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A quantitative synchronization model for smooth pursuit target tracking

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Abstract We propose a quantitative model for human smooth pursuit tracking of a continuously moving visual target which is based on synchronization of an internal expectancy model of the target position coupled to the retinal target signal. The model predictions are tested in a smooth circular pursuit eye tracking experiment with transient target blanking of variable duration. In subjects with a high tracking accuracy, the model accounts for smooth pursuit and repeatedly reproduces quantitatively characteristic patterns of the eye dynamics during target blanking. In its simplest form, the model has only one free parameter, a coupling constant. An extended model with a second parameter, a time delay or memory term, accounts for predictive smooth pursuit eye movements which advance the target. The model constitutes an example of synchronization of a complex biological system with perceived sensory signals.

Keywords Smooth pursuit · Synchronization · Dynamical Modeling

1 Introduction

The human eyes can perform two distinctive forms of motion: Rapid movement of the eye from one fixation point to another, known as saccadic movement, and smooth pursuit eye movements which is much slower and allow us

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to stabilize the images from moving objects on the retina, thereby enabling us to perceive the moving objects in detail. Contrary to saccades during which vision is highly deteriorated, vision is maintained during smooth pursuit. It is well-known and intriguing that smooth eye movements normally cannot be induced voluntarily but require a continuously moving object in the visual field [47,27,34,32]. In the theory of synchronization of dynamical systems this fact could be seen in a new light: If smooth pursuit depended on synchronization between an internal model for the object position as part of a driven system (the oculomotor system) coupled to a driving system (the object), smooth eye movements would become impossible with the absence of a smoothly moving object. Smooth eye movements would manifest itself only in the form of smooth pursuit but not independently from a moving object.

Synchronization between a driven system and a driving system is a well-known and well-investigated general phenomenon in dynamical systems [49,60]. In particular, the concept of phase synchronization has been found wide applicability in physiology [21,46] and the neurosciences [61,67]. Synchronization of biological systems with environmental signals has been proposed as a mechanism which may allow for real-time reactions of biological systems to predictable signals [73,75]. In general, synchronization can be observed in coupled dissipative dynamical systems which possess a negative feedback coupling. In the realm of the oculomotor system [10], negative feedback is also known as on-line gain control [53,54].

It is difficult to prove synchronization alone from observations of the driving and the driven system, because in the synchronous state, in the ideal case the driven system follows the driving system exactly, and nothing can be inferred about the equations of motion of the driven system and its coupling to the driving system. But systems can be tested for synchronization by looking at irregular motion [13], for example after a brief perturbation [11], and then comparing the resulting dynamics with what the equations of motion of the driven

system would predict. Following this line, we designed an experiment in which the visual target transiently disappears for short times, thus perturbing the coupling, and compare the resulting eye dynamics with the dynamics that a simple synchronization model would predict. The model is in fact the simplest nontrivial continuous system synchronization model one can think of and contains only the coupling constant as a free parameter. Although it does not account for noisy irregularities of smooth pursuit or the amplitude and velocity profile of saccadic movements, its predictions can be tested in experiments.

2 Methods

2.1 Subjects

The experiment was performed on 30 healthy subjects. 29 subjects were performing two identical experiments, one subject performed only one experiment. The subjects were of ages 15–60 without prior history of drug or alcohol abuse, pregnancy, traumatic brain injury, or neurological or psychiatric diagnosis. They were naive as to the goals of this study and not trained in this experiment. All subjects gave informed consent to participate in this study.

2.2 Oculomotor testing

An eyechart was used to verify that all subjects had normal or corrected-to-normal vision. The subjects were seated in a darkened room, facing a computer screen in a distance of 40 cm, and their heads were stabilized via a bite bar system. A single target was presented on the computer screen over a black background as a circularly clockwise rotating red sphere (Fig. 1a). The target was moving with constant angular velocity of 2.51 rad/s or a frequency of 0.4 Hz. The circular trajectory had an amplitude of 7° . At each 12 o'clock position, the target was made invisible in a pseudo-random fashion for a duration of 208, 312, 416, 520, 625, 833, or 937 ms (corresponding to angles of 30, 45, 60, 75, 90, 120, or 135° , respectively), referred to as “target blanking intervals” in the following. This paradigm was repeated in two blocks of about 90 s each. If the subject expressed any signs of fatigue or inconvenience, the session was stopped and the subject was allowed to take a break, after which the session was resumed. Eye movements were recorded by a human infrared eye tracking system (Eyelink II) with 500 Hz temporal resolution. Before each session, the system was calibrated, based on 9 points, including center and peripheral. The signal representing eye and target movements was low-pass filtered at 50 Hz and stored on a computer for further analysis. Occasionally, short segments of data in which no signal was recorded were removed.

2.3 Data analysis

The performance of the 30 subjects was ranked by the root-mean-square deviations between the eye coordinates (averaged for right and left eye) and the target coordinates. Only the six subjects with the best performance were used for data analysis, since it was observed that for subjects with lower accuracy in smooth pursuit eye movement, the actual performance rapidly deteriorated, rendering the data useless for the studies. This was observed, for example, as more frequent phase slips (a cycle is missed or jumped over) in the lower ranked subjects. The six subjects with the best performance are labeled A to F, the order reflecting decreasing performance.

2.4 Reduction to one-dimensional time series data

We are interested in modeling how the eye follows the clockwise rotating target. It is more important to model how the eye follows the rotary component of the target motion instead of the target amplitude which is constant anyway. Therefore, as a first step, the amplitude of the eye is eliminated by introducing phase angles. This way, the two-dimensional problem reduces to a one-dimensional problem which is, furthermore, also dynamically much simpler; the target phase is simply a linearly decreasing function in time.

The phase angles of the eyes and the target are defined as follows: The phase angle of the eyes is $\Phi(t) = \text{unwrap}[\arctan(y_e(t)/x_e(t))]$, and the phase angle of the target is $\Theta(t) = \text{unwrap}[\arctan(y_t(t)/x_t(t))]$. Here, $(x_e(t), y_e(t))$ and $(x_t(t), y_t(t))$ are the coordinates of the eyes and the target, respectively, depending on time t . The eye coordinates are the averages over the two eyes, and “unwrap” denotes a phase-unwrapping operation. The coordinates of the eyes and target were normalized to zero mean and unit standard deviation, and the target phase was smoothed by a boxcar filter to remove digital sampling errors. Note that the unwrapped target phase is a linearly decreasing function in time (Fig. 1b). Phase slips in Φ where removed, such that the absolute difference to Θ never exceeded 2π . Finally, the variable of interest is the *phase error* $\Delta(t)$ between the target and eye,

$$\Delta(t) = \Theta(t) - \Phi(t) . \quad (1)$$

Figures 2a,b show the phase error $\Delta(t)$ for subject A and E. Subject A performs reactive smooth pursuit without advancing the target signal (Fig. 2a), subject E shows predictive smooth pursuit that advances the target signal (Fig. 2b).

2.5 Model fitting

Coupling constants K (see “Theory”) were fitted to each cycle in the following way: For each target blanking, K

was fitted to Eq. (12) using a numerical minimization routine applied to the first 300 ms of data after the disappearance of the target. During this time, the eye velocity usually still differs from zero (Fig. 5c), allowing for fitting the coupling constant K to the data. Saccades were not removed and can lead to occasional outliers or unrealistic negative values of the coupling constant K , since the model does not take saccades into account. Outliers ($K > 0.03 \text{ s}^{-1}$) and negative K were discarded from further analysis, no matter of their origin.

3 Theory

3.1 Control by Synchronization

We first consider the simplest nontrivial synchronization scheme one can think of (Fig. 3): A target variable $\Theta(t)$, where t is time, drives a system with state variable $\Phi(t)$. In our experiment, $\Theta(t)$ is the phase angle of the target on the screen, which is assumed to be identical to the phase angle on the retina, and $\Phi(t)$ is the phase angle in an internal expectancy model for the target position (Fig. 1b). The actual manifestation of the expectancy model in the brain will be discussed in the ‘‘Discussion’’ section.

We assume that the expected target position directly determines the eye position, as long as the eyes are performing smooth movements. In this case, ‘‘expected target position’’ and ‘‘eye position’’ are the same. In the case of saccades, the position of the eye does not necessarily match the expected target position any more. Rather, we will later hypothesize that saccades are triggered when the discrepancy of the expected target position and the signal on the retina exceeds a threshold.

If the target is rotating clockwise with angular velocity ω , its dynamics is described by the differential equation $\dot{\Theta} = \omega$ ($\omega < 0$) with the solution $\Theta(t) = \Theta(0) + \omega t$, a steadily and uniformly decreasing phase. The phase angle in the expectancy model is coupled to the target by a linear coupling term with coupling constant $K > 0$ which is constant over each cycle, such that the coupled system can be described by

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega + K(\tilde{\Theta} - \Phi). \quad (2)$$

Here, $\tilde{\Theta} = \Theta$ if the target is visible, and $\tilde{\Theta} = \Theta_0$ if the target is invisible, where Θ_0 is the last position before target blanking. This modeling of the target blanking interval is crucial for the following; the movement during the blanking interval is modeled by ‘‘freezing’’ the drive variable to a constant value until the target reappears.

3.2 Model predictions

Of main interest is the dynamics of the phase error $\Delta(t) = \Theta(t) - \Phi(t)$.

(I) *Visible target:* For a visible target, one has from system (2)

$$\dot{\Delta} = \dot{\Theta} - \dot{\Phi} = -K\Delta \quad (3)$$

with the solution

$$\Delta(t) = \Delta(t_1)e^{-K(t-t_1)} \quad (t > t_1), \quad (4)$$

an exponentially decreasing phase error. Here, t_1 is the time when the target becomes visible. Therefore, the model predicts that the phase difference between actual and expected target position decays exponentially with a characteristic time constant $1/K$. For large times, asymptotically one has $\Delta(t) = 0$, i.e., complete synchronization; target position and expected position are identical, and smooth pursuit is observed. This relaxation to equilibrium in the phase error is the reason for why one cannot infer properties of the driven system without perturbing the coupled system.

(II) *Invisible target:* In our experiment, a perturbation is imposed by transient disappearances of the target for intervals of variable duration. The solution for target blanking starting at time t_0 can be found in the following way: During target blanking, we have from system (2)

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega + K(\Theta_0 - \Phi), \quad (5)$$

since target blanking starts with a fixed target angle, as discussed before. To shorten notation, we define a constant $\omega_1 = \omega + K\Theta_0$ such that the system becomes

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega_1 - K\Phi. \quad (6)$$

For the phase of the internal expectancy model position one has the solution

$$\Phi(t) = e^{-K(t-t_0)}\Phi_0 + \int_{t_0}^t e^{K(u-t)}\omega_1 du \quad (7)$$

$$= e^{-K(t-t_0)}\Phi_0 + \omega_1/K - \omega_1/K e^{-K(t-t_0)} \quad (8)$$

$$= e^{-K(t-t_0)}(\Phi_0 - \omega_1/K) + \omega_1/K. \quad (9)$$

Now, the phase error is (note that $\Theta(t) = \Theta_0 + \omega(t-t_0)$)

$$\Delta(t) = \Theta(t) - \Phi(t) \quad (10)$$

$$= \Theta_0 + \omega(t-t_0) - \omega_1/K - (\Phi_0 - \omega_1/K)e^{-K(t-t_0)} \quad (11)$$

$$= \omega(t-t_0) - \omega/K + (\Delta(t_0) + \omega/K)e^{-K(t-t_0)} \quad (12)$$

Equations (4) and (12) are the main results of our model. They model the phase difference, or phase error, between expected and target position after and during the transient disappearance of the target, respectively. These equations predict that during target blanking the expected position is lagging the invisible target position after a while, and that the phase error is otherwise described by two superimposed dynamical episodes:

(i) *The initial episode:* Immediately after target blanking the expected position is dominated by the exponential term in Eq. (12), $e^{-K(t-t_0)}$. This will be denoted as the ‘‘initial episode’’. Depending on the sign of the phase error at the time of target blanking, $\Delta(t_0)$, there

are two different scenarios: (a) For $\Delta(t_0) > 0$, the initial slope of $\Delta(t)$ is negative, and there is no extremum of $\Delta(t)$ during target blanking. (b) For $\Delta(t_0) < 0$, i.e., when the expected position is initially lagging the target position, the initial slope of $\Delta(t)$ is positive, and there is a local minimum of the absolute value of $\Delta(t)$ at time $t_0 + 1/K \ln(K\Delta(t_0)/\omega + 1)$. In this local minimum, the slope of $\Delta(t)$ changes sign, and from here on the dynamics starts to resemble case (a). In other words, for negative initial phase errors, the eye does not slow down immediately but *accelerates* briefly towards the now invisible target before slowing down. This is a particularly crucial prediction of the model since it produces another rather characteristic dynamical pattern which can be tested for in experiments as well.

(ii) *The linear episode:* For increasing time, the phase error is dominated by the terms $\omega(t - t_0) - \omega/K$ in Eq. (12) and becomes more and more linear in time. This can be understood by that the eye becomes slower and slower, and for infinitely large times it stands still. The endpoint is at the angle ω/K . Note that for a still eye the absolute phase error increases linearly, since the target is moving on with angular velocity ω . Since $\omega < 0$, the eye is lagging. This will be denoted as the “linear episode”. Both initial and linear episode together make up the de-synchronization episode during target blanking.

(III) *After end of target blanking:* When the target becomes visible again, re-synchronization begins, identical to the behavior before target blanking, i.e., the eye follows Eq. (4).

3.3 Model with a time delay

The model can be extended to predictive smooth pursuit that advances or “anticipates” the target signal by introducing a time delay τ into the driven system (the oculomotor system). It is well known that for sinusoidal stimuli as in our study there is a predictive mechanism in smooth pursuit [2] since phase errors are less than expected from the time delays in the oculomotor system [15], or even become positive, i.e., the eye advances the target position. This time delay can be interpreted as a short term memory which may be realized by time delayed feedback in the participating control loops governing smooth pursuit. The duration of the time delay in our model exactly specifies the amount of prediction. It is usually much shorter than a full cycle duration and does not contain any information about previous cycles or target blanking durations. The notion that the introduction of a memory can lead to the opposite effect of prediction or prospective control [68] is somewhat counterintuitive but has been described extensively in theory, where it is known as “anticipatory synchronization” [70, 71, 30]. Anticipatory synchronization has been validated in physical experiments [63, 74], and has been postulated as being utilized in communication within neuronal systems [65, 14]. Time delayed oscillators also have

been used to model processes related to internal timing and pitch perception [40, 55].

Introducing the delayed value of the expected phase angle, $\Phi_\tau(t) = \Phi(t - \tau)$, the coupled system is now defined as

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega + K(\Theta - \Phi_\tau). \quad (13)$$

Therefore, the driven system (only) has been modified by introducing a time delay into the coupling term. This time delay models a short term “memory” of the phase angle at a fixed time τ before the actual time of eye motion. The phase error has to be re-defined accordingly as $\Delta^{(\tau)}(t) = \Theta(t) - \Phi(t - \tau)$.

(I) *Visible target:*

The phase error is

$$\dot{\Delta}^{(\tau)} = \dot{\Theta} - \dot{\Phi}_\tau = -K\Delta^{(\tau)}. \quad (14)$$

This is a delay differential equation, which, in contrast to the linear equation (3), may have not only exponentially decaying but also oscillatory and unstable solutions [43, 23, 26, 16]. These solutions occur if $K\tau > \pi/2$. At this point, oscillations with period 4τ will occur. For realistic fits of K to the data (see “Results”) and observed anticipation time τ it turns out that we are usually below this threshold, and no oscillations are to be expected.

Note that now the trivial fixed point, i.e., the synchronous state, is given by $\Delta^{(\tau)} = 0$. This means that during synchronization $\Theta = \Phi_\tau$, which is equivalent to $\Phi(t) = \Theta(t + \tau)$. This expression states the counterintuitive behavior of a target anticipation; the eye advances the target. This way, the apparent nuisance of a time delay can be seen rather as a beneficial component of the nervous system [70, 73, 14]. Further dynamical effects of time delays in the nervous system have been described recently [17].

(II) *Invisible target:* During target blanking, we have from system (13)

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega + K(\Theta_0 - \Phi_\tau). \quad (15)$$

Using again $\omega_1 = \omega + K\Theta_0$, this becomes

$$\dot{\Theta} = \omega, \quad \dot{\Phi} = \omega_1 - K\Phi_\tau. \quad (16)$$

Since the solution of these delay-differential equations depend on an initial condition which is defined on the whole interval $[-\tau, 0]$, we do not give general analytic solutions and model solutions are obtained numerically.

3.4 Model simulations

The model (2) was numerically simulated using Matlab (The MathWorks, Inc., 2004). Figure 4a shows a section with the three episodes de-synchronization, re-synchronization, and synchronization. Figure 2c shows a longer free-run solution. It was verified that the numerical solutions are identical to the analytic expression (12). The analogous results for the model with the time delay, Eq. (13), are shown in Figs. 4d and 2d, respectively.

4 Results

Over the six subjects with the best performance, the model predictions could be verified in repeating patterns, as detailed below. The measurements do not always reflect the model predictions, but the typical pattern consisting of the three episodes can be observed across subjects in a number of repetitions. In some subjects, the predicted dynamical patterns could be found repeatedly over the whole data set.

Generally, five of the six subjects show both reactive (eye position equals target position) and predictive (eye position advances target position) pursuit. One subject shows reactive pursuit only. On average, about 50% of trajectories during target presentation are predictive.

4.1 De-synchronization

The de-synchronization episode of the model consists of an initial part and a following dominantly linear behavior.

(i) *Initial episode:* The predicted dynamical patterns of the initial episode during target blanking are the most characteristic ones. There are two scenarios: (a) The initial phase error is zero or positive, and the model predicts an initial exponential slowing down of the eye (Fig. 5b). In subject A with the best smooth pursuit accuracy, in the first run 85% and in the second run 95% of all trajectories show this behavior shortly after target blanking (Fig. 5a). All other five subjects show this behavior as well; for example, subject B and C which have mostly positive initial phase errors show this behavior in more than 40% of all trajectories. Figures 6b, d show examples for the other subjects. (b) The initial phase error is negative, and the model predicts an initial positive slope of the phase error and a local maximum shortly after onset of target blanking. In this maximum, the absolute phase error is minimal. This behavior is present in two out of four subjects with initially negative phase error (Fig. 6c). In the subject with the better performance, in the first run 75% and in the second run 50% of all trajectories show this behavior. However, subject F with the worst performance occasionally shows local maxima in the phase error also for positive initial phase errors, which would not be explainable by the model.

(ii) *Linear episode:* In the linear episode, the phase dynamics is dominated by a slowing-down of the eye. This slowing-down is a natural behavior of the model during target blanking. All six subjects show the linear episode, and it is seen in 95% of all observed trajectories. Figure 5a shows the linear episode for subject A during all target blanking intervals, and Fig. 6 shows the linear episode for subjects F, E, D, and A for selected cycles.

4.2 Re-synchronization

The re-synchronization episode is modeled as a smooth trajectory of the expected target position, like the de-synchronization episode. However, after reappearance of the target the eye performs saccadic movements (most often directed towards the target) which differ from the expected target position. Therefore, the exponential re-synchronization episode is not directly observable after reappearance of the target.

However, it can be found frequently that in the first half-second after target reappearance the eye trajectory briefly meets the expected trajectory again, and new saccades are triggered not later or almost exactly at this point (Figs. 6a, d). In subject A with the best performance, there is evidence for this behavior after about 50% of all target reappearances in the second run of the experiment. This behavior can also be observed occasionally in three other subjects.

When this behavior happens, occasionally a subsequent series of trigger points can be observed during which the phase error shows an exponentially decaying behavior for the first two or three saccades, and the expectancy model trajectory provides an envelope to the eye trajectory. This behavior persists up to one second after target reappearance, i.e., during the re-synchronization episode. The envelope of the eye's dynamics during saccades after the end of a transient disappearance is described by the theoretical trajectory of the expectancy model state, Eqs. (4) and (12). Note that the expectancy model position influences the eye dynamics even if the target is visible again. It seems like that for a short time, the expectancy model position is preferred over the updated image on the retina. It is interesting to note that the coupling constant K has been fitted only to the first 300 ms of each data segment after onset of target blanking and that the same K accounts for the re-synchronization episodes, without an explicit fit to this episode.

4.3 Coupling constant

The coupling constant K , which is the only free parameter in our model without time delay, has been assumed to be constant for each cycle from one target blanking to the beginning of the next one. Graphs of the coupling constant K over time show that K is fluctuating. It can be observed in all six subjects that after small values of K at the beginning of the trial K increases slightly. Frequently, it can be observed that K decreases after a while. To summarize this observation, Fig. 7 shows the mean value of K over all six subjects and trials in dependence of time. The line is a quadratic function fit to these values.

5 Discussion

5.1 Model significance

Our model is a *quantitative* model. The main significance of our model lies in the fact that a single parameter, the coupling constant, can be made accountable for both the initial and the linear de-synchronization behavior during target blanking. Furthermore, it was hypothesized that also the re-synchronization behavior after reappearance of the target can be modeled if the expectancy model target trajectory is seen as an envelope of the eye trajectory which is interrupted by saccadic movements directed towards the target. This observation was not persistent over all target blanking intervals and subjects, but could be seen repeatedly. Within this respect, the model partially accounts for post-saccadic events whereas most known approaches of smooth pursuit are about pre-saccadic events.

Whereas the model describes the initial and subsequent linear increase of the magnitude of the observed phase error at the beginning of target blanking accurately, after the first saccade the expectancy model state is not directly observable since due to saccades it does not coincide with the actual position of the eyes any more. But it happens occasionally that after target reappearance saccades directed towards the target are apparently triggered by the expectancy model state. This could be explained by the following hypothesis: Although the target is visible again, it is in conflict with the expected target position which would predict, due to synchronization, that the target is more behind its actual position. The eye control system waits until the target reaches its expected position, cannot find it there, and initiates a saccade as a quick search step. This scheme is in agreement with the recent finding that smooth pursuit and saccadic target tracking may share a similar functional architecture [41,35,36]. We note that the initial and the linear episodes are in partial agreement with the observation that after target disappearance smooth pursuit continues at a reduced gain if subjects expect the target to reappear [4], although our model does not explain a residual velocity.

5.2 Application to step-ramp paradigms

In the re-synchronization phase after target reappearance, rather than a smooth onset of smooth pursuit as predicted for the expectancy model state, almost always saccades were observed. We believe that the main reason is that during the target blanking interval the eyes are significantly slowing down (Fig. 5c), and, unlike to the Rashbass paradigm [50], the target motion continues in the same direction after target reappearance. In our experiment we did not use step-ramp paradigms because the crucial point in the validation of our model is

the target blanking interval in which it is assumed that the driving signal is “frozen” to its last value before the blanking interval. However, our theoretical results are not generally in disagreement with a possible smooth onset of smooth pursuit in experiments using the Rashbass paradigm. This is demonstrated in Fig. 8 which shows an application of the model to a target trajectory undergoing several step-ramps. These data, in particular Fig. 8a, show a good agreement with experimental data published by [7], Fig. 1D.

5.3 Reductionistic top down approach

Our model is a reductionistic top-down approach for describing motor control [25]. Unlike models describing, for example, cerebellar control loops [58,59,39,62,31] or specific neural networks [33], our model does not refer to specific feedback loops involved. Even if the latter approaches are very promising, we believe that our reductionistic model can shed light onto how biological systems interact with a complex environment: Synchronization of biological systems with environmental signals in general, rather than synchronization between individuals, which has been studied more thoroughly, has been proposed as a mechanism which may allow for optimal real-time reactions [73,75] of the system to signals that can be described by dissipative laws of motion. If an anticipatory component is included, these models may produce predictive motion. In the here proposed model the dynamics of the target is a simple linear function in time and only the coupling provides the dissipation which is necessary for the stability of the trivial fixed point $\Delta = 0$. This special case has been studied in detail by Calvo et al. [8].

Towards this end, the main finding of our top-down approach is that certain features of smooth pursuit can be described by a simple control theory approach with only one degree of freedom and only one free parameter. As it is described for example in a similar modeling approach to human speech [48], in the top-down approach the proposed functional loops are not directly observable. Rather, one measures only the behavior of a performance control loop which may be composed of a group of nested lower-level loops. At the performance level, one can observe and quantify only the actions of all these loops acting together.

We hypothesize that the actual manifestation of the internal expectancy model may be found to some extent in the frontal eye field (FEF). In general, cortical areas with extraretinal information, such as the FEF, are involved in smooth pursuit in target blanking experiments, as is known from fMRI studies [38]. Several studies have suggested that FEF neurons encode an internal three-dimensional representation of smooth pursuit eye movements [20,24] or object velocity [6] using the efference copy signal. Therefore, a representation of object posi-

tion may be derived from the integration of the object velocity information in the FEF [5, 1].

5.4 Dynamical approach

As was pointed out previously, both the position and velocity of the retinal image have to be controlled in visual target tracking [10].

Because our model is based on differential equations which relate the velocity of the eye to its position (given by the phase angle), it accounts both for position and velocity in one instance. This does not effect the validity of theories of anticipatory pursuit in which position and velocity are treated separately, for example in the remembered pursuit task [76, 3, 2]. Our approach to model smooth pursuit by differential equations is based on the common methodology of mathematically describing continuous dynamical systems, less on assumptions about whether the system is based on velocity or position information processing or storage.

The time delay in our model equals the anticipation time and does thus not contain information about previous cycles. The model only contains negative feedback control and no “switches” or varying parameters during one cycle. In particular, the initial phase in eye velocity is modeled correctly after disappearance of the target as an exponential decay of eye velocity [37]. Furthermore, the model solutions predict that the initial phase of the de-synchronization episode depends on whether the phase error at the onset of target blanking is positive or negative; the subsequent evolution of the trajectory into the linear de-synchronization phase (when the eye slows down) is taken account for automatically by the model equations and is also a pure result of synchronization between an expectancy model for the target position and the actual target position on the retina.

5.5 More complex models

Our model is an attempt to reconcile the mechanical view and the cognitive view of smooth pursuit, both of which have been found to be incomplete if each taken alone [12]. It describes the cognitive view in a dynamical way by introducing coupling constants as a measure of a yet unknown process. Our model can be seen as a linear approximation of more complex models, for example with nonlinear coupling terms, or models using chains of coupled oscillators [72]. The coupling constant crucially determines the shape of the model trajectories, and it is not possible to model an entire trial with equal quality with a constant coupling constant. The coupling may depend on several parameters which are not included in our model, like attention, fatigue, and eye blinking.

Since the eye motion is relatively slow if no saccades occur, our model does not involve an optimal control

strategy or the search for that by the system, as in [64] and references therein. The theoretically described three characteristic episodes of motion in and after transient target blanking are the pure result of feedback control, and due to the slowness of the eye motion, there is no optimization necessary with respect to minimal variance, minimal jerks, etc.

5.6 Unexplained variability

Our model does not account for most of the variability in the data during saccades and smooth pursuit, and also not for much of the variability during transient target blanking across all six subjects. The main finding is that three characteristic patterns of dynamical episodes could be found repeatedly in and shortly after target blanking. Over the whole dataset of all six subjects considered, there remains unexplained data variability. One source of unexplained variability could be that smooth pursuit is not only elicited by the image on the retina but also by perceived motion signals, as was observed by [57] through correlations in direction variations in perceptual and pursuit responses to stimulus presentations with randomly varying directions. That experiment indicated that the pursued and perceived motion directions are influenced by the same stochastic noise source.

Future work will concentrate on models with stochastic components that may better take account for this variability. Further modifications of the experiment are the inclusion of an occluder during target absence which has been found to have a profound effect to the outcome of smooth pursuit [12].

The statistical properties of the timing of saccades in visual search between multiple targets has been investigated by van Loon et al. [51, 66]. It is found that a Gamma distribution describes timing better than a Gaussian distribution. In [66] the Gamma distribution has not been tested against other alternatives. It is not clear so far which timing is predicted by our model, since the model does not describe the amplitude and dynamics of saccadic movements.

5.7 Coupling constant

We interpret the initial increase of the coupling constant K as a learning effect [42, 45] and the subsequent decrease of K as fatigue or decreased attention. The coupling constant could reflect the degree of attention via synchronization between the expectancy model and the signal input [29, 44]. These hypotheses need further experimental evaluation, for example by performing distraction experiments [18]. Also, the exact relationship between the coupling constant and gain control [11, 9], if there is any, is unknown.

5.8 Further model implications

Our model implies that the synchronization characteristics would become even more predominant for larger target rotation frequencies. To keep up with a faster moving target, we expect that in particular the triggering of saccades during the re-synchronization episode is modeled better. Vice versa, we predict that for slower target motion our model breaks down since then synchronization is not required as a means of rapid adjustment to the target signal.

We have not much further explored the meaning of the time delay τ for smooth pursuit that advances the target. It has been mentioned that our model solutions could become unstable, leading to oscillations with a characteristic frequency. Spontaneous oscillations are known to occur, for example, in the pursuit system of monkeys during ramp target tracking and can be modeled by feedback loops [22]. It would be very interesting whether these oscillations could be observed in experiments with a higher target rotation frequency. Applying methods of time-delayed feedback equation fitting to these data [69,28,56] could reveal more about the stability properties of the oculomotor system [52]. Using generalized phase diagrams, this approach has recently been pursued successfully for a manual tracking experiment with delayed visual feedback [19].

It would be interesting to see if our model applies as well to other movements which are believed to have both a mechanical and a cognitive aspect like limb movements.

6 Summary

We presented and tested a mathematical model of smooth pursuit eye tracking which is based on the dynamical principle of synchronization between a driving and a driven system. Our one-dimensional model for the phase error of smooth pursuit of a transiently disappearing circular rotating target predicts several different characteristic dynamical patterns which all could be found repeatedly in experimental data of individuals that have a high smooth pursuit accuracy. The model could explain why smooth voluntarily eye movement is impossible without a smoothly moving target. The model depends only on one free parameter, a coupling constant between the actual and the expected target position. This parameter can be fitted to data. The model predicts three characteristic dynamical episodes of eye motion during and after target blanking: An initial de-synchronization episode, a linear de-synchronization episode, and a re-synchronization episode after the re-emergence of the target.

The reproducibility of the initial and the linear part of the de-synchronization episode across subjects and over time is our main result in favor of a dynamical synchronization model for smooth pursuit. The unexpected

result that our model occasionally seems to be able to correctly predict the onset of saccades in a short time interval after target reappearance, with the same coupling constant K that is fitted in the de-synchronization episode, provides further evidence for our model. A fit of the model's only free parameter, the coupling constant, shows that this parameter has a characteristic time evolution for all considered subjects, which is hypothetically interpreted as arising from learning and fatigue. An extension of the model by introducing a time delay in the coupling allows for modeling smooth pursuit which advances the target in a simple but plausible way by the concept of anticipatory synchronization. Eye movement that advances the target position would be the result of short time delays in oculomotor feedback loops, whereas the anticipation time is determined by the time delay.

We believe that our quantitative dynamic approach to model oculomotor control provides a promising way to efficiently describe other motor control systems as well. Our hope is that models like the presented one may yield a better understanding of damaged neuronal control loops for the benefit of brain trauma patients.

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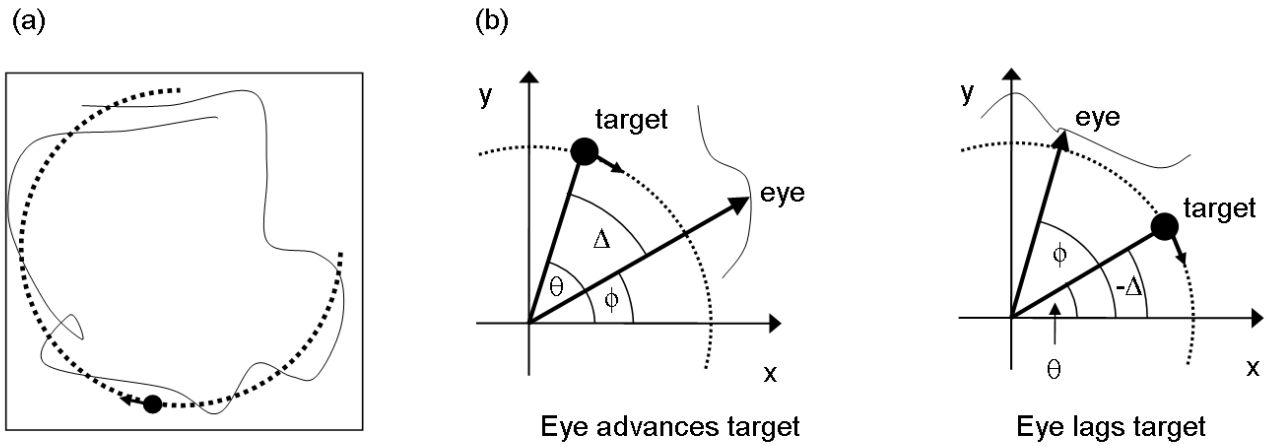


Fig. 1 (a) Schematic view of the target trajectory presented to the subjects (dotted line). The target was blanked during intervals of pseudo-randomly varying duration as described in the text. Here, the time when the target is invisible covers 90° of the full circle, corresponding to a duration of 625 ms. The curvy line represents a possible trajectory of an expectancy model target position, which, during smooth pursuit, is assumed to coincide with the actual eye position. (b) Definition of the phase error $\Delta(t)$ as the only dynamical variable. The phase error is defined as the difference between the phase of the target position, $\Theta(t)$, and the phase of the expectancy model target position, $\Phi(t)$, which coincides with the eye position during smooth pursuit. It does not matter for the definition of the phase error if the target is actually visible or not. For clockwise target motion, a positive phase error corresponds to a leading expected target position, a negative phase error to a lagging expected target position. The phase error is independent of the length of the vectors describing expected and actual target position, thus reducing the two-dimensional configuration space to the one-dimensional rotary component of the target motion and expectancy model dynamics.

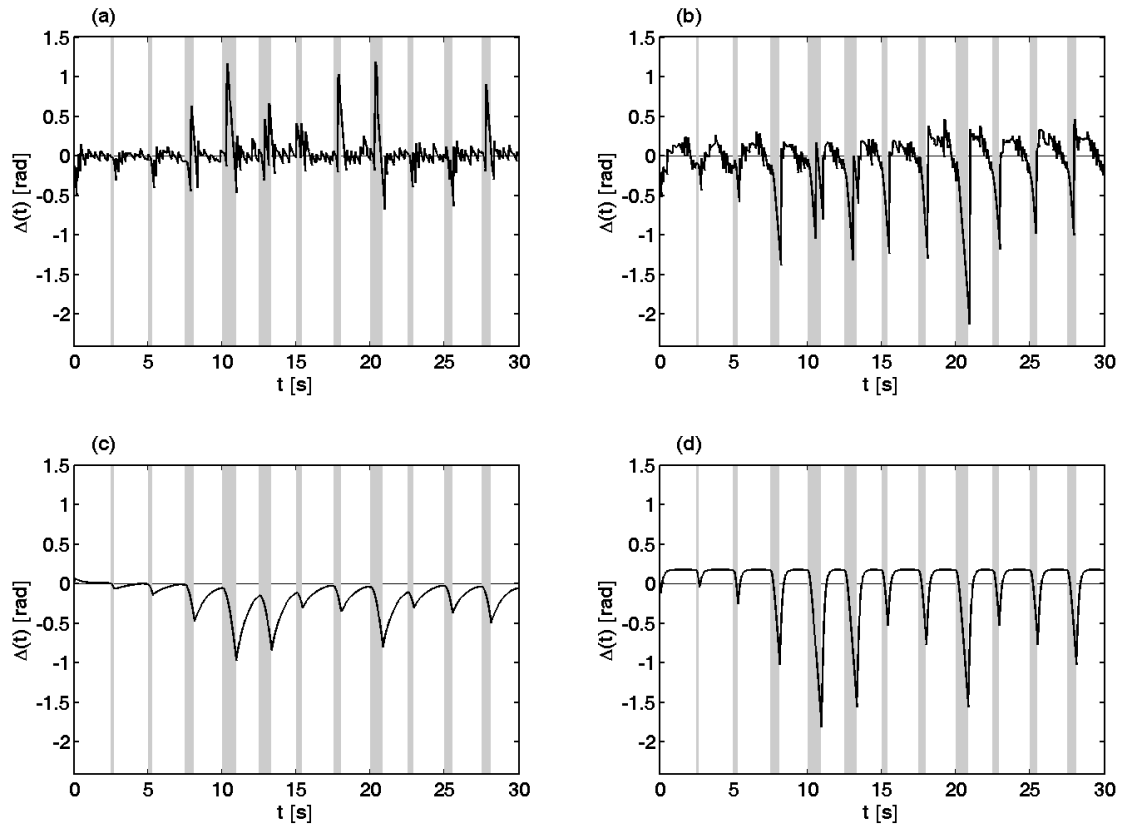


Fig. 2 Experimental (a,b) and modeled (c,d) phase errors $\Delta(t)$ over time t . The shaded areas indicate intervals during which the target is invisible. At all other times, the target performs a continuous clockwise rotating motion. Positive $\Delta(t)$ mean that the eyes advance the target, negative $\Delta(t)$ mean that the eyes are lagging the target, and $\Delta(t) = 0$ corresponds to exact smooth pursuit. (a) Phase errors of subject A. During some target blanking intervals, saccades towards the target can be seen. (b) The same for subject E who is showing predictive pursuit during target visibility, reflected by the on average more positive phase error. (c) Free run model solutions with coupling constant $K=0.0012 \text{ s}^{-1}$ and model delay $\tau = 0 \text{ ms}$. The initial condition of the model solution does not depend on the data shown in (a), but the coupling constant used is an average fit to the data in (a). Saccades are, as always, not modeled. (d) The same for $K = 0.0045 \text{ s}^{-1}$ and $\tau = 70 \text{ ms}$. In this case, the phase errors are mainly positive during target visibility, which is a characteristic of anticipatory synchronization. Again, the model initial conditions do not depend on the data shown in (b). Both the delay and the coupling constant are an average fit to the data in (a).

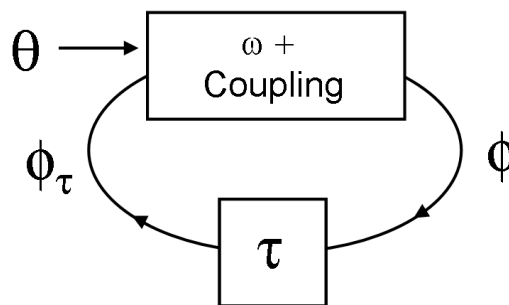


Fig. 3 Block diagram for the synchronization of a driven variable Φ to a driving variable (target) Θ . A generalized model that accounts for anticipatory synchronization contains also a time delay τ between the driven state Φ and coupling, i.e., the driven state Φ is delayed before coupled to the target variable Θ , according to Eq. (13).

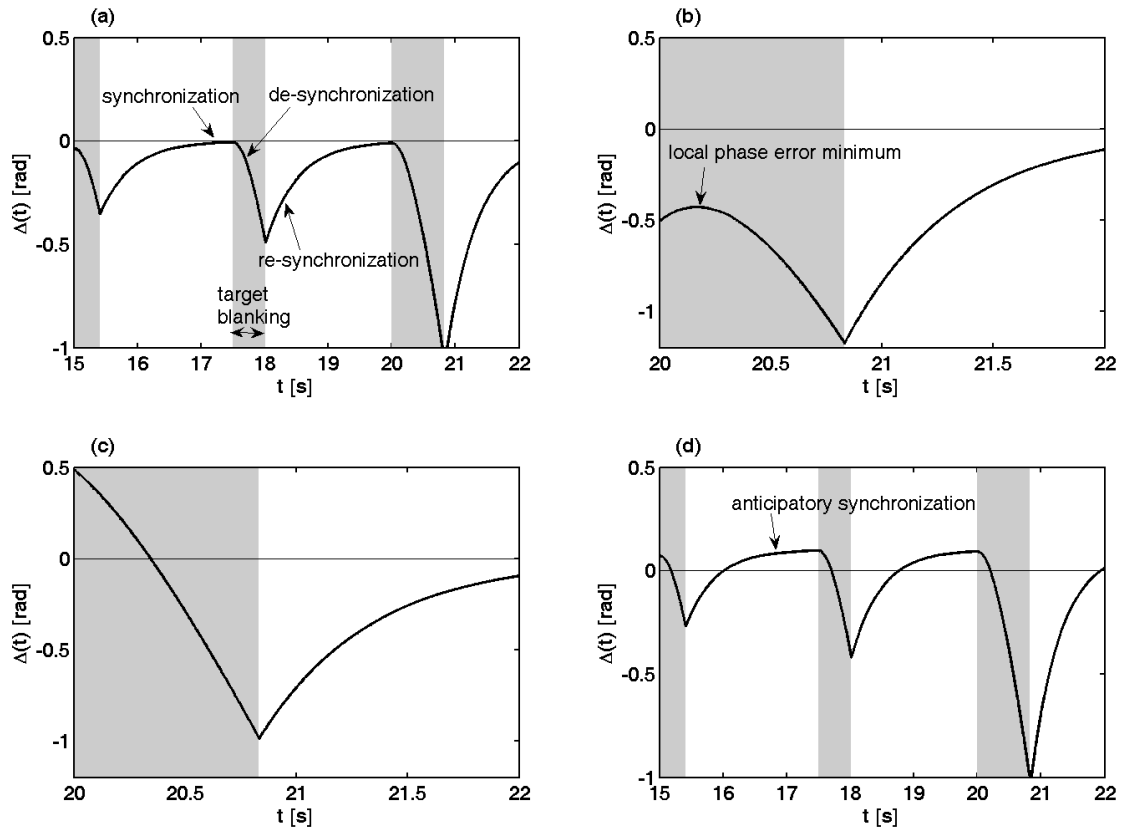


Fig. 4 Behavior of the synchronization model (2) in the absence and following onset of an ideal driving signal $\Theta(t)$, for input delay $\tau = 0$ (a,b,c) and $\tau = 40$ ms (d). **(a)** When the driving signal is turned off (shaded areas), de-synchronization begins, which means that the phase error $\Delta(t)$ becomes nonzero. In this case, $\Delta(t) < 0$, i.e., the driven system falls behind the driving target. After turning the drive on again, re-synchronization begins, $\Delta(t)$ approaches zero again. This dynamics is described analytically by Eq. (12). **(b)** When the initial phase error is negative (eye lags target), the de-synchronization phase error has a local minimum. **(c)** When the initial phase error is positive (eye leads target), the de-synchronization phase has no local minimum. **(d)** With a time delay, the system behaves differently (Eqs. (14) and (16)): First, de-synchronization sets in, i.e., the driven system advances the drive signal for a while until it finally lags behind the driving signal. Re-synchronization appears to be similar to the non-delayed case. In the synchronization case, the phase error does not vanish any more but is a constant $\Delta > 0$, i.e., the eye advances the target. Since $\tau = 40$ ms, the phase error in this anticipatory synchronous case is $\Delta = 0.4 \text{ Hz} \times 2\pi \times 40 \text{ ms} = 0.10$ rad.

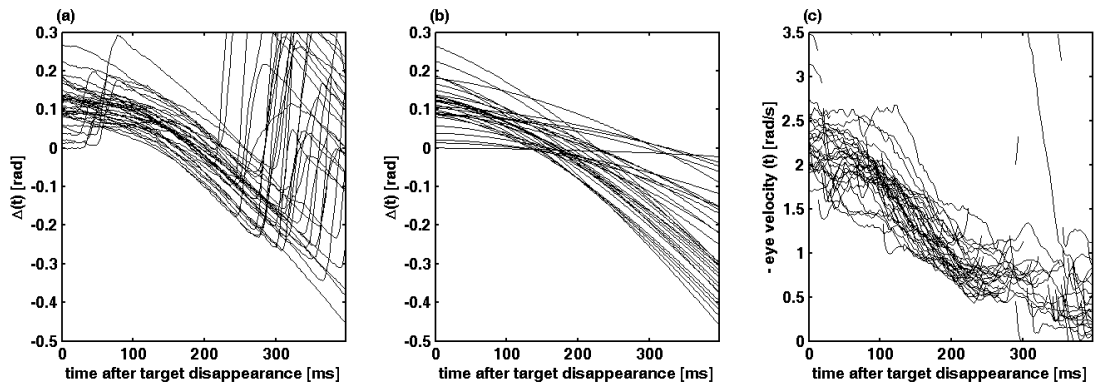


Fig. 5 Observed phase error during all target blanking episodes for subject A for the first 400 ms (a), and comparison with model trajectories (b). (The saccades directed towards the target visible in the data plot are not accounted for by the model fit and can lead to a unrealistic negative value of K . The solutions of four negative K are removed from the model plot.) (c) shows the eye angular velocity during target blanking, as estimated from the position data by numerical time derivation and with saccades removed.

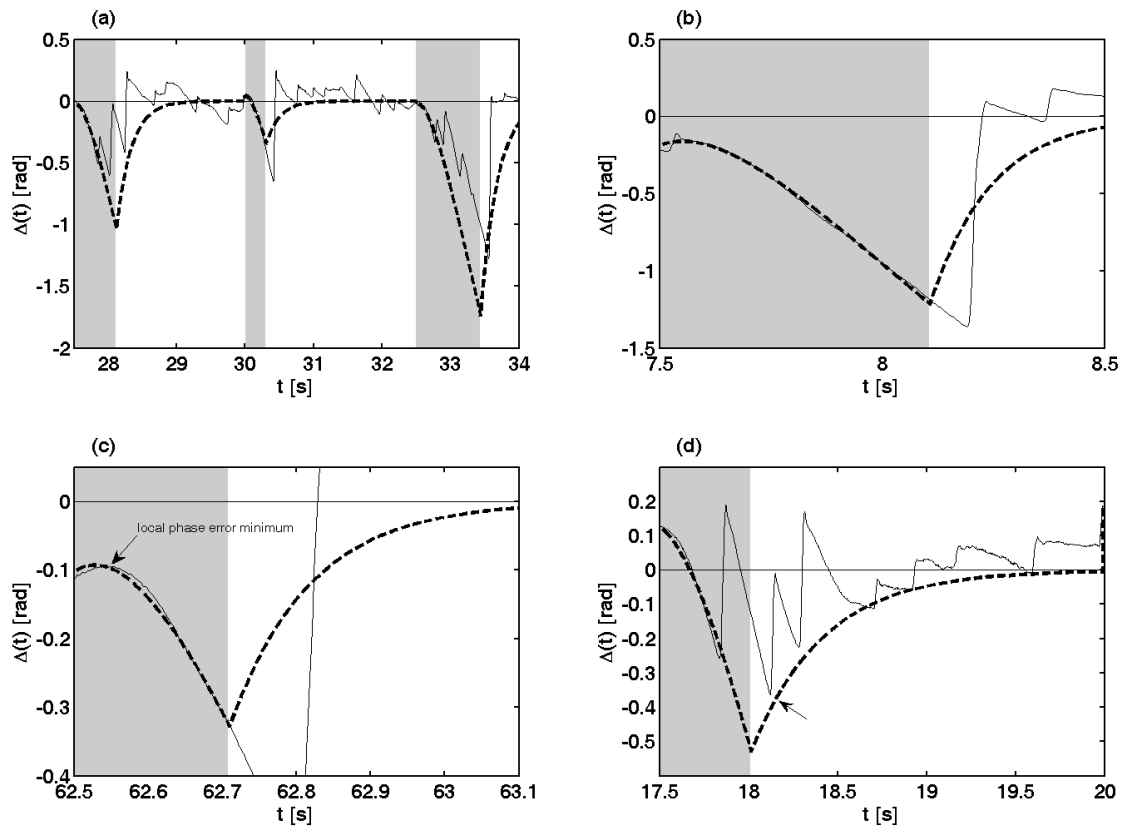


Fig. 6 Comparison of experimental (continuous lines) and modeled (dashed lines) phase error in subjects F (a), E (b), D (c), A (d). The interval during which the target is invisible is depicted as the shaded area. **(a)** The model reproduces the de-synchronization phases (at the beginning of the shaded areas) three times in succession. **(b)** The dynamics of the phase error in the de-synchronization episode during target blanking coincides well with the model prediction. Both the initial and the linear part of the de-synchronization episode are modeled correctly. **(c)** The de-synchronization episode for an initially negative phase error. The negative initial phase error of the subject leads to a local minimum of the phase error shortly after onset of target blanking, as predicted by the model. The model also predicts correctly the subsequent linear part of the de-synchronization episode. **(d)** The initial and linear part of the de-synchronization episode, and re-synchronization. In this example, the model simulates the de-synchronization episode well and partly predicts when small saccades directed towards the target are triggered, in particular immediately after the reappearance of the target. Saccades appear as jumps towards positive $\Delta(t)$ (eye advances target). After the first saccadic movement, the phase error $\Delta(t)$ increases in magnitude until a level is reached which corresponds to the expected target position after the reappearance of the target (dashed line, arrow), although the target is visible again. Note that the model neither predicts the first onset nor the amplitude of saccadic eye movements.

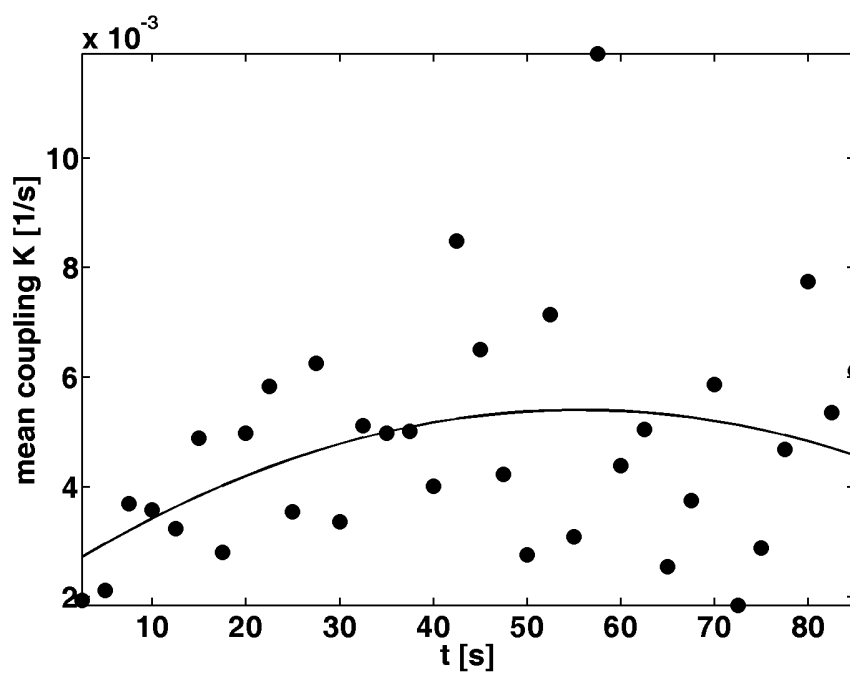


Fig. 7 Mean values of fitted coupling constants K over time for all six subjects. The line is a quadratic function fit to the mean coupling constants. (Outliers, i.e., unrealistic negative K and $K > 0.03 \text{ s}^{-1}$, have been removed prior to averaging.)

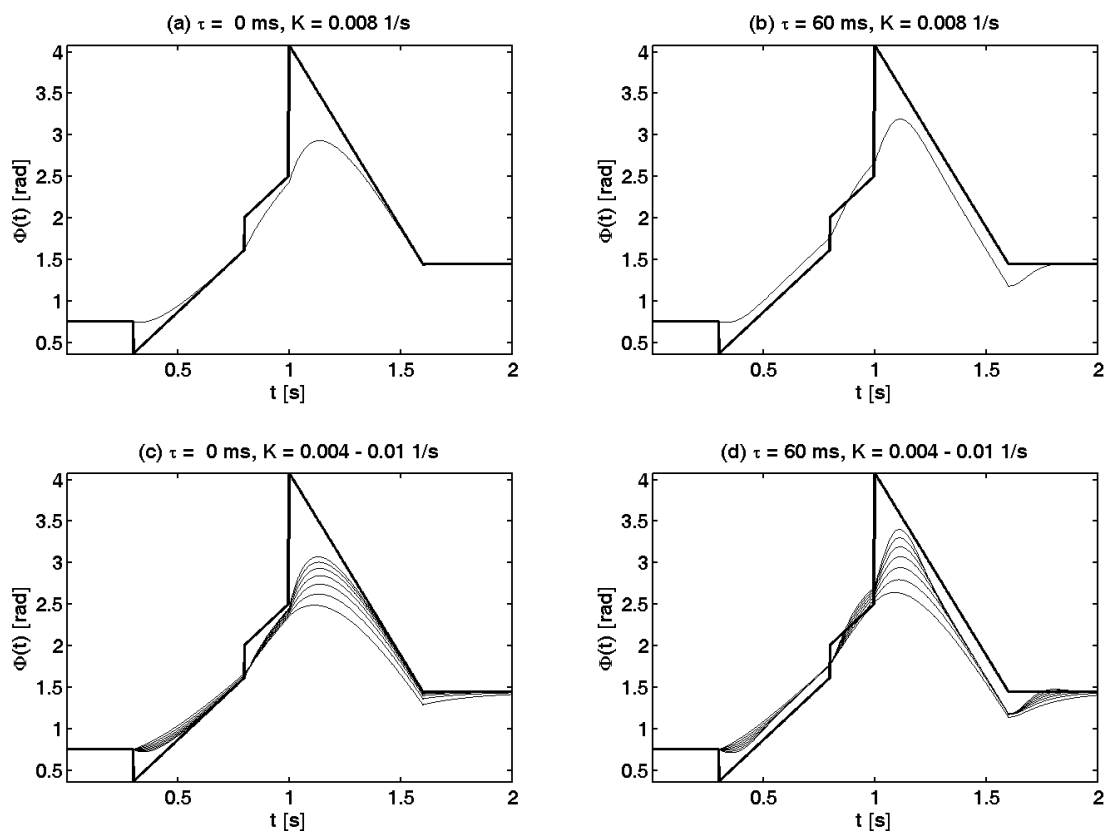


Fig. 8 Application of the model (thin lines) to a circular step-ramp paradigm of the target phase (thick lines), for varying delays and coupling constants as given in the title of each plot. The chosen coupling constants are typical for our experimental values, as shown in Fig. 7.