

# S1 Properties and Extension of Modified Tau

## S1.1 Size and Velocity Effect

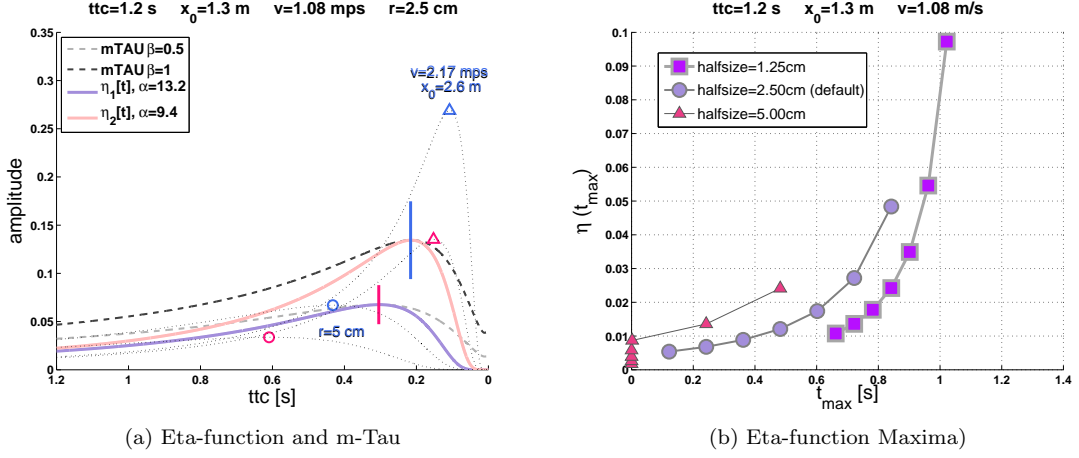


Figure S1: **The  $\eta$ -function.** (a) Same as Figure 1b, but here two  $\eta$ -functions with  $\alpha = 13.2$  and  $\alpha = 9.4$  are shown. For comparison, two  $\tau_{\text{mod}}$ -functions with  $\beta_1 = 0.5$  and  $\beta_1 = 1$ , respectively, are also plotted, whose maxima coincide with those of  $\eta$  (amplitudes of  $\tau_{\text{mod}}$  functions were correspondingly rescaled). Note that both  $\eta$ -functions have a more pronounced decrease after the maximum than the corresponding  $\tau_{\text{mod}}$ -functions: Whereas the  $\eta$ -functions approach zero before  $t_c$ , the  $\tau_{\text{mod}}$ -functions do not. The default maxima are marked by vertical bars, and correspond to stimulus parameters  $t_c = 1.2\text{ s}$ ,  $x_0 = 1.3\text{ m}$ ,  $v = 1.08\text{ m/s}$ , and  $l = 2.5\text{ cm}$ . Their shift directions (as a result of doubling either object size or velocity) are identical with the m-Tau function (Figure 1): Both maxima of the  $\eta$ -function shift to the left (circles) upon multiplying the object's default halfsize  $l$  by two ("size effect"). A shift in the opposite direction (triangles) occurs upon doubling approach velocity  $v$  and initial distance  $x_0$  ("velocity effect",  $t_c = 1.2\text{ s}$ ). (b) Same as Figure 1b, but here the size effect is demonstrated for the  $\eta$ -function. Unlike m-Tau, the maxima of the  $\eta$ -function do not lie nor shift on a straight line. Circle symbols represent the default case, with  $\eta$ -function maxima allocated at times  $t_{\max} \in \{0.12, 0.24, 0.36, 0.48, 0.60, 0.72, 0.84\}\text{ s}$ . The velocity effect is illustrated with Figure S2.

## S1.2 Remarks on Equation 1

1. In the m-Tau function  $\tau_{\text{mod}}(t) \equiv \gamma(t) \cdot \tau(t)$ , the factor  $\gamma(t)$  provides gain control to  $\tau(t)$ :

$$\lim_{\dot{\Theta} \rightarrow 0} \gamma(t) = \lim_{\dot{\Theta} \rightarrow 0} \frac{\dot{\Theta}}{\dot{\Theta} + \beta_1} = 0 \quad (\text{S1})$$

$$\lim_{\dot{\Theta} \rightarrow \infty} \gamma(t) = 1$$

if  $|\beta_1| > 0$  and constant, and thus  $\gamma(t)$  is constrained to the interval from zero to one, with asymptotic interval boundaries.

2. The m-Tau function can be interpreted as steady-state solution of the differential equation

$$\frac{d\tau_{\text{mod}}(t)}{dt} = -\beta_1\tau_{\text{mod}}(t) - \dot{\Theta}(t)\tau_{\text{mod}}(t) + \Theta(t) \quad (\text{S2})$$

The last equation describes a neuron which encodes  $\tau_{\text{mod}}$  in its mean firing rate [1]. The decay rate (leakage conductance) is set by  $\beta_1$ , with resting level at zero. The neuron receives silent or

shunting inhibition (i.e. reversal potential equal to the neuron's resting potential) with strength  $\dot{\Theta}$ . Excitatory input is provided by  $\Theta$ .

3. In summary, the m-Tau function comprises three desirable properties with one equation: (i) it remains finite (“computationally stable”) for  $\Theta = 0$ , (ii) it can be formally expressed as providing a gain control for the  $\tau$ -function, and (iii) it can be readily cast into a differential equation for neuronal firing rate.

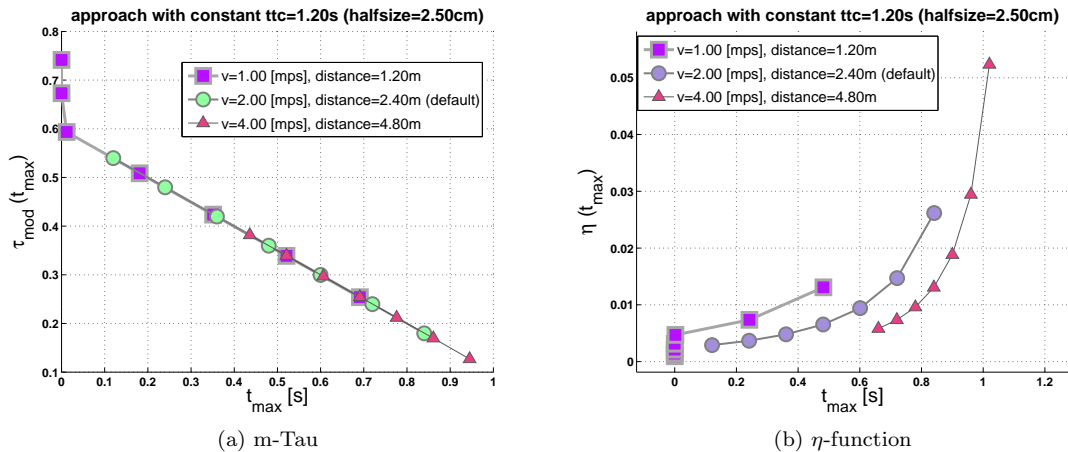
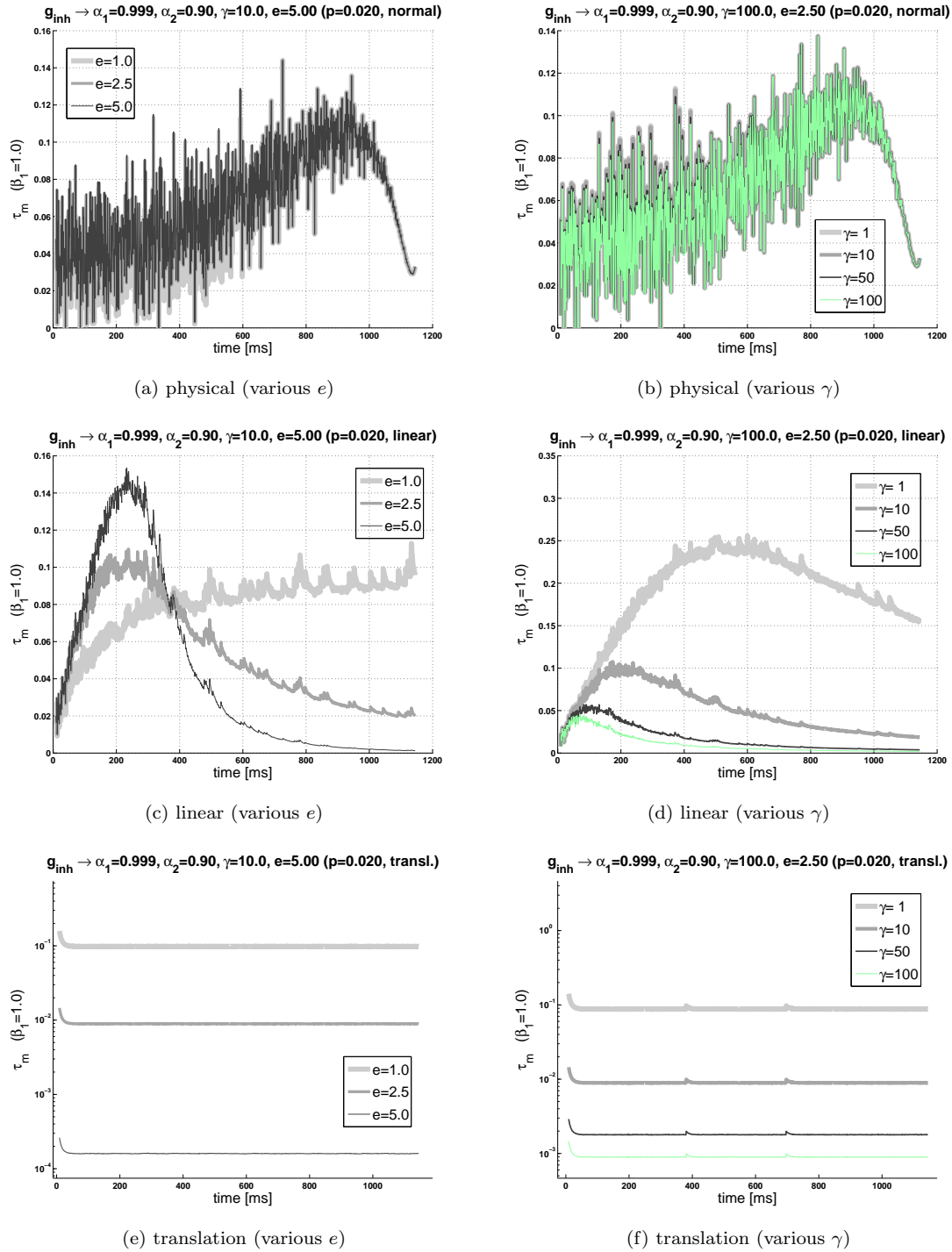


Figure S2: **Velocity effect.** The figure illustrates how the maxima of m-Tau function and  $\eta$ -function behave upon changing the velocity of an approaching object. Notice that, in order to maintain  $t_c = 1.2$  s, the initial object-observer distance had to be modified accordingly (see legend). The rest of the parameters are identical with Figures 1 and S1, respectively, and are indicated at the top of each figure panel. The default values for speed and initial distance were  $v = 2.0$  m/s and  $x_0 = 2.4$  m, respectively. Maxima corresponding to the default values are indicated by circle symbols. (a) Changes in speed translate to shifting the default data points to the left ( $v = 1.0$  m/s) and to the right ( $v = 4.0$  m/s). Similar to the size effect (Figure 1b), default and shifted data points lie on a straight line (except for some numerical inaccuracies associated with the two leftmost points). (b) Compared to the m-Tau function, variation in speed leads to separates curves for the maxima of the  $\eta$ -function. All curves are furthermore nonlinear, with their amplitudes  $\eta(t_{\text{max}})$  increasing when maxima move closer to  $ttc$ .

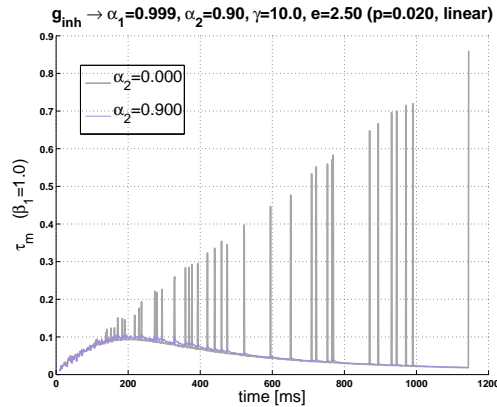


**Figure S3: Simulation results I: Modified Tau with additional inhibition.** Simulation of equation (S3) for different types of object approaches, and for different values of  $e$  (left figure panels) and  $\gamma$  (right panels) of equation (S4). Default parameters were  $\alpha_1 = 0.999$  (memory coefficient for filtering  $\Theta$ ),  $\alpha_2 = 0.9$  (memory coefficient for low-pass filtering of  $x$ ),  $\gamma = 10$  (constant gain factor), and  $e = 2.5$  (power law exponent). Noise was added to angular variables according to equation (9), with  $p_1 = p_2 = 0.020$ . **(a, b)** “Normal” object approach (approaching speed  $1.13m/s$ , object half-size  $l = 0.025m$ , distance  $x_0 = 1.3m$ ). Inhibition stays silent ( $g_{\text{inh}}(t) = 0\forall t$ ) because  $\dot{\Theta}(t)$  exceeds the threshold value  $5 \times 10^{-5}$  most of the time. **(c, d)** A linear approach (i.e.  $\Theta = \text{const.}$ ) triggers inhibition proportional to  $\Theta^e$  (equation S4), and suppresses  $\tau_{\text{mod}}$ -responses for  $e > 1$  after an initial transient. This behavior is consistent with corresponding experimental observations [2]. **(e, f)** Perhaps an ecologically more relevant situation is the suppression of responses to translating objects, or ego-motion as consequence of translation movement (both of which  $\dot{\Theta} \approx 0$ ). Suppression of such responses occurs again after some initial transient.

### S1.3 At a glance: The $\eta$ -Function and the m-Tau Function

	eta-function $\eta(t)$	m-Tau-function $\tau_{\text{mod}}(t)$
<b>definition</b>	$A \cdot \dot{\Theta} / \exp(\alpha \Theta)$	$\Theta / (\dot{\Theta} + \beta_1)$
<b>peak location <math>t_{\text{max}} = \dots</math></b>	$t_c - \alpha \cdot \kappa$	$t_c - \sqrt{\kappa(\frac{2}{\beta_1} + \kappa)}$
<b>place peak at <math>t_{\text{max}} \rightsquigarrow</math></b>	$\alpha = (t_c - t_{\text{max}}) / \kappa$	$\beta_1 = 2 [(t_c - t_{\text{max}})^2 / \kappa - \kappa]^{-1}$
<b>shift of maximum</b>	$\alpha^{(1)} > \alpha^{(2)} \rightsquigarrow t_{\text{max}}^{(1)}$ before $t_{\text{max}}^{(2)}$	$\beta_1^{(1)} > \beta_1^{(2)} \rightsquigarrow t_{\text{max}}^{(1)}$ after $t_{\text{max}}^{(2)}$
<b>inhibitory input</b>	$\exp(\alpha \cdot \Theta)$	angular velocity $\dot{\Theta}$
<b>firing rate equation</b>	not straightforward (cf. [3])	$\frac{d\tau_{\text{mod}}(t)}{dt} = -\tau_{\text{mod}}(\beta_1 + \dot{\Theta}) + \Theta$
<b>stability issues</b>	no	none for $\beta_1 > 0$
<b>direct relation to <math>t_c</math></b>	no	$\tau_{\text{mod}}(t) = \gamma(t) \cdot \tau(t)$
<b>lower parameter limit</b>	$\lim_{\alpha \rightarrow 0} \eta(t) = \dot{\Theta}$	$\lim_{\beta_1 \rightarrow 0} \tau_{\text{mod}}(t) = \tau(t)$
<b>upper parameter limit</b>	$\lim_{\alpha \rightarrow \infty} \eta(t) = 0$	$\lim_{\beta_1 \rightarrow \infty} \tau_{\text{mod}}(t) = 0$

**Additional information:**  $\kappa \equiv 1/v$  is the ratio of object radius (“half-size”) to object velocity;  $\gamma(t) \equiv \dot{\Theta} / (\dot{\Theta} + \beta_1)$  is a gain control factor; and  $\tau \equiv \Theta / \dot{\Theta}$  is the  $\tau$ -function. “**Place peak at  $t_{\text{max}}$ ”** means that  $\eta$  and  $\tau_{\text{mod}}$  adopt their respective maxima at  $t_{\text{max}}$  if  $\alpha$  and  $\beta_1$  are calculated with the formulas as shown in the table.



(a)

Figure S4: **Simulation results II: Modified Tau with additional inhibition.** Inhibition  $g_{\text{inh}} = g_{\text{inh}}(x, t)$  is assumed to be a low-pass filtered version of  $x$  (equation S4). The degree of low-pass filtering is specified by the memory coefficient  $\alpha_2$ . Without noise, we could in principle directly use  $x$  as inhibitory conductance (i.e.  $\alpha_2 = 0$ ). In the presence of sufficiently high noise levels, though,  $x$  would get zero at random times. This could lead to random drop-outs of inhibition in  $\tau_{\text{mod}}(t)$ , what is indicated by the “spikes” in the figure (legend: curve for  $\alpha_2 = 0$ ). Low-pass filtering of  $x$  with  $\alpha_2 > 0$  converts  $g_{\text{inh}}$  into a sluggish process, which bridges the gaps where  $x$  is zero (curve for  $\alpha_2 = 0.9$ ).

### S1.4 Shut Down of m-Tau Responses for $\dot{\Theta} = \text{const.}$

This section is thought as a proof of two concepts: *First*, the m-Tau function can be easily extended to accept further excitatory or inhibitory inputs. Important, these inputs can be incorporated in a biophys-

ically plausible way [1]. *Second*, m-Tau as it stands (“vanilla”  $\tau_{\text{mod}}$ ) cannot reproduce the experimental data with constant angular velocity from reference [2]. Situations with  $\dot{\Theta} = \text{const.}$  may occur if self-motion creates a translatory flow field across the retina, or if any object crosses a visual scene rather than approaching the observer on a collision course. In order to shut down m-Tau responses to such linear object “approaches”, we will define a corresponding inhibitory process. We start by adding an inhibitory conductance  $g_{\text{inh}}$  to the differential equation (S2):

$$\frac{d\tau_{\text{mod}}}{dt} = -\beta_1\tau_{\text{mod}} - \dot{\Theta}\tau_{\text{mod}} + g_{\text{inh}}[V_{\text{inh}} - \tau_{\text{mod}}] + \Theta \quad (\text{S3})$$

Without loss of generality, we assume  $V_{\text{inh}} = 0$  for the inhibitory reversal potential. For the sake of clarity, we omitted biophysical constants for transforming the terms to units of voltage (the state variable  $\tau_{\text{mod}}$  represents voltage). Our goal is to inhibit m-Tau responses for translation movement or ego-motion. To a first approximation, both of the latter movement patterns will have  $\dot{\Theta} = \text{const.}$ , and thus  $\ddot{\Theta} = 0$ . The idea is to engage inhibition in the latter case, while it should stay silent during any “normal” object approach. To this end we define a *gating process*  $\mathcal{G} = \mathcal{G}(\ddot{\Theta}) \in [0, 1]$ , with  $\lim_{|\ddot{\Theta}| \rightarrow 0} \mathcal{G} = 1$ , and 0 otherwise. An explicit implementation of  $\mathcal{G}$  could be defined via a Heaviside or sigmoid function, respectively. For the simulations shown in figure S3,  $\mathcal{G} = 1$  if  $|\dot{\vartheta}(t + \Delta t) - \dot{\vartheta}(t)| < 5 \cdot 10^{-5}$ , (low-pass filtering analogous to equation 4). Strong low-pass filtering of angular velocity (here with filter memory coefficient  $\alpha_1 = 0.999$ ) increases the resilience of the gating process even in the presence of high noise levels. Inhibition is furthermore assumed to be a nonlinear function of  $x = x(t)$ ,

$$x = \gamma\Theta^e \cdot \mathcal{G}(\ddot{\Theta}) \quad (\text{S4})$$

with exponent  $e = 2.5$  (further values: Figure S3a,c,e) and (here constant!) gain  $\gamma = 10$  (further values: Figure S3b,d,f). Finally, the inhibitory conductance  $g_{\text{inh}} = g_{\text{inh}}(x, t)$  of equation (S3) is just a low-pass filtered version of  $x$ , where we used a memory coefficient  $\alpha_2 = 0.9$ . Without noise, one could relinquish filtering (i.e.  $\alpha_2 = 0$ ), and directly use  $x$ . However, in the presence of noise, inhibition would then randomly switch-off. These drop outs would cause corresponding “spikes” for the linear approach (Figure S4). Note that, unlike the  $\eta$ -function, we did not use an exponential function in equation (S4). A “moderate” power law with  $e = 2.5$  is sufficient to get the job done (see also reference [4]). In figures S3 and S4 noise was added to optical variables, according to equation (9). This means that optical variables  $\Theta$  and  $\dot{\Theta}$  were replaced by  $\tilde{\Theta}$  and  $\dot{\tilde{\Theta}}$ , respectively, in all equations within this section.

## References

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