Anticipatory pursuit is influenced by a concurrent timing task

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The ability to predict upcoming events is important to compensate for relatively long sensory-motor delays. When stimuli are temporally regular, their prediction depends on a representation of elapsed time. However, it is well known that the allocation of attention to the timing of an upcoming event alters this representation. The role of attention on the temporal processing component of prediction was investigated in a visual smooth pursuit task that was performed either in isolation or concurrently with a manual response task. Subjects used smooth pursuit eye movements to accurately track a moving target after a constant-duration delay interval. In the manual response task, subjects had to estimate the instant of target motion onset by pressing a button. The onset of anticipatory pursuit eye movements was used to quantify the subject's estimate of elapsed time. We found that onset times were delayed significantly in the presence of the concurrent manual task relative to the pursuit task in isolation. There was also a correlation between the oculomotor and manual response latencies. In the framework of Scalar Timing Theory, the results are consistent with a centralized attentional gating mechanism that allocates clock resources between smooth pursuit preparation and the parallel timing task.

Keywords: prediction, smooth pursuit, manual response, attention, human

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Introduction

In the behavioral repertoire of an organism, most actions depend at least to some degree on an internal sense of elapsed time. From sleep–wake cycles and foraging behavior to pursuit-evasion and fine motor control, successful execution depends on the ability to perceive and reproduce different intervals of time (Buhusi & Meck, 2005). Time as an explicit phenomenon has been studied for years in the psychology literature, in both humans and animals (Gallistel & Gibbon, 2000; Mauk & Buonomano, 2004). In the class of experiments referred to as "interval reproduction," subjects are typically presented a standard reference time interval, delineated by tones or visual cues. They are then required to reproduce the reference interval using a manual action such as a button press. The subjects match the reference with a precision that depends on the stimulus length (Gibbon, Malapani, Dale, & Gallistel, 1997), the cue modality (Penney, 2003), and other factors (Merchant, Zarco, & Prado, 2008). A simultaneous task, such as monitoring additional intervals (Brown, Stubbs, & West, 1992; Brown & West, 1990), causes the subject to overestimate durations and therefore respond later. This effect could be due to the allocation of attention to a concurrent process that could change the perception of elapsed time (Casini & Macar, 1997; Fortin, 2003; Macar, Grondin, & Casini, 1994).

A perception of elapsed time is essential to predict when an upcoming event is likely to occur. Prediction is often studied using anticipatory smooth pursuit eye movements as a tool (Badler & Heinen, 2006; Barnes & Asselman, 1991; de Hemptinne, Lefèvre, & Missal, 2006; Heinen, Badler, & Ting, 2005; Kowler, 1989; Missal & Heinen, 2004). Anticipatory pursuit is defined as a smooth (non-saccadic) eye movement that occurs in the absence of a visual target (i.e., before it appears). Anticipatory eye movements are enhanced when the upcoming target is predictable (de Hemptinne et al., 2006; Heinen et al., 2005; Kao & Morrow, 1994, Kowler, 1989), when it moves at high speed (Heinen et al., 2005; Kao & Morrow, 1994), and when its motion is preceded by a blank delay interval or "gap" (Boman & Hotson, 1988). The timing of anticipatory pursuit is dependent on the timing of the

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pursuit target (de Hemptinne, Nozaradan, Duvivier, Lefèvre, & Missal, 2007; Heinen et al., 2005).

Since a concurrent task degrades manual timing performance, it should do the same for anticipatory smooth pursuit if the two systems share a common system for representing elapsed time. We designed a task where anticipatory pursuit movements were frequently observed because the timing of target motion onset was kept constant in blocks of trials. For the concurrent task, subjects needed to make a manual predictive response to the same stimulus. We hypothesized that attention devoted to the concurrent task could alter the initiation of the anticipatory smooth pursuit response. Portions of this research have been published previously in abstract form (Badler, Lefèvre, & Missal, 2008).

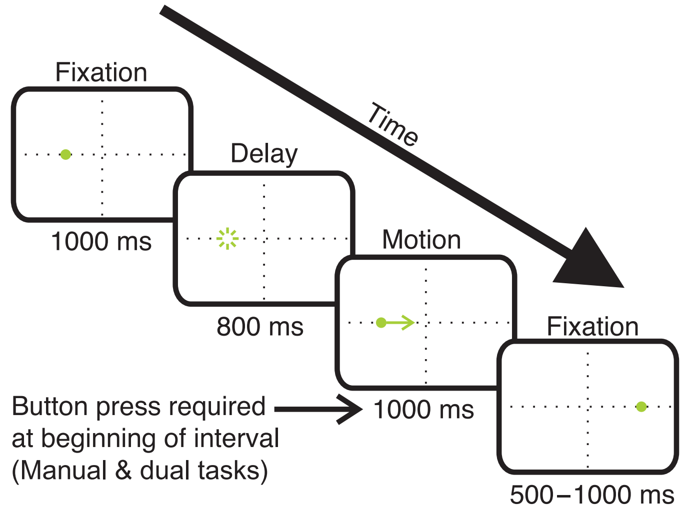

Figure 1. Experimental paradigm. A spot target appeared slightly offset to the left or right of the screen (first panel) and was fixated by the subject. The target disappeared during the delay period (second panel). After the delay in non-catch trials, the spot reappeared moving towards the center of the screen (third panel). It came to rest on the opposite side for a random amount of time (fourth panel). Only the spot was visible on the screen; the horizontal and vertical dashed lines are shown here for reference. The numbers below the panels indicate the duration of each interval.

Methods

General methods

Five healthy right-handed subjects (four females) between the ages of 22 and 33 were used. Subjects EC, LM, and MC were naive to the design and purpose of the study. All subjects gave informed consent.

Subjects were seated in a darkened room facing a dimly lit projection screen (Barco, Kortrijk, Belgium). The viewable screen area measured 195 × 146 cm, the resolution was 800 × 600 pixels, and the refresh rate was 100 Hz. Their heads rested on a chin-rest 150 cm from the screen. Subjects CD, EC, JB, and LM wore a helmet containing a video eye-tracking system (Chronos Vision, Berlin, Germany), and their eye movements were recorded at 200 Hz. Subject ML had eye movements recorded at 1000 Hz using an EyeLink 1000 fixed camera (SR Research, Mississauga, Ontario, Canada). In trials where manual responses were recorded, the subjects also held a small response box with three buttons (Cambridge Research Systems, Rochester, Kent, U.K.), which recorded button presses at a resolution of 1 ms. Subjects used their dominant hand, but otherwise were not restricted as to which button to use.

Before each session, subjects viewed a calibration pattern consisting of a blue dot 0.37 deg in diameter that appeared in a sequence starting at the screen center, followed by positions vertical ±5 and ±10 deg, horizontal ±5, ±10, and ±15 deg, and finally ending back in the center. All fixations lasted 2000 ms save the last two horizontal ones (±15), which lasted 3000 ms. These trials were used for offline computation of offsets and gains.

Visual stimulus

The visual pursuit stimulus was identical for all experiments (Figure 1). It consisted of a 0.75 deg green dot with a luminance of 0.5 cd/m^2. In a single trial, the dot first appeared in the center of the screen offset by 7 deg either to the right or to the left. After a fixation period of 1000 ms, the target disappeared, indicating the start of the delay interval. The delay lasted 800 ms, after which in 75% of trials the target reappeared, offset by an additional 3 deg toward the periphery (total offset = 10 deg). It immediately moved toward the center of the screen at a velocity of 33 deg/s. After a 33 deg excursion the target stopped and remained static for a random amount of time (500, 750, or 1000 ms) before disappearing again, marking the end of the trial. With a probability of 25% the target did not reappear after the delay (catch trials); instead the blank screen persisted for the remainder of the trial. The inter-trial interval was 1000 ms. Note that the target onset time and trajectory was completely predictable for each non-catch trial (via the fixed delay duration and initial direction offset, respectively). However, the randomized post-movement fixation interval maintained the temporal independence of the individual trials. That is, it prevented them from forming an overlying rhythm when assembled as a sequence, which could introduce undesired context effects (Jones & Boltz, 1989). A trial block consisted of 50 trials.

There were three types of trial blocks, which differed only in the instructions given to (and behavior of) the subject. In **pursuit-only** blocks, subjects were asked to follow the moving target with the eyes as accurately as possible. In **manual-only** blocks, subjects were asked to try to predict the occurrence of the target, by pressing a response button to coincide with the reappearance of the target after the delay. Note that this was not a simple reaction task; subjects could not wait for visual information before making their response. In **dual-task** blocks, the subjects received the same instructions as to the button press, but they were instructed to pursue the target as well. Between 200 and 550 trials were collected from each subject for each task type.

A single experimental session consisted of up to 12 blocks, but the exact number depended on the available time and tolerance of the subject. One to six blocks of a single type were presented in sequence, before changing to a different type. Subjects were always presented with one of the simpler block types in their first session (pursuit-only or manual-only); subjects naive to pursuit tasks were given an additional 20–50 practice trials of the pursuit-only task before recordings began. After the first session, the presentation order of the sequences of block types was randomized for each subject.

Eye movements

For subjects recorded using the Chronos eyetracker, eye position data were extracted from the video files using a contour detection algorithm provided by the company (circle approximation for pupil). The EyeLink eyetracker recorded pupil position directly. Subsequent analysis was performed in MATLAB (The MathWorks, Natick, Mass.) using in-house software. Horizontal and vertical eye positions were digitally differentiated and filtered (25 Hz cutoff) to compute eye velocity. Eye acceleration was also computed by differentiation, using a 40-Hz cutoff filter instead. For the calibration trial, periods of stable gaze at each target position were manually selected by an operator, following which offsets and gains were computed using linear regression.

Anticipatory pursuit onset was detected using the algorithm of de Hemptinne et al. (2007). Filtered velocity was required to exceed a threshold of 1.5 deg/s for at least 100 ms to meet the requirement of anticipation. To allow for oscillations of eye velocity, which sometimes occurred around the threshold, sub-threshold intervals were allowed so long as they did not exceed 50 ms in duration. Sub-threshold periods did not count toward the 100 ms requirement, however. All trials were checked by an operator to assure anticipatory pursuit onset could be determined unambiguously. Anticipatory pursuit onset was marked as indeterminate in trials, which contained any of the following: slow eye drifts that began before the delay period, saccades or blinks that occurred during the last 200 ms of the delay period or within 100 ms of anticipatory pursuit onset, or excessive noise in the eye movement trace.

If present in the trial block, manual response times of indeterminate pursuit trials were included in the analysis, with the following exception: trials were rejected outright if the manual response fell more than 500 ms before or after target motion onset or if it failed to occur at all. Anticipatory pursuit onset times were not used in these cases, since the subject essentially failed to follow the task instructions. The first four trials of every block were also rejected outright, to provide the subject with enough repetitions to formulate a reliable estimate of the delay duration (cf., Barnes & Asselman, 1991).

Statistical analyses were performed on all subjects individually, using a Bonferroni-corrected alpha of 0.01 (0.05 / 5). Mean response times between the different experiment types were compared using a 2-sided *t*-test. For the dual task data, anticipatory pursuit and manual response times were compared using the following correlation analysis: for each trial block, the mean was subtracted from each set of response times, and a cross-covariance analysis was performed on the resulting values. The lag-zero peaks of each trial block were then averaged for each subject. Bootstrap estimates of significance were obtained by rerunning the analysis 1000 times with shuffled anticipatory pursuit onset values (the corresponding manual response times were left unchanged), then checking the real value against the 99.5th percentile of the ranked simulated values.

Results

A total of 6110 trials were recorded from all subjects. 8.3% of those trials were rejected because the subject's manual response fell outside of the allowed range. In an additional 8.6% of trials, anticipatory pursuit (or lack thereof) could not be determined. In the two experiment types where pursuit was required, 81.7% of the trials had a detectable anticipatory pursuit response (Figure 2). The delay before target onset, predictable timing, and high target velocity all contributed to robust anticipatory pursuit. Limiting the data set to only catch trials did not qualitatively change any results. It did, however, decrease the sample size, so for all analyses both the catch and non-catch trials were included.

Anticipatory pursuit latencies for one subject (EC) are plotted as cumulative frequency distributions in Figure 3. Data from the pursuit-only task are shown in blue, and data from the dual task are in red. Both distributions are approximately sigmoidal and are centered before the onset of target motion (as expected of a predictive eye movement). They are not exactly symmetric, as the appearance of the visual target in non-catch trials eliminates possible late response points. Importantly, the dual-task distribution is shifted rightward relative to the single-task one. This means that, on average, anticipatory pursuit was initiated later during the dual-task blocks.

The delay in anticipatory pursuit onset induced by the concurrent manual task was consistent in the subject

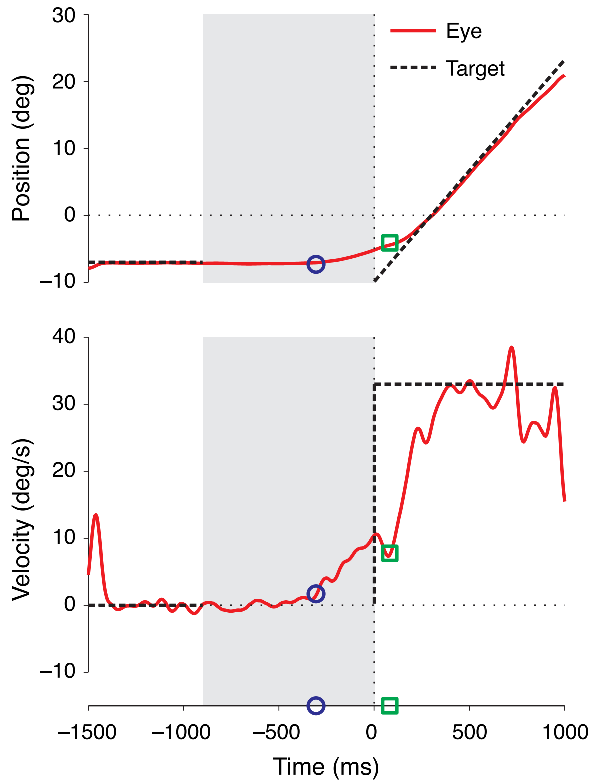

Figure 2. Sample response during the dual task for subject LM. Top panel, eye and target position. Bottom panel, eye and target velocity. The shaded region indicates the delay interval. The detected anticipatory pursuit onset (blue circle) and recorded time of the button press (green square) are marked on both eye traces as well as the *x*-axis.

population (Figure 4, blue bars; see also Supplementary Figure 1). Shown in Figure 4 are the mean latencies from the single task subtracted from those of the dual task (thus,

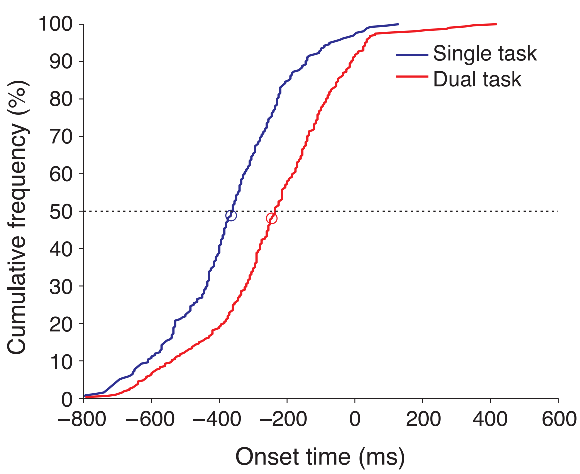

Figure 3. Anticipatory pursuit distributions. Cumulative distributions of anticipatory pursuit onset times for the single and dual tasks. The circles indicate the response mean values; response medians are indicated by the 50th percentile line. Responses occurred significantly later during the dual task. Subject EC.

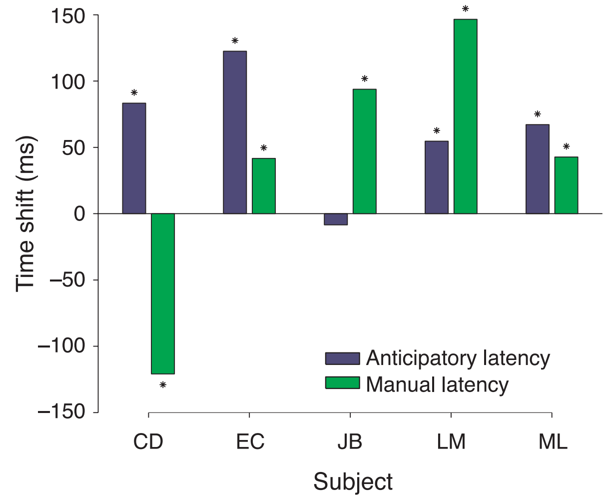

Figure 4. Summary of response time shifts for anticipatory pursuit and button-press responses. Bar height is equal to mean dual task response minus mean single task response. For four out of five subjects, the mean onset of anticipatory pursuit was shifted significantly later in time during the dual task. Four out of five subjects also showed a significantly later shift for the manual response data. Asterisks indicate significance at the 0.01 level.

positive numbers indicate later average responses during the dual task). For four out of five subjects, the delay was significant (Table 1).

Having established that anticipatory pursuit was affected by the concurrent manual task, we wished to see if the manual response itself showed a similar effect. Although several studies have shown delayed response times in the presence of distracter tasks (e.g., Brown, 1997; Migliore, Messineo, Cardaci, & Ayala, 2001), none to our knowledge have used ocular pursuit as the distracter. Figure 4 also shows the difference in the mean manual response time between the single and dual tasks (green bars). Again, four of five subjects were significant (Table 2). The magnitudes of the differences were also similar to those of the anticipation data. Therefore, the effect on response timing appears to be similar, whether the response is made by the eye or voluntarily by the hand.

	Pursuit only task			Pursuit dual task			
Subject	Mean	*SD*	*N*	Mean	*SD*	*N*	Shift
CD	−219	138	330	−135	119	380	83*
EC	−366	179	260	−243	201	314	122*
JB	−194	202	383	−203	182	474	−8
LM	−192	116	348	−137	79	436	55*
ML	−120	184	199	−52	61	214	67*

Table 1. Mean, standard deviation (*SD*), and number (*N*) of anticipatory pursuit onset measurements for each subject and task type. Shift, rounded difference equal to dual task mean minus single task mean. Asterisks indicate significance ($p < 0.01$). Mean and *SD* values are in ms.

	Manual-only task			Manual dual task			
Subject	Mean	*SD*	*N*	Mean	*SD*	*N*	Shift
CD	−101	63	276	−222	118	501	−121
EC	−55	120	276	−14	176	407	42*
JB	−47	67	368	47	73	552	94*
LM	7	108	184	154	86	452	147*
ML	−178	131	274	−135	85	276	43*

Table 2. Mean, standard deviation, and number of manual response time measurements for each subject and experiment. Asterisks indicate a significant difference ($p < 0.01$) that is positive. Other details as in Table 1.

Trial interactions

Since anticipatory pursuit showed a delayed onset similar to the effect observed for manual actions when both were performed simultaneously, the possibility arises that their underlying control systems may share some components. To test this possibility, we examined the correlations between both movements during the dual task. We first performed a linear regression on all data points of anticipatory pursuit onset plotted against manual response time, for all subjects. Figure 5 shows the regression plot for subject LM, lying in the middle of the data set with a correlation coefficient (r^2) of 0.18. The other subjects were as follows: CD, 0.20; EC, 0.02; JB, 0.01; ML, 0.44. All regressions except JB had a significant positive slope ($p < 0.01$). Although the results are variable and do not account for differences between trial blocks, they suggest that anticipatory pursuit and the manual responses may derive a fraction of their variance from a common source.

To confirm the presence of covariation while correcting for inter-block differences, we subtracted the means from both the anticipatory pursuit and manual response data for each block individually. Figure 6 shows a running average of response times (window = 5 trials) for all trials in sequence, also for subject LM. There appears to be a correspondence between the variations around the mean responses, as the two curves visibly follow each other during most blocks.

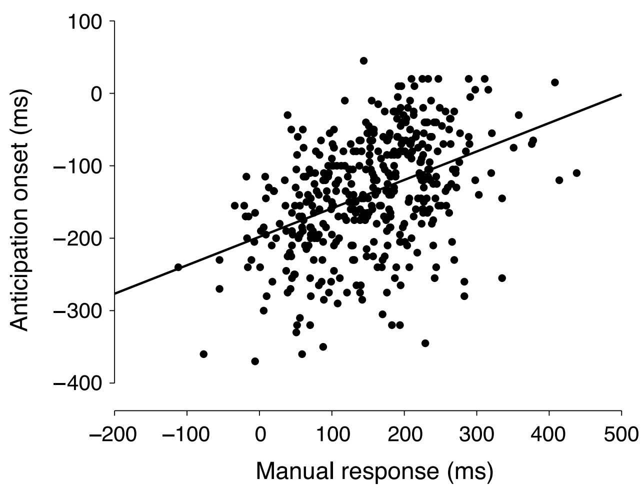

Figure 5. Linear regression of all responses. Each trial in the dual task data set is plotted as a point. The linear regression line is also shown. There is a modest correlation between the responses (r^2 = 0.18). Subject LM.

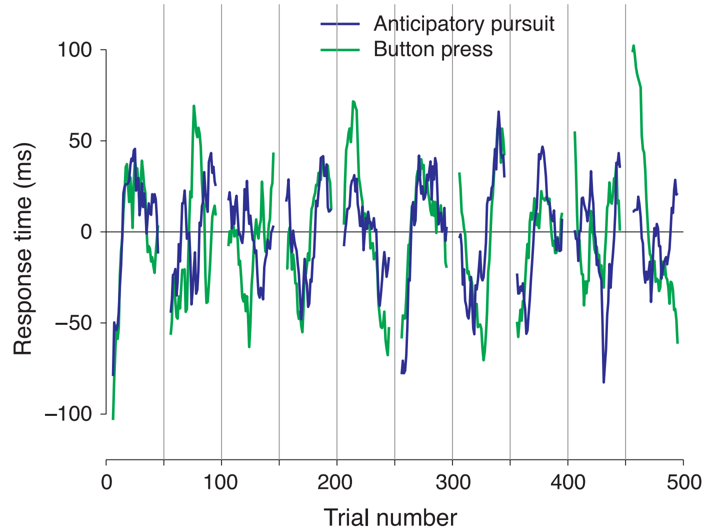

Figure 6. Responses over time. For each trial block (demarcated by the light gray lines), the mean was subtracted from the button-press responses and from the anticipatory pursuit onset times. Corresponding running averages of response times were then computed using a window size of five trials. Note the degree of correspondence between the average curves. Subject LM.

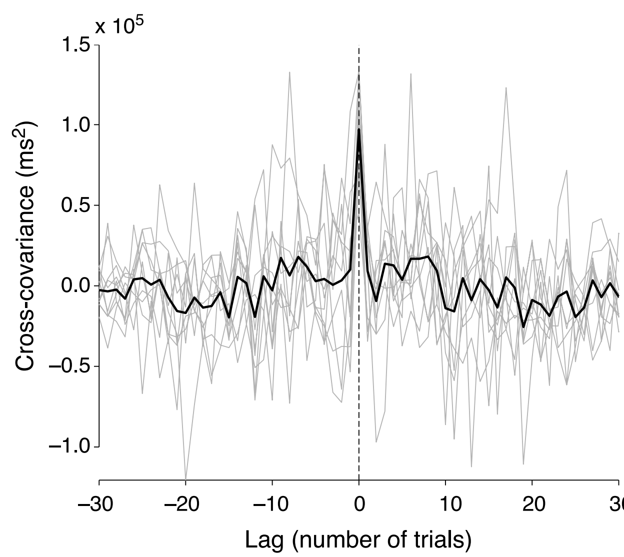

Figure 7. Cross-covariance analysis. For each trial block in the dual task the cross-covariance was computed between anticipatory pursuit onset and manual response times (light gray lines). The mean (dark line) is also shown. The single peak at lag = 0 results from trial-by-trial correlations between the two responses. Subject LM.

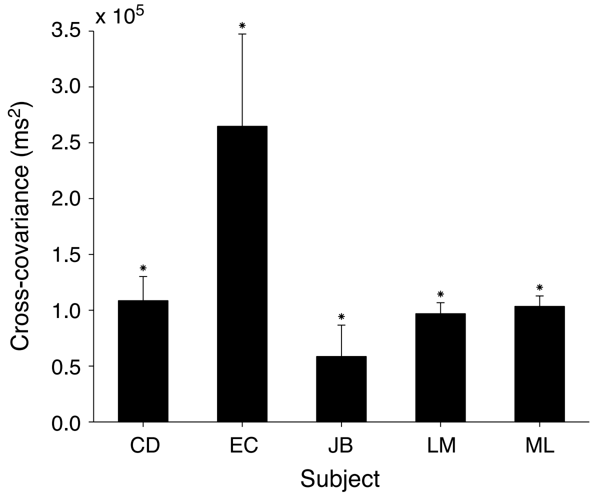

Figure 8. Summary of response correlations. Mean cross-covariance at lag = 0 between all response times, averaged over all trial blocks. Error bars indicate standard error of the between-block mean, and asterisks indicate significance as computed from the bootstrap (see Methods section). All subjects showed significant correlations between ocular and manual timing.

To quantify the degree of correspondence, a cross-covariance analysis was performed on each block and the results averaged (Figure 7). Here, the covariance between the two signals is plotted against lag, or the amount that one signal is shifted relative to the other. The covariance curves for each trial block are plotted in light gray, while the average of all blocks is in black. The response covariance is manifested as a strong peak at lag = 0, relative to the other lag values. All subjects showed a significant lag-zero peak (Figure 8), although JB was marginal with a $p \approx 0.01$ (repeated applications of the bootstrap procedure using different random seeds rejected the null hypothesis about 75% of the time). The correlation analysis suggests that the system responsible for timing anticipatory pursuit initiation shares components with the system for general motor timing (as measured by the button press).

Discussion

We have established that the timing of anticipatory smooth pursuit was delayed when a manual timing task was performed simultaneously. The manual response itself was also delayed by the requirement to pursue. Furthermore, anticipatory pursuit onset tended to covary with the manual response on trials where they were performed together. To explain the preceding results, we propose that the mechanism for generating predictive pursuit is modulated by an attentional component, which itself is shared by other, volitional timing systems in the brain.

Timing model

To illustrate the relationship between anticipatory pursuit and manual response timing, we use a common model of interval timing derived from Scalar Timing Theory (STT), first developed by Gibbon, Church, and Meck (1984). Our version of the model is shown in Figure 9. The clock element emits pulses at regular intervals. The clock pulses must pass through the switch or gate, which is regulated by attention (Meck, 1984). If they pass the gate, the pulses are then counted by the accumulator. At every time step the value in the accumulator is compared to a reference value from memory. When the two values are sufficiently close based on a decision criterion (Wearden, 2004), a response is initiated. For a trial-based experiment such as ours, the system is then reinitialized to its baseline values in preparation for the next trial.

Our model includes a second response process, linked to the first via the attentional gate (cf. Buhusi, 2003). Functionally, the attention module controls the allocation of clock pulses to the accumulators of each concurrent process. However, the need to divide attention between multiple processes increases the computational load, so that some fraction of clock pulses are "missed", i.e., not counted because the switch is left open due to inattention (Fortin, 2003). Thus, it takes longer for the number of pulses stored in the accumulator to approach the value in reference memory, and the response is delayed. To illustrate, one can imagine that ten ticks of real time have elapsed and the corresponding ten pulses have been emitted by the clock component. If the switch is open 20% of the time because the attentional modulator is

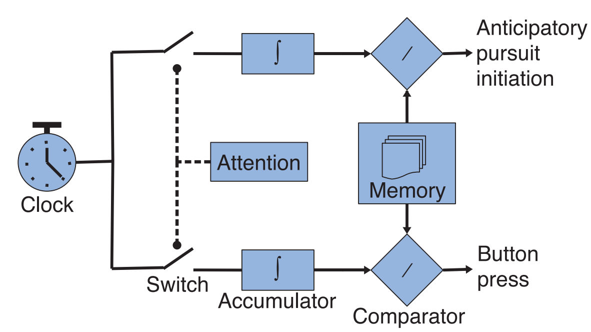

Figure 9. Timing model. The components are based on STT. The clock emits regular pulses that must pass a switch held closed by attention. Pulses that pass through are counted by the accumulator, whose value is checked against a reference stored in memory. When the accumulator and reference values are sufficiently close as determined by the comparator, a response is initiated. Insufficient attention allows the switch to open, causing pulses to be blocked. Thus it takes longer for the accumulator to reach a value close to reference memory, causing a delayed response. During a dual task both branches are active, increasing the load on the attentional component and consequently decreasing the amount of time that the switches are held closed.

distracted by the concurrent task, only eight of those pulses will have been counted by the integrator. If the reference interval (stored in memory) is also eight ticks, the model will then issue a response, but it is 25% too late. This example illustrates the difference between subjective and objective time, and how a late response can result when the subjective clock is slowed due to divided attention.

The second principal result, the correlation between responses in the dual task, supports the idea that anticipatory pursuit shares at least some processing components with the system responsible for more general timing tasks. This is in contrast with other motor actions such as continuous circle drawing, which appear to use a largely separate timing system (Zelaznik, Spencer, & Ivry, 2002). We suggest that the clock, attention, and memory components could be shared, with the remaining processing units segregated (perhaps corresponding to downstream structures closer to the motor outputs of the brain). However, we cannot rule out alternative configurations with more or less overlap. For example, a shared attentional component alone may be sufficient to cause the response correlations we observe: attention is known to fluctuate and is correlated to the timing performance of various tasks (West & Alain, 2000). Thus a period of low attention or arousal could cause *both* processing branches to lose clock pulses and thus yield later than average responses, whereas a period of high arousal would have the opposite effect. Note that the model does not necessarily predict that subjects will have the same magnitude response shift for their eye and hand movements. Individual differences in the downstream components (e.g., the decision criterion) can differentially affect the response times, despite the common contribution of the attention module.

Although the model is based on STT, the individual components need not be necessarily localized to discrete areas of the brain. Indeed, the question of centralized versus distributed timing is controversial (Ivry & Spencer, 2004; Mauk & Buonomano, 2004; Nobre, Correa, & Coull, 2007), and models considerably different from STT have been proposed (Hopson, 2003; Staddon, 2005). The goal of our model was to provide a plausible framework to describe the effect of a concurrent task on the timing of anticipatory smooth pursuit. With the analogous branch that controls manual response timing, it can also account for the analogous effect of smooth pursuit on the performance of the button-press task.

General discussion

We have shown an interaction between the timing of a predictive manual response and the timing of anticipatory pursuit. To our knowledge, this is the first study to directly compare the timing characteristics of anticipatory ocular pursuit with a manual response in parallel. Barnes and Marsden (2002) performed a series of experiments where subjects pursed a target with the eyes, while simultaneously tracking it with the hand by means of a manipulandum. In their experiment using predictable targets, they found that anticipatory pursuit began marginally *earlier* during the dual tracking task (-158.7 ± 20.0 ms, mean ± *SEM*) than the pursuit-only task (-124.0 ± 35.1 ms). They attributed this result to the "synergy" of the tasks; i.e., the impending hand movement creates both an expectancy of the upcoming movement and a parallel source of information about the dynamics of that movement. By contrast, the button press in our task does not share any motion characteristics with the desired smooth pursuit movement, allowing it to serve simply as a drain on shared timing resources. In addition, the design of Barnes and Marsden's experiments precluded them from running "hands-only" trials, and they did not examine trial-by-trial correlations between the two movement types.

On the other hand, studies using multiple timing tasks have been performed using manual responses alone. Brown and West (1990) and Brown et al. (1992) showed that when human subjects had to time multiple intervals, they tended to overestimate their duration. In addition, performing pursuit rotor tracking (Brown, 1997) or other non-timing tasks in parallel also caused temporal productions to lengthen (Brown & Merchant, 2007). Fortin (2003) and Fortin and Massé (2000) found that when subjects were required to pause their timing during an interval reproduction task, they responded later when they were cued about the upcoming timing pause. In each of these studies the authors attributed the response shifts to an attentional process. In other words, the subjects' performance of a distracting task, or even the expectation of one, was sufficient to draw their attention away from the primary timing task.

Overall, the data in our study were robust and consistent with previous research. However, there are a few exceptions worth addressing. The first is the large negative latency shift in the manual response data for subject CD. In other words, this subject pressed the button ~120 ms *earlier,* on average, during the dual task. It may have been due to the use of a cognitive strategy, whereby the subject overcompensated for the increased difficulty of the dual task by consciously responding too early. There was also an insignificant negative shift for anticipatory pursuit latency for subject JB, who also had the weakest eye–hand correlations. This may have been due to overtraining, since the subject had extensive experience in pursuit tasks in general and making anticipatory pursuit movements in particular.

Conclusions

The timing of anticipatory pursuit appears to behave similarly to the timing of voluntary predictive motor actions. The mutual response delay observed when the tasks are performed in parallel suggests that they are limited by the same attentional system. In addition, the response correlation observed on dual task trials suggests that their two timing systems share some common processing components. Anticipatory pursuit follows other established properties of timing, such as having variance that scales with the duration to estimate (de Hemptinne et al., 2007), but at the same time is less vulnerable to conscious cognitive interference. Thus, it can be a useful tool for measuring timing processes in the brain.

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References

Badler, J. B., & Heinen, S. J. (2006). Anticipatory movement timing using prediction and external cues. *Journal of Neuroscience, 26,* 4519–4525. [PubMed] [Article]

Badler, J. B., Lefèvre, P., & Missal, M. (2008). Anticipatory pursuit is influenced by a concurrent duration reproduction task [Abstract]. *Journal of Vision, 8*(6):672, 672a, http://journalofvision.org/8/6/672/, doi:10.1167/8.6.672.

Barnes, G. R., & Asselman, P. T. (1991). The mechanism of prediction in human smooth pursuit eye movements. *The Journal of Physiology, 439,* 439–461. [PubMed] [Article]

Barnes, G. R., & Marsden, J. F. (2002). Anticipatory control of hand and eye movements in humans during oculo-manual tracking. *The Journal of Physiology, 539,* 317–330. [PubMed] [Article]

Boman, D. K., & Hotson, J. R. (1988). Stimulus conditions that enhance anticipatory slow eye movements. *Vision Research, 28,* 1157–1165. [PubMed]

Brown, S. W. (1997). Attentional resources in timing: Interference effects in concurrent temporal and nontemporal working memory tasks. *Perception & Psychophysics, 59,* 1118–1140. [PubMed]

Brown, S. W., & Merchant, S. M. (2007). Processing resources in timing and sequencing tasks. *Perception & Psychophysics, 69,* 439–449. [PubMed]

Brown, S. W., Stubbs, D. A., & West, A. N. (1992). Attention, multiple timing, and psychophysical scaling of temporal judgments. In F. Macar, V. Pouthas, & W. J. Friedman (Eds.), *Time, action and cognition: Towards bridging the gap* (pp. 129–140). Dordrecht, The Netherlands: Kluwer Academic.

Brown, S. W., & West, A. N. (1990). Multiple timing and the allocation of attention. *Acta Psychologica, 75,* 103–121. [PubMed]

Buhusi, C. V. (2003). Dopaminergic mechanisms of interval timing and attention. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 317–338). Boca Raton, FL: CRC Press.

Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews, Neuroscience, 6,* 755–765. [PubMed]

Casini, L., & Macar, F. (1997). Effects of attention manipulation on judgments of duration and of intensity in the visual modality. *Memory & Cognition, 25,* 812–818. [PubMed]

de Hemptinne, C., Lefèvre, P., & Missal, M. (2006). Influence of cognitive expectation on the initiation of anticipatory and visual pursuit eye movements in the rhesus monkey. *Journal of Neurophysiology, 95,* 3770–3782. [PubMed] [Article]

de Hemptinne, C., Nozaradan, S., Duvivier, Q., Lefèvre, P., & Missal, M. (2007). How do primates anticipate uncertain future events? *Journal of Neuroscience, 27,* 4334–4341. [PubMed] [Article]

Fortin, C. (2003). Attentional time-sharing in interval timing. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 235–260). Boca Raton, FL: CRC Press.

Fortin, C., & Massé, N. (2000). Expecting a break in time estimation: Attentional time-sharing without concurrent processing. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1788–1796. [PubMed]

Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review, 107,* 289–344. [PubMed]

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of Sciences, 423,* 52–77. [PubMed]

Gibbon, J., Malapani, C., Dale, C. L., & Gallistel, C. (1997). Toward a neurobiology of temporal cognition: Advances and challenges. *Current Opinion in Neurobiology, 7,* 170–184. [PubMed]

Heinen, S. J., Badler, J. B., & Ting, W. (2005). Timing and velocity randomization similarly affect anticipatory pursuit. *Journal of Vision, 5*(6):1, 493–503, http://journalofvision.org/5/6/1/, doi:10.1167/5.6.1. [PubMed] [Article]

Hopson, J. W. (2003). Timing without a clock. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 23–60). Boca Raton, FL: CRC Press.

Ivry, R. B., & Spencer, R. M. (2004). The neural representation of time. *Current Opinion in Neurobiology, 14,* 225–232. [PubMed]

Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review, 96,* 459–491. [PubMed]

Kao, G. W., & Morrow, M. J. (1994). The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Research, 34,* 3027–3036. [PubMed]

Kowler, E. (1989). Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vision Research, 29,* 1049–1057. [PubMed]

Macar, F., Grondin, S., & Casini, L. (1994). Controlled attention sharing influences time estimation. *Memory & Cognition, 22,* 673–686. [PubMed]

Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience, 27,* 307–340. [PubMed]

Meck, W. H. (1984). Attentional bias between modalities: Effect on the internal clock, memory, and decision stages used in animal time discrimination. *Annals of the New York Academy of Sciences, 423,* 528–541. [PubMed]

Merchant, H., Zarco, W., & Prado, L. (2008). Do we have a common mechanism for measuring time in the hundreds of millisecond range? Evidence from multiple-interval timing tasks. *Journal of Neurophysiology, 99,* 939–949. [PubMed]

Migliore, M., Messineo, L., Cardaci, M., & Ayala, G. F. (2001). Quantitative modeling of perception and production of time intervals. *Journal of Neurophysiology, 86,* 2754–2760. [PubMed] [Article]

Missal, M., & Heinen, S. J. (2004). Supplementary eye fields stimulation facilitates anticipatory pursuit. *Journal of Neurophysiology, 92,* 1257–1262. [PubMed] [Article]

Nobre, A., Correa, A., & Coull, J. (2007). The hazards of time. *Current Opinion in Neurobiology, 17,* 465–470. [PubMed]

Penney, T. B. (2003). Modality differences in interval timing: Attention, clock speed, and memory. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 209–234). Boca Raton, FL: CRC Press.

Staddon, J. E. (2005). Interval timing: Memory, not a clock. *Trends in Cognitive Sciences, 9,* 312–314. [PubMed]

Wearden, J. H. (2004). Decision processes in models of timing. *Acta Neurobiologiae Experimentalis (Warsaw), 64,* 303–317. [PubMed]

West, R., & Alain, C. (2000). Effects of task context and fluctuations of attention on neural activity supporting performance of the Stroop task. *Brain Research, 873,* 102–111. [PubMed]

Zelaznik, H. N., Spencer, R. M., & Ivry, R. B. (2002). Dissociation of explicit and implicit timing in repetitive tapping and drawing movements. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 575–588. [PubMed]