



The effects of enhanced attention and working memory on smooth pursuit eye movement

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Abstract

It has long been suggested that increasing attentional demands can alter smooth pursuit eye movements, but the precise nature of the changes generated is not clear. Our goal was to examine smooth pursuit with a task that enhanced attention to the target and that increased demands on working memory, without distracting from the target. 15 subjects tracked a target moving around a predictable circular trajectory at a constant tangential velocity. An *n*-back task with two levels of additional working memory load was integrated into the pursuit target to increase cognitive demands. In the single-task conditions, subjects either performed pursuit alone or the *n*-back task with a stationary target. In the dual-task conditions, pursuit and the *n*-back task were performed together. Performance of the *n*-back tasks was not impaired by simultaneous smooth pursuit. The *n*-back tasks had negligible effects on horizontal or vertical pursuit gain, but generated increased phase lag and reduced the variability of position error during pursuit. Increasing the difficulty of the *n*-back task further reduced the variability of position errors. We conclude that enhanced attention does not alter the velocity gain of smooth pursuit but rather improves its consistency. As long as attention remains focused on the target, increased attentional demands further reduce pursuit variability. Increases in phase lag may serve to improve attentional processing of the target.

Keywords Ocular motor · Velocity gain · Phase · Consistency · Variability · *n*-Back

Introduction

Smooth pursuit is the ocular tracking of a moving target, the goal of which is to maintain a stable target image on the fovea (Kowler 2011). It is often conceived as the operation of a control system that uses feedback information about target velocity and eye velocity to create a situation where these are equal, ideally reducing the velocity of the image of the target on the retina (retinal image slip) to zero (Lisberger et al. 1987). In humans, the operation of this system is imperfect, leading to smooth pursuit being supplemented by small ‘catch-up’ saccades to maintain stable fixation on the target. The efficiency of smooth pursuit varies with target parameters: it is worse with faster velocities, more rapid frequencies of oscillation, higher accelerations, more unpredictable trajectories, and lower target contrast (Sharpe and Sylvester 1978; Barnes 2008). Pursuit also varies with subject factors such as age (Sharpe and Sylvester 1978; Spooner et al. 1980).

Cognitive factors can also influence pursuit performance. In particular, the effect of attention has often been studied. Attention has many dimensions, however, and its effects

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on smooth pursuit varies with the nature of the attentional demands (Hutton and Tegally 2005). One class of attentional effects that has often been studied is that of enhanced attention to the target. This has generally been achieved by having the pursuit target change form during pursuit, either as a varying letter or digit (Shagass et al. 1976; Cegalis et al. 1983; Clementz et al. 1990; Sweeney et al. 1994; Van Gelder et al. 1995), the appearance of a dot (Iacono et al. 1981, 1982), or simple dimming (Van Gelder et al. 1990), frequently with instructions to the subject to keep track or indicate the occurrence of these changes—i.e., a dual-task design where the second task involves the ocular motor target. These types of studies consistently conclude that enhanced attention to the target improves smooth pursuit.

On the other hand, another group of studies have used a different type of dual-task design in which subjects perform a cognitive or perceptual task unrelated to the ocular motor target while engaged in smooth pursuit. The results of these dual-task experiments have been mixed. Some studies document no effect of serial subtraction (Brezinova and Kendell 1977; Lipton et al. 1980) or auditory noise (Kaufman and Abel 1986) on smooth pursuit quality. Others found that smooth pursuit worsened when subjects performed serial subtraction (Acker and Toone 1978), auditory discrimination and motor tasks (Hutton and Tegally 2005), or discrimination of a grating orientation in the visual periphery (Kerzel et al. 2009). Such deterioration suggests that attentional resources are limited, with deleterious consequences when attention is divided between tracking of the target and a second, unrelated task. On the other hand, two studies reported that secondary auditory oddball or discrimination tasks actually improved pursuit (Van Gelder et al. 1995; Kathmann et al. 1999). To explain this seemingly paradoxical effect, the authors suggested that pursuit is a skilled automatic task that was performed better when attention or controlled processing was directed elsewhere, an explanation that has been challenged by others who failed to replicate the result (Hutton and Tegally 2005).

One problem with interpreting the prior literature about attentional effects on smooth pursuit is the variability in the methods used to evaluate pursuit performance. Concerns have been expressed regarding the ‘relatively crude’ nature of some of the qualitative parameters reported (Hutton and Tegally 2005). In the papers that reported quantitative indices, a frequently used parameter has been root mean square error (Iacono et al. 1981, 1982; Van Gelder et al. 1990, 1995; Kathmann et al. 1999; Hutton and Tegally 2005). This measures the difference between eye position and target position at each point in time sampled, squares it, and then takes the square root of the average of those squares. Root mean square error thus reflects the average absolute distance between the eye and the target over the period of measurement. However, this metric of

eye position error is limited in its ability to capture the performance of the pursuit system. First, it incorporates both pursuit and saccadic elements of ocular tracking, and therefore, it does not provide precise information about the operation of pursuit alone. Second, because it is an unsigned error, it does not distinguish between tracking that is too fast or too slow. These problems limit our ability to infer the specific mechanisms behind attentional effects on smooth pursuit from reports that use root mean square error as the main outcome variable. Velocity gain, the ratio of eye to target velocity during segments of pursuit only—i.e., after saccades have been edited from the trace—better captures the adequacy of the sensorimotor operation generating smooth pursuit, but only a few studies have reported the effects of attentional tasks on velocity gain (Kaufman and Abel 1986; Van Gelder et al. 1995; Hutton and Tegally 2005).

In this study, our primary goals were to determine the effects of enhanced attention to the pursuit target. We evaluated classic control-system parameters such as velocity gain, which can be considered the amplitude of the pursuit system’s response, and phase, which reflects the timing of the response. In addition, we evaluated the consistency of the pursuit response, by assessing the variability of the spatial accuracy of pursuit. If attentional improvements in pursuit are the result of augmenting the basic sensorimotor computation generating smooth pursuit, then we should find that attention increases the velocity gain of pursuit. On the other hand, given that one of the effects of attention on the other tasks is greater consistency of performance (Bartolomeo et al. 2001; Baird et al. 2014), another possible outcome is that attentional enhancement reduces the variability of position error during pursuit, rather than increasing the gain of pursuit.

Our second goal was to examine the effects of further increases in attention by using a working memory task that varied in the degree of difficulty. We integrated a visual *n*-back task that varied in the demands on working memory (1-back and 2-back levels of load), but that still required attention to the pursuit target for the performance of the secondary task. Integrating the secondary task into the target allowed us to vary the amount of attentional load while avoiding the confound of attentional distraction that is present in the second type of dual-task design discussed above, where the secondary task is unrelated to the target. If the deleterious results on pursuit in those studies are truly related to increased attentional or cognitive load, then a similar decline should be seen with increasing demands from the secondary task. However, if those deleterious effects are due to distraction and divided attention, then we should see no effect or even improvement in pursuit parameters.

Methods

Subjects

15 (mean age = 31.1 ± 7.9 years, 13 female) subjects were recruited through an institutional newsletter. Subjects were excluded from participation if they had a history of traumatic brain injury, cranial nerve abnormalities, neurological or psychiatric illness, used nicotine or psychotropic medication, had a history of drug or alcohol abuse, were pregnant, or were exposed to general anesthetic during the 2 weeks prior to testing.

Apparatus and stimuli

Stimuli were generated with a custom in-house developed python program presented on a ViewSonic VX2268wm monitor (ViewSonic Corp. USA) with a refresh rate of 120 Hz and 8 bits per channel, placed 60 cm away from the subject. Monitor resolution was set to 800×600 for the smoothest possible target presentation. The graphics card was a 128-bit PNY Quadro K620 (PNY Technologies Inc., USA), and key presses were made on a Logitech F310 gamepad (Logitech International S.A., Switzerland). Eye movements were recorded monocularly with an EyeLink 1000

at 500 Hz (SR Research, Canada), with a tower mount for head stabilization.

The target was a white ring subtending 0.5° of visual angle with an inner disc having a diameter of 0.25° of visual angle, displayed on a dark grey background (RGB colour code: 75 75 75). During stationary trials, the target appeared at the center of the screen (Fig. 1). On all pursuit trials, the target moved clockwise around a circular trajectory with a radius of 10.5° of visual angle, with a period of 2.5 s (i.e., 0.4 Hz), resulting in a constant tangential velocity of $26^\circ/\text{s}$. The spatial span and frequency of this motion were chosen to match those of many prior studies of attentional effects on horizontal sinusoidal pursuit (Brezinova and Kendell 1977; Lipton et al. 1980; Iacono et al. 1981, 1982; Spohn et al. 1988; Sweeney et al. 1994).

The secondary n -back tasks involved attention to the colour of the inner disc of the target. This changed between nine colours in pseudo-random order. During the 1-back task, the disc alternated between one of those nine colours shown for 1000 ms and a period of 1000 ms when the disc matched the grey background (i.e., is not visible). The task was to press a key when a colour matched the colour presented one previously (e.g., blue–grey–yellow–grey–orange–grey–orange...). During the 2-back task, the central disc alternated between one of the nine colours every 1000 ms. The task was to press the key if the

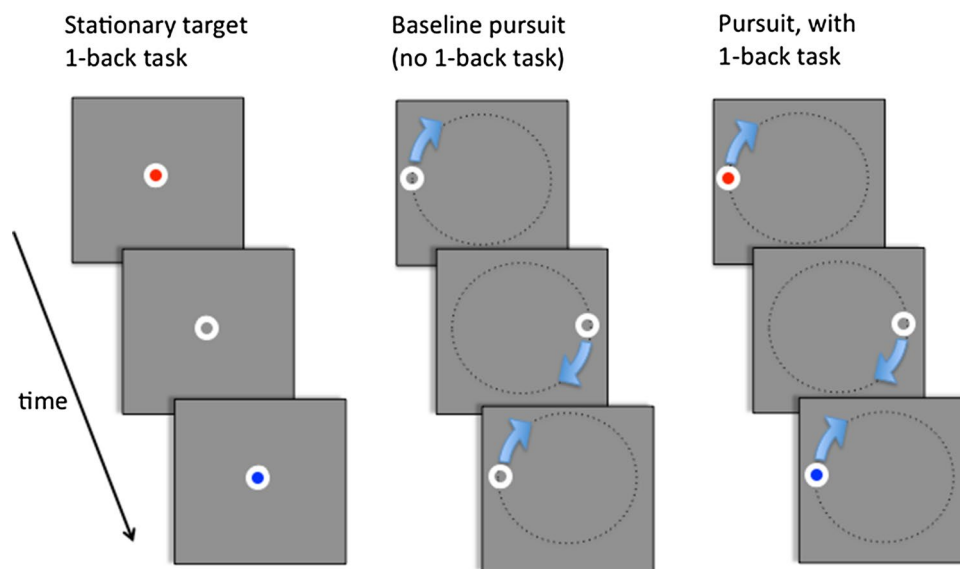


Fig. 1 Depiction of trials within the 1-back block. The block begins with a 1-back trial with a stationary target at screen center, whose central disc has one of the nine colours. Each colour appears for 1 s and alternates with 1 s when the central disc is the same colour as the background (i.e., disappears). The subject indicates if the current colour is the same as the previous colour. After 1 min of this trial, subjects perform a baseline pursuit trial. They follow a moving target along a circular path, indicated by the dotted circle, in a clockwise

direction, as shown by the blue arrows. The central disc is invisible. Finally, they perform pursuit with the 1-back task. The pursuit target follows the same trajectory, but the central disc changes colour as it did with the stationary trial, and subjects also perform a 1-back trial. The 2-back block has similar trials. The difference in the n -back task is that the central disc never disappears but changes colour every second, and the task is to indicate whether the current colour matches the second most recent colour

colour matched that presented two colours previously (e.g., orange–blue–red–green–**red**...).

On baseline pursuit trials, the central disc was grey and thus not visible.

Procedure

Chair and chin-rest height were adjusted for each subject. Instructions were presented on the screen and any questions answered by a research assistant. Nine-point calibration and validation procedures were performed before each component, and were redone if the average margin of error exceeded 0.5° of visual angle. Calibration points were presented in a three-by-three rectangular grid, spanning 22.4° horizontally and 19.6° vertically. Half of the subjects were randomized to perform the 1-back block first and the 2-back block second, while the remaining half performed these two blocks in the reverse order.

In each block, subjects performed three tasks in sequence (Fig. 1). First, they performed an n -back task while watching a stationary target. This began with the white-ring target at screen center. When subjects were ready, they pressed a key which began the sequence of colour changes to the target described above, while the target remained at the center of the screen. This continued for 1 min, and ended with disappearance of the target. Second, they performed a baseline pursuit assessment, without the n -back task. This began with the white-ring target located to the right on the horizontal meridian, and when subjects were ready, they triggered the target's clockwise motion along its circular trajectory by a keypress. The motion continued for 1 min and again ended with disappearance of the target. Third, they performed the dual-task condition, with simultaneous smooth pursuit and the n -back task. This began in similar fashion to the baseline pursuit assessment, with the white-ring target to the right on the horizontal meridian, and triggered to move along its trajectory by a keypress, only now the central disc changed colour every second, as described above. Again, the motion ended after 1 min with disappearance of the target. After completing this first block, they then repeated the same process with the other n -back block.

At the 30s mark of each pursuit trial, a drift correction was performed to compensate for any inadvertent signal drift during the trial.

Data variables

Reaction time and raw eye movement data were extracted using EyeLink Data Viewer (SR Research, Canada). Means and standard deviations were calculated for reaction times for responses made between 200 and 1000 ms after the target change. False alarms were any keypress when no cue was presented, and misses were failures to respond during this

time window. The sum of misses and false alarms was the 'error rate'.

For the pursuit blocks, the EyeLink parser was used to detect blinks and saccades. Saccades were defined as an eye movement with velocity above $35^\circ/\text{s}$ or acceleration above $9500^\circ/\text{s}^2$, which were excised from the data prior to analysis. The remaining eye movement data were analyzed using an in-house developed MATLAB script (The MathWorks, USA). We excluded the first full cycle of each pursuit block, so that our analysis focused on steady-state pursuit.

We first characterized pursuit performance for the remaining trace with traditional one-dimensional (horizontal and vertical) measures of gain and phase. We used a cross-correlation procedure that varied the offset between eye and target velocity, to find the offset that gave the smallest residual error. This offset was the phase, expressed in degrees per cycle. Once phase offset was corrected, gain was defined as the slope of the linear regression of eye velocity against target velocity.

We next performed a two-dimensional analysis, as used previously by others (Maruta et al. 2010, 2013). This assessed positional errors after converting the data to polar coordinates. For each sample along the target trajectory, we calculated the tangential error, which was the vector between the eye and target position as projected onto the direction of instantaneous target motion, and the radial error, the vector orthogonal to instantaneous target motion, both expressed in degrees of visual angle (see Fig. 2). Related to tangential error, circular phase was defined as the angular difference between the gaze and target from screen center, in degrees. Positive values indicate phase lead or tangential error with eye position ahead of the target. For radial error, a positive value indicates an eye position that is further away from screen center than the target. For each of these three position variables, we calculated the standard deviations as indices of the variability of pursuit, where smaller values would indicate more consistent pursuit.

Finally, to capture the variability of error in both radial and tangential directions in a single metric, we multiplied the standard deviation of radial error by that of tangential error, and then by π , which can be visualized as the area of an ellipse, and which we termed the 'overall variability'.

Statistical analysis

For the subject's keypress responses for n -back tasks with either a stationary or moving target, we analyzed the variables of reaction time and error rate using a general linear model, with main factors of type of task (1-back task and 2-back task) and target motion (stationary and moving), with subject as a random factor. For reaction time, we performed this for both the means and the medians of each subject's performance.

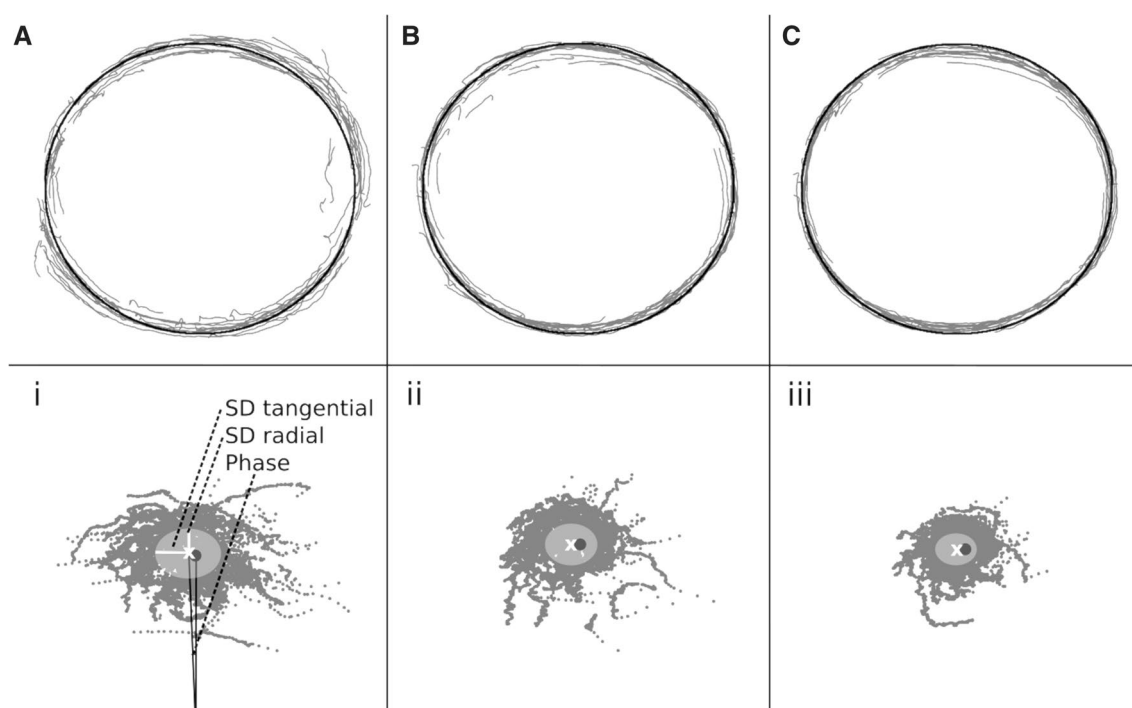
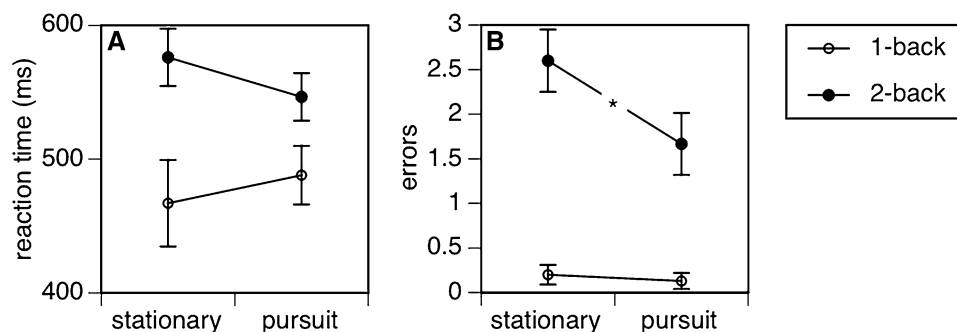


Fig. 2 Examples of smooth pursuit during the different conditions. **a–c** Are 30-s samples of a representative subject's gaze trace (light grey), following the target trajectory (black), for **a** one baseline condition, **b** pursuit during the 1-back task and (**c**) pursuit during the 2-back task. In **i–iii**, the data from **a–c** are transformed so that current target position is collapsed to a single location at 90° (vertical),

shown as a black dot, with simultaneous eye position depicted as a scatter around this target location. **i** is for the baseline condition, **ii** for the 1-back task, and **iii** for the 2-back task. **i** Also illustrates the standard deviation (SD) of radial and tangential position and the phase error. In all three panels, the white cross indicates mean eye position and the shaded ellipse the overall variability

Fig. 3 Performance on the n -back tasks for **a** reaction time, and **b** task errors. Performance is shown while the target is both stationary and moving during smooth pursuit. *Indicates linear contrasts that were significant. Error bars indicate one standard error



For pursuit performance, we analyzed the pursuit variables above using a similar general linear model. Here, the main factors were block (1-back block, 2-back block) and condition (baseline pursuit, pursuit with n -back task), with subject as a random factor. Because standard deviations are not normally distributed, we applied a \log_{10} transform to those data prior to analysis. We examined specified a priori contrasts, between each n -back task and its baseline condition, and between the 1-back and the 2-back tasks.

Compliance with ethical standards

Informed consent was obtained for all participants prior to beginning the study. Ethical approval in accordance with the principles of the Declaration of Helsinki was granted by the Clinical Research Ethics Board at the University of British Columbia.

Results

Performance of the *n*-back task

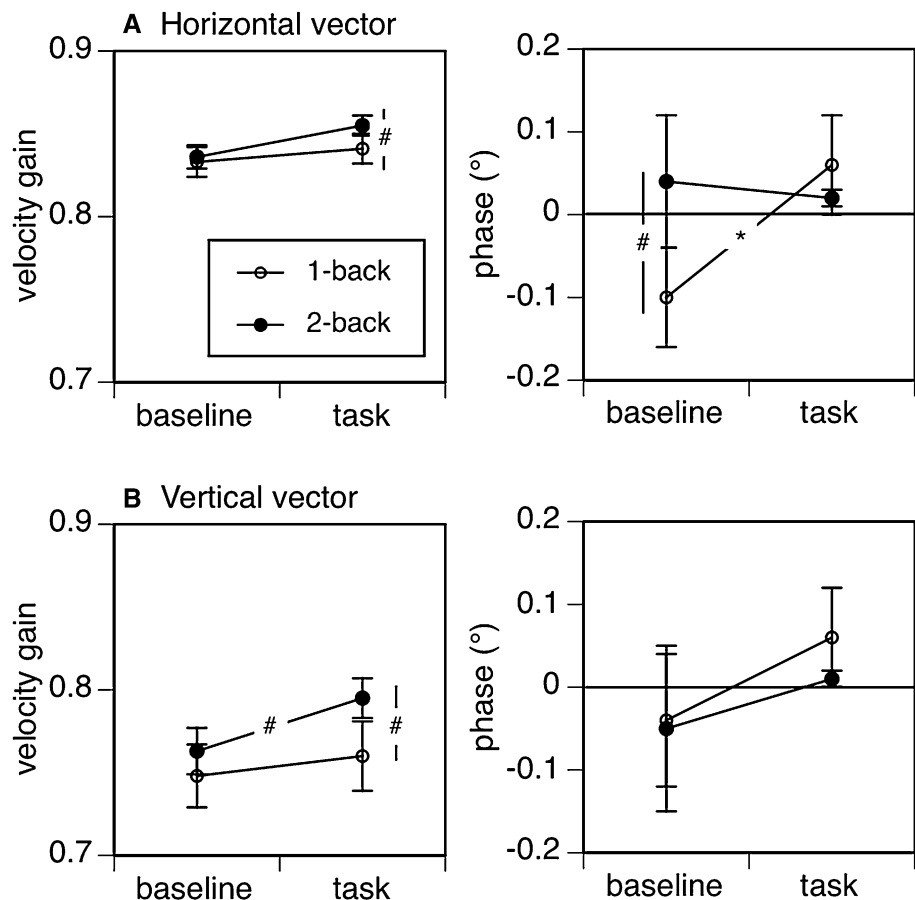
For reaction time, there was a main effect of task [$F_{(1,42)} = 23.8$, $p < 0.0001$] due to longer reaction times for the 2-back task (Fig. 3). There was no effect of target motion, nor any interaction between task and target motion. Linear contrasts confirmed that reaction times for the 2-back task were prolonged both for stationary [$F_{(1,42)} = 20.1$, $p < 0.0001$] and moving targets [$F_{(1,42)} = 5.79$, $p = 0.02$]. Contrasts between stationary and moving target conditions were not significant for either the 1-back or 2-back tasks.

Repeating this analysis using the median reaction times of each subject gave a similar result: a main effect of task [$F_{(1,42)} = 27.1$, $p < 0.0001$] due to longer reaction times for the 2-back block (mean 555 ms, SD 78) than the 1-back block (mean 453 ms, SD 120), but no effect of target motion or interaction between task and target motion.

For task errors, there was again a main effect of task [$F_{(1,42)} = 71.4$, $p < 0.0001$] due to more errors with the 2-back task, but now also a main effect of target motion [$F_{(1,42)} = 4.61$, $p = 0.037$], due to more errors with the stationary target. There was a trend to an interaction [$F_{(1,42)} = 3.46$, $p = 0.07$]. Linear contrasts confirmed more errors for the 2-back task with both stationary [$F_{(1,42)} = 53.1$, $p < 0.0001$] and moving targets [$F_{(1,42)} = 21.68$, $p < 0.0001$]. The linear contrast between stationary and moving targets was not significant for the 1-back task, but there were fewer errors for the 2-back task with the moving target than with the stationary target [$F_{(1,42)} = 8.03$, $p = 0.007$].

These data thus confirm increased task difficulty with the 2-back than the 1-back task, regardless of whether the target is a stationary one or a moving target for smooth pursuit. Second, there is no significant difference in *n*-back task performance between watching a stationary target or pursuing a moving one. A two one-sided test (TOST procedure) (Schuirmann 1987) confirmed non-inferiority of response times during pursuit compared to the stationary trials for an equivalence margin of 60 ms, for $\alpha = 0.025$.

Fig. 4 One-dimensional smooth pursuit results, for **a** horizontal and **b** vertical velocity gain. Performance is shown for both baseline pursuit and dual-task conditions. Left graphs show velocity gain, right graphs phase offset, with negative values indicating phase lag. *Indicates linear contrasts that were significant, # indicates contrasts with a trend to significance ($0.05 < p < 0.10$). Error bars indicate one standard error



Eye movement data

Traditional one-dimensional Cartesian analyses

Horizontal velocity gain showed a trend to an effect of block [$F_{(1,42)} = 3.71$, $p = 0.061$], but no effect of condition or interaction (Fig. 4). Linear contrasts showed a trend to improved gain during the 2-back task compared to the 1-back task [$F_{(1,42)} = 3.48$, $p = 0.069$], but neither differed from their baseline conditions. The phase of horizontal pursuit showed a trend to an interaction between block and condition [$F_{(1,42)} = 3.35$, $p = 0.074$], with contrasts showing a phase difference between the 1-back task and its baseline condition [$F_{(1,42)} = 5.36$, $p = 0.026$] and a small difference between the two baseline conditions [$F_{(1,42)} = 4.17$, $p = 0.047$].

Vertical velocity gain showed a trend to an effect of condition [$F_{(1,42)} = 3.54$, $p = 0.067$] but no effect of block or interaction. Linear contrasts showed a trend to better gain for the 2-back task than for either its baseline condition [$F_{(1,42)} = 3.46$, $p = 0.069$] or the 1-back task [$F_{(1,42)} = 2.86$, $p = 0.098$]. Vertical phase did not show any effects.

Two-dimensional analyses

For radial position error, there was an effect of condition [$F_{(1,42)} = 4.49$, $p = 0.04$]: mean eye eccentricity was slightly hypometric during the baseline conditions but normometric during the n -back tasks (Fig. 5). There was no effect of block or interaction. For radial variability (the standard deviation of radial position error), there was an effect of both block [$F_{(1,42)} = 12.03$, $p = 0.0012$] and condition [$F_{(1,42)} = 5.12$, $p = 0.029$] but no interaction. Linear contrasts showed less variable pursuit during the 2-back task than during the 1-back task [$F_{(1,42)} = 7.80$, $p = 0.008$], and a trend for less variable pursuit during the 2-back task compared to its baseline condition [$F_{(1,42)} = 3.77$, $p = 0.059$]. The baseline conditions of the two blocks also differed slightly [$F_{(1,42)} = 4.46$, $p = 0.041$].

For tangential position error there was an effect of condition [$F_{(1,42)} = 26.8$, $p < 0.0001$] but no effect of block or interaction. Linear contrasts showed that there was a slight lag of eye position during the baseline condition that increased when subjects simultaneously performed the n -back task, for both the 1-back [$F_{(1,42)} = 8.89$, $p = 0.005$] and 2-back conditions [$F_{(1,42)} = 18.89$, $p < 0.0001$]. The difference between the 1-back and 2-back conditions was not significant. For tangential variability, there was an effect of block [$F_{(1,42)} = 5.06$,

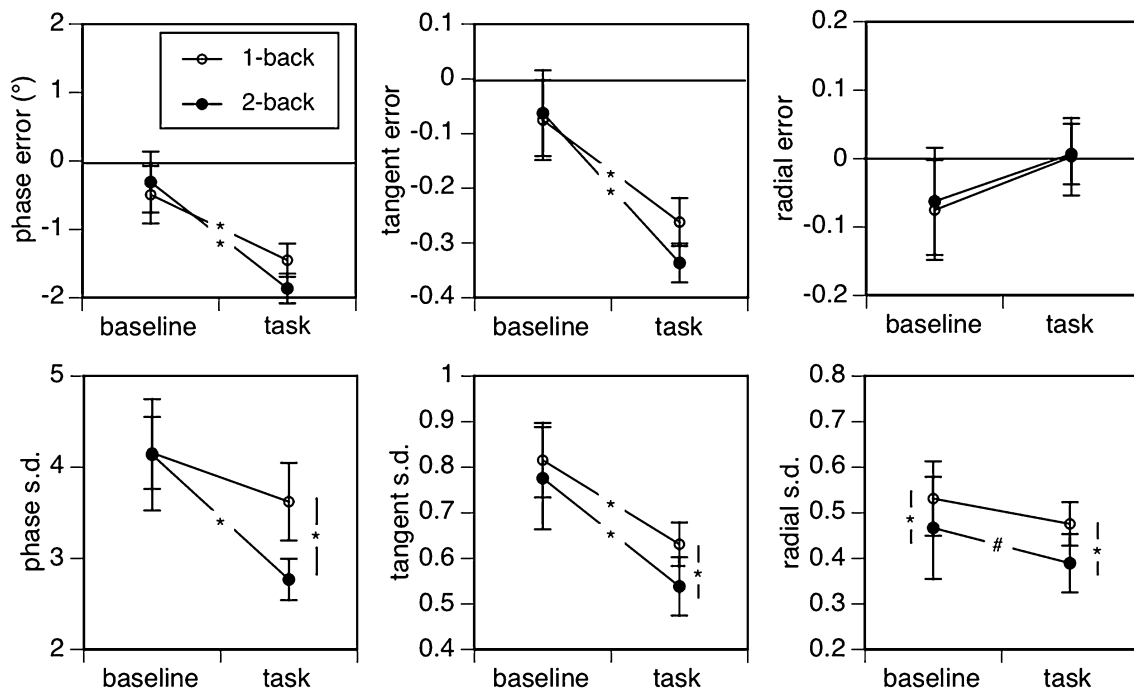


Fig. 5 Two-dimensional smooth pursuit results. Top graphs show mean errors, and bottom graphs show standard deviations for gaze position (i.e., gaze variability). Left graphs show data for circular phase, middle graphs for tangential gaze position, and right graphs for radial gaze position. Negative results for phase and tangential error

indicate the gaze lagging behind the target, and for radial error a gaze position that is less eccentric than the target. *Indicates linear contrasts that were significant, #indicates contrasts with a trend to significance ($0.05 < p < 0.10$). Error bars indicate one standard error

$p=0.03$] and condition [$F_{(1,42)}=18.55$, $p<0.0001$] but no interaction. Linear contrasts showed that, compared to the baseline conditions, the dual task reduced the tangential variability of pursuit in both the 1-back [$F_{(1,42)}=6.18$, $p=0.017$] and 2-back conditions [$F_{(1,42)}=12.96$, $p=0.0008$]. In addition, pursuit during the 2-back task was less variable than with the 1-back task [$F_{(1,42)}=4.62$, $p=0.038$].

For circular phase, there was an effect of condition [$F_{(1,42)}=23.7$, $p<0.0001$] but no effect of block or interaction. Linear contrasts showed more phase lag in the dual task than the baseline conditions for both the 1-back [$F_{(1,42)}=6.88$, $p=0.012$] and 2-back tasks [$F_{(1,42)}=18.14$, $p<0.0001$]. However, the difference in phase between pursuit with the 1-back and 2-back tasks was not significant. Circular phase variability also showed an effect of block [$F_{(1,42)}=4.29$, $p=0.045$] and condition [$F_{(1,42)}=11.18$, $p=0.002$] but no interaction. Linear contrasts showed that pursuit with the 2-back task had less phase variability than either its control condition [$F_{(1,42)}=10.58$, $p=0.002$] or pursuit with the 1-back task [$F_{(1,42)}=5.54$, $p=0.023$].

Overall variability showed an effect of block [$F_{(1,42)}=7.15$, $p=0.011$] and condition [$F_{(1,42)}=16.8$, $p=0.0002$] but no interaction (Fig. 6). Linear contrasts showed that, compared to their baseline conditions, there was less overall spatial error when pursuit was combined with an n -back task, for both the 1-back [$F_{(1,42)}=4.45$, $p=0.041$] and 2-back tasks [$F_{(1,42)}=13.58$, $p=0.0006$]. Spatial variability of pursuit was significantly less with the 2-back than the 1-back task [$F_{(1,42)}=7.17$, $p=0.01$].

Discussion

Our results showed that enhanced attention to the target with the 1-back task neither improved nor degraded the classic metric of gain in either horizontal or vertical directions. Rather, it led to slightly greater phase lag and tangential

lag, and tracking became less hypometric in terms of eccentricity. Pursuit also became more consistent, with less variability in tangential error and overall spatial error. These effects were replicated with the 2-back task. In addition, the added demands of working memory during the 2-back task further improved the consistency of pursuit, whether this was measured as the variability of radial position, tangential position, or phase, or our combined metric of overall variability. In contrast, the effects on pursuit gain were modest or non-existent.

Benefits of enhanced attention have been shown in prior studies. However, as others have remarked (Hutton and Tegally 2005), some of the earlier studies reported qualitative impressions or secondary features such as saccadic frequency (Shagass et al. 1976; Brezinova and Kendell 1977; Lipton et al. 1980; Cegalis et al. 1983; Clementz et al. 1990), while others reported root mean square error (Iacono et al. 1981, 1982; Van Gelder et al. 1990, 1995; Sweeney et al. 1994), a quantitative parameter that is an approximate measure of smooth pursuit performance. Only two studies reported the effects of attentional enhancement on velocity gain. Using letter targets that did or did not change while moving at constant velocity, one study found mixed results: horizontal but not vertical pursuit was better when subjects had to read silently changing letters than when they pursued a target that did not change (Van Gelder et al. 1995). Another found that discriminating the position of a small dot on the horizontally moving target had no effect on pursuit gain (Kerzel et al. 2009). The circular pursuit method we used, which is equivalent to sinusoidal pursuit in horizontal and vertical directions simultaneously, showed no change in velocity gain with our 1-back task.

On the other hand, there was a greater tendency for the eye to lag target position, reflected in both a phase lag and negative tangential error. This was replicated in both the 1-back and 2-back conditions. To our knowledge, attentional effects on phase during pursuit have not been previously reported. The reason why enhanced attention produces a phase lag is not certain, but one can speculate that a phase lag might optimize attentional processing of the pursuit target, given what is known about the spatial distribution of attention during pursuit. Despite some contrary results (Lovejoy et al. 2009), studies of manual reaction times (van Donkelaar 1999; Khan et al. 2010) and saccadic latencies (Krauzlis and Miles 1996; Tanaka et al. 1998; Khan et al. 2010) show that the fastest responses to targets appearing during smooth pursuit occur at or just ahead by 1° – 3° of the current target location. Using a different approach, a recent EEG study of flickering stimuli found an increase in EEG power when the stimulus was 1.5° – 3.5° ahead of the target (Chen et al. 2017). If attention is indeed located ahead of the point of pursuit, then an eye position that lags slightly behind the location of the target may be optimal for placing

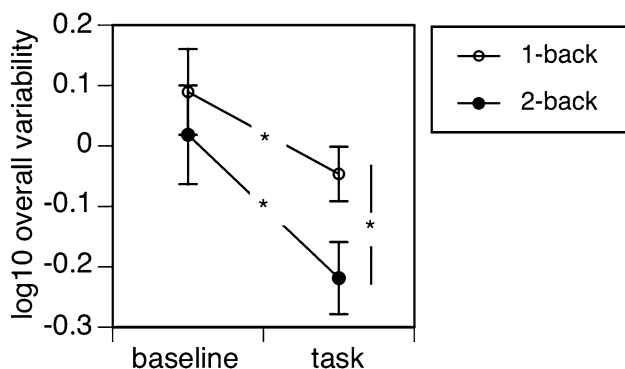


Fig. 6 Overall variability. This measure incorporates both radial and tangential position variability. *Indicates linear contrasts that were significant. Error bars indicate one standard error

attention on the target. Alternatively, with predictable target motion as in our paradigm, phase lag is reduced through the operation of predictive or anticipatory mechanisms in classic or optimal control theory (Pavel 1990), and one could speculate that the increased cognitive demands of n -back tasks compete with and reduce the efficacy of those operations.

Finally, likely, the strongest effect of enhanced attention to the target we found was reduced variability of smooth pursuit. Related to this effect are observations that suggest that performance consistency may be one of the benefits of enhanced attention. One of the effects of intensive attentional training is reduced variability of reaction times and greater consistency of event-related potentials (Lutz et al. 2009). Conversely, reaction time variability increases during mind-wandering, when the subject's attention has strayed from the task at hand (Baird et al. 2014), and performance becomes less consistent when attention is diverted (Bartolomeo et al. 2001). In the neuropsychological literature, increased performance variability is one of the features of conditions associated with impaired attention, such as attention deficit with hyperactivity (Rubia et al. 1999; Castellanos et al. 2006), cerebral trauma (Stuss et al. 1989), and frontal lobe lesions (Stuss et al. 2003).

A second attentional effect we explored in this study was that of increased demands on working memory. Our behavioural data demonstrated longer reaction times and more errors for the 2-back than the 1-back task, indicating that these differed in difficulty. These data are consistent with the other results showing a correlation between reaction time and increasing values of n in the other n -back tasks (Jaeggi et al. 2010). Unlike prior studies, this increased demand was not accompanied by a distraction of attention away from the target to another visual or sensory modality, or to a cognitive task irrelevant to pursuit. Rather, sustained attention to the pursuit target was required to perform our secondary task. Hence, our design allowed us to explore the effects of increased cognitive processing without divided attention or distraction. Our results showed that rather than a worsening of pursuit performance, there was first, minimal effect on velocity gain, and second, further improvement in pursuit consistency as the n -back task became more challenging.

Again, most of the older studies claim a lack of change or worsening of smooth pursuit with distraction from tasks such as serial subtraction or writing reported rudimentary, qualitative assessments of pursuit (Brezinova and Kendell 1977; Acker and Toone 1978; Lipton et al. 1980). Studies measuring pursuit gain found either no effect of auditory noise (Kaufman and Abel 1986) or reduced gain when subjects performed auditory discrimination or tapping tasks (Hutton and Tegally 2005), or reported the orientation of a grating in their peripheral vision (Kerzel et al. 2009). Studies that included multiple levels of difficulty for the secondary task reported no effect of additional cognitive load (Brezinova

and Kendell 1977), worse pursuit with more difficult backward subtractions (Acker and Toone 1978), or worse gain with more complex tapping tasks (Hutton and Tegally 2005). It has been suggested that the impact of secondary tasks may vary with the demand on attentional resources, with less impact of easier tasks, and with the specific type of attention required, particularly as they may relate to the processes involved in smooth pursuit (Hutton and Tegally 2005). Our results show that as long as increased attentional demands remain focused on the target of pursuit, there is no decline in velocity gain, but rather a reduction in pursuit variability. At this point, there are few other data concerning the impact of working memory on the variability of smooth pursuit. One metric that also reflects variability is the eye-target synchronization index reported by Contreras et al. (2011). This study used word recall as the dual task during smooth pursuit; however, it is unclear from their data if the changes in healthy subjects were significant (Contreras et al. 2011).

Also of interest is the impact of pursuit on the performance of the secondary task. Many previous studies did not evaluate this aspect of the dual-task paradigm (Shagass et al. 1976; Van Gelder et al. 1995; Hutton and Tegally 2005). When it was evaluated, the other studies found no difference in task performance between stationary or pursuit conditions, for discrimination of a peripheral grating orientation or memory for object colour in the visual periphery (Kerzel and Ziegler 2005; Kerzel et al. 2009), or auditory tasks of detection or discrimination (Kathmann et al. 1999). Consistent with these results, we found that both the 1-back and 2-back tasks were performed equally well whether the subject was watching a stationary target or pursuing a moving one at the time. While a ceiling effect might obscure a pursuit-induced change with the 1-back task, this is likely not the case for the more difficult 2-back task. Thus, our data do not indicate a performance trade-off between the secondary attentional task and smooth pursuit, which others have speculated might occur (Hutton and Tegally 2005). Others have suggested that this lack of effect of pursuit on secondary task performance indicates that smooth pursuit and colour discrimination tasks do not share processing resources, even if both share the same stimulus (Kerzel et al. 2009).

In summary, we found that enhancing attention to the target does not alter a fundamental characteristic of the sensorimotor computations that generate smooth pursuit, namely pursuit velocity gain. Rather, it serves to make performance more consistent, reducing the variability of position error, an effect that may parallel the other observations on the effect of attention (or inattention) on within-subject performance variability of the other tasks (Lutz et al. 2009; Baird et al. 2014). This effect on performance variability can account for the previous observations of qualitative improvement and reduced root mean square error of smooth pursuit with attentional enhancement. We also found increased phase lag,

a novel effect that we speculate may serve to enhance attentional processing of target features. Finally, we found that increasing task difficulty and demands on working memory further reduced the variability of position errors of pursuit. In our design, subjects had to attend to the target to perform the more difficult task. This suggests that the deleterious effects of secondary tasks in older reports may be related more to distraction and divided attention than simply to increased attentional load. This is consistent with the proposal of others (Hutton and Tegally 2005) that the effects of attention on smooth pursuit are not unitary, but may depend upon both the degree and type of attention being demanded and its relationship to the act of smooth pursuit.

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Author contributions JLS, SLC, WJP, and JJSB conceptualized the experiment and BK assisted with computer programming. JLS conducted the testing of participants, pursuit analysis, and wrote the initial draft. JJSB performed the statistical analysis. All authors contributed to the interpretation of results, writing and approval of the final draft.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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