

Comparison Principles and Asymptotic Behavior of Delayed Age-Structured Neuron Models

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Abstract

In the context of neuroscience the elapsed-time model is an age-structured equation that describes the behavior of interconnected spiking neurons through the time since the last discharge, with many interesting dynamics depending on the type of interactions between neurons. We investigate the asymptotic behavior of this equation in the case of both discrete and distributed delays that account for the time needed to transmit a nerve impulse from one neuron to the rest of the ensemble. To prove the convergence to the equilibrium, we follow an approach based on comparison principles for Volterra equations involving the total activity, which provides a simpler and more straightforward alternative technique than those in the existing literature on the elapsed-time model.

Keywords Age-structured models \cdot Delay equations \cdot Comparison principles \cdot Volterra equations

Mathematics Subject Classification 35F15 · 35F20 · 92-10

1 Introduction

Several mean-field models have been proposed to describe the electrical activity of a large group of interconnected neurons. They usually take the form of a partial differential equation with a time variable and additional variables, often called structure variables, which describe one or more additional quantities of the system. For example, models structured by the membrane potential of neurons such as the integrate-and-fire systems are well-known with a vast literature [1–8].

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This article is devoted to the study of an age-structured model for an interconnected ensemble of neurons described by the elapsed time since last discharge at the membrane potential, which is known as the elapsed-time equation (ET). In this model neurons are subjected to random discharges so that when they reach the firing potential, they stimulate (or inhibit) other neurons to spike. Depending on the type of interaction, different possible behaviors of the brain activity are possible.

This equation was initially proposed in [9] and then subsequently developed by many authors with different extensions by incorporating new elements such as the fragmentation equation [10], spatial dependence with connectivity kernel in [11], a multiple-renewal equation in [12] and a leaky memory variable in [13]. Moreover, like the case of membrane potential models such as the Fokker-Planck equation, this model can be obtained as a mean-field limit of a microscopic model and it establishes a bridge of the dynamics of a single neuron with a population-based approach, whose aspects have been investigated in [14–19]. Readers seeking further information may consult [20] for a comprehensive review of non-linear partial differential equations in neuroscience.

We begin by introducing the model and summarizing its background, followed by a description of the results addressed in this article.

In all models in this paper, n = n(t, a) represents the density at time $t \ge 0$ of neurons which fired $a \ge 0$ units of time ago. The time elapsed since the last spike is commonly referred to as the *neuron's age*. We always write the models in dimensionless form to simplify the mathematical treatment, but units can be easily added by standard procedures. In this work we focus on the *elapsed-time model with distributed delay*, which correspond to the nonlinear system given by

$$\partial_t n + \partial_a n + S(a, X(t))n = 0, t, a > 0, (1a)$$

$$n(t, a = 0) = r(t) := \int_0^\infty S(a, X(t)) n(t, a) da,$$
 $t > 0,$ (1b)

$$X(t) = \int_{-\infty}^{t} \alpha(t - s)r(s) \, \mathrm{d}s, \qquad t > 0.$$
 (1c)

The quantity r = r(t) represents the total number (or density) of neurons which fire at time t, which means that the membrane potential reaches a threshold value and then resets to a baseline value. This term r(t) determines the *total activity* of the neuron network, represented by the quantity X = X(t) through a convolution with a certain nonnegative function $\alpha \in L^1(\mathbb{R}^+)$ with $\int_0^\infty \alpha(s) \, ds = 1$, which is known as the kernel of distributed delay. This convolution takes into account the delay in transmission after a neuron spikes and the value $\alpha(s)$ represents the influence in the total activity at time t of a neuron which fired at time t - s. In this context, it is understood that the history of the rate r(t) for t < 0 is fixed as an initial condition (as we explain later in (1e))

The nonnegative function S(a, X) is called the *firing coefficient* and it represents the susceptibility of neurons to discharge. This function accounts for the effect that a total activity X has on neurons of age a. As we see in the boundary condition (1b) of n at a = 0, when a neuron discharges at time t its age is reset 0, so that the firing rate r(t) is determined by an integral involving the firing coefficient S and the total activity X(t), which depends on the previous states of the system for the firing rate and the delay kernel α .

A typical choice for the firing coefficient is $S(a, X) = \varphi(X) \mathbb{1}_{a > \sigma}$, which represents a network of neurons with an absolute refractory time $\sigma \ge 0$ during which they cannot fire again after a given discharge. Furthermore, the function S may be increasing or decreasing



in X, to allow for excitatory of inhibitory interactions respectively and it determines the type of regime of the system. In the case that S does not depend on X the model becomes linear, and its study is considerably simpler. We notice that r(t) can be calculated by knowing n(s, a) for times s < t, so equation (1c) is a type of delayed boundary condition.

The above equation should be complemented by a suitable initial condition,

$$n(t = 0, a) = n^{0}(a), \qquad a > 0,$$
 (1d)

$$r(t) = r^0(t), t < 0,$$
 (1e)

where $n^0 \in L^1(\mathbb{R}^+)$ is a given nonnegative function, and r^0 is defined on $(-\infty,0)$. Since (1a)–(1e) is a delay equation, it would be natural to specify n(t,a) for $t \in (-\infty,0]$ as an initial condition, but only the firing rate r(t) = n(t,0) is actually used, so we emphasize that it is enough to set r(t) for negative times t. Thus we allow for "infinite delay" in the equation. The statement of the model in [9] is equivalent to assuming r(t) = 0 for all t < 0. If for a certain t > 0 one assumes that t = 0 for all t > 0, then it is clearly enough to give t = 0 for t = 0 as initial data (since the values of t = 0 for t < -d do not play any role).

Moreover, we formally have the following mass-conservation property

$$\int_0^\infty n(t,a) \, da = \int_0^\infty n^0(a) \, da, \qquad \forall t \ge 0, \tag{2}$$

and without loss of generality, we will normalize it to 1 so that $n(t, \cdot)$ can be interpreted as the probability distribution at time t of the time since the last spike.

There are two important situations which are limiting cases of this one. First, if we take the limit as $\alpha \to \delta_d$ (a Dirac delta function at t = d) for some d > 0 we formally obtain the model with *single discrete delay*:

$$\partial_t n + \partial_a n + S(a, r(t-d))n = 0, t, a > 0, (3a)$$

$$n(t, a = 0) = r(t) := \int_0^\infty S(a, r(t - d)) n(t, a) da.$$
 $t > 0.$ (3b)

This system is known as the case with discrete delay, where the total activity is just the firing rate at time t - d. Now the natural initial condition involves setting

$$n(t = 0, a) = n^{0}(a), a > 0,$$
 (3c)

$$r(t) = r^{0}(t), -d \le t < 0.$$
 (3d)

In turn, if we consider the limit d = 0 then this system becomes

$$\partial_t n + \partial_a n + S(a, r(t))n = 0, t, a > 0, (4a)$$

$$n(t, a = 0) = r(t) = \int_0^\infty S(a, r(t))n(t, a) da.$$
 t > 0. (4b)

This system is known as the case with instantaneous transmission. Now the definition of r(t) is an independent equation, which has to be solved together with the whole system and the only initial condition to set is n(0, a) for a > 0. If n(t, a) is known for a certain t, then finding an r(t) which satisfies $r(t) = \int_0^\infty S(a, r(t))n(t, a) \, da$ may be an ill-posed problem;



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see [9] or [21] for a simple example, and more recently [22] for an analysis of the conditions which may stop this system from being well-posed.

Concerning the steady states, the equilibria of (1a)–(1e) are given by the equation:

$$\begin{cases} \partial_{a}n^{*} + S(a, X^{*})n^{*} = 0 & a > 0, \\ r^{*} := n^{*}(a = 0) = \int_{0}^{\infty} S(a, X^{*})n^{*}(a) \, \mathrm{d}a, \\ X^{*} = r^{*} \int_{0}^{\infty} \alpha(s) \, \mathrm{d}s. \end{cases}$$
 (5)

Thanks to the normalization $\int_0^\infty \alpha(s) \, ds = 1$ we have $X^* = r^*$. From the first equation of the system we get that $n^*(a) := r^* e^{-\int_0^a S(a', X^*) \, da'}$ and the following equation holds for r^* :

$$r^*I(r^*) = 1$$
, with $I(r) := \int_0^\infty e^{-\int_0^a S(s,r) \, ds} \, da$, (6)

as a consequence of the mass-conservation property.

For simplicity we call the steady state as the pair (n^*, r^*) , since $X^* = r^*$. Moreover, for the case of instantaneous transmission (4a)–(4b) and the case with discrete delay (1a)–(1e) the definition of an equilibrium is analogous and in all cases we have the same steady states for a given firing coefficient S. We also remark that when the system is inhibitory it has a unique steady state, while in the excitatory case multiple steady states may arise [9].

Finally, if we fix $X = \bar{r} \ge 0$ as parameter in the coefficient S we obtain the following linear equation, which is fundamental to understand the non-linear problems (1a)–(1e) and (3a)–(3d).

$$\begin{cases} \partial_t n + \partial_a n + S(a, \bar{r})n = 0 & t, a > 0, \\ n(t, a = 0) = r(t) := \int_0^\infty S(a, \bar{r})n(t, a) \, da & t > 0, \\ n(t = 0, a) = n^0(a) & a > 0. \end{cases}$$
 (7)

Observe that this linear equation does not have any explicit delay and in this case it can be cast in the form of an abstract ODE in the space $\mathcal{M}(\mathbb{R}^+)$ of finite signed Borel measures, given by

$$\partial_t n = L_{\bar{r}}[n] := -\partial_a n - S(a, \bar{r})n + \delta_0 \int_0^\infty S(a, \bar{r})n(a) \, \mathrm{d}a. \tag{8}$$

For the sake of simplicity of the notation in the computations, we treat the elements in $\mathcal{M}(\mathbb{R}^+)$ as if they were integrable functions with corresponding generalization. The solution of this linear problem determines a positive and mass-preserving semigroup in $\mathcal{M}(\mathbb{R}^+)$, which will be denoted as $e^{tL_{\bar{r}}}$ in the sequel. In other words, $e^{tL_{\bar{r}}}$ is a Markov semigroup. The asymptotic behavior of $e^{tL_{\bar{r}}}$ is well-known, as we state in the following result.

Proposition 1 (Linear spectral gap) Assume that S satisfies Hypothesis 1, and let $\bar{r} \geq 0$ be given. Then the pair $\left(\bar{n}^* := \bar{r}^* e^{-\int_0^a S(s,\bar{r}) \ ds}, \bar{r}^* := \left(\int_0^\infty e^{-\int_0^a S(s,\bar{r}) \ ds} \ da\right)^{-1}\right)$ is the unique positive stationary solution to Equation (7) such that $n^* \in L^1(0,\infty)$ with $\int_0^\infty n^* \ da = 1$. And there exist constants C_0 , $\lambda > 0$ such that for all initial data $n^0 \in \mathcal{M}(\mathbb{R}^+)$ it holds that,



for all t > 0,

$$\|e^{tL_{\bar{r}}}n^{0} - \langle n^{0}\rangle \bar{n}^{*}\|_{TV} \le C_{0}e^{-\lambda t}\|n^{0} - \langle n^{0}\rangle \bar{n}^{*}\|_{TV}$$

$$|r(t) - \langle n^{0}\rangle \bar{r}^{*}| < C_{0}e^{-\lambda t}\|n^{0} - \langle n^{0}\rangle \bar{n}^{*}\|_{TV}$$
(9)

with $\langle n^0 \rangle := \int_0^\infty n^0 \, \mathrm{d}a$.

We remark that the constant λ gives the natural speed of convergence to equilibrium of (7). This result can be proved through different techniques such as the entropy method [23], Doeblin's theory [21] and Kato's inequality [24].

Concerning the nonlinear case, global well-posedness of weak solutions has been studied in the case with instantaneous transmission and also distributed delay [9, 17, 21, 24] and more recently in [22] with a numerical scheme inspired in fixed-point problems.

Regarding long-time behavior, global results are comparatively rare: no general results on convergence to equilibrium are available, and no useful entropy or Lyapunov functional is known for the nonlinear model. Some partial results in this direction include [25], where the existence of periodic solutions with jump discontinuities was established in the case of strong non-linearities.

However, a quite complete analysis can be carried out in perturbative situations, when the system is close to a linear system. In this regard, the following properties are expected to hold:

- 1. There exists a unique probability equilibrium n^* , with its associated firing rate r^* .
- All solutions with an initial probability distribution converge to this equilibrium as t → +∞ at an exponential rate.

It is reasonable to study these properties when the nonlinearity is weak, meaning that the following holds for a small enough ℓ :

$$|S(a,r) - S(a,r')| \le \ell |r - r'|$$
 for all $a, r, r' > 0$. (10)

In previous papers a very similar condition to this is always used. In the literature on neuron dynamics this condition corresponds to either "weak connectivity" or "strong connectivity" regimes. To understand the meaning of weak and strong regimes it is important to notice that the firing coefficient is usually written as $\widetilde{S}(a,JX)$ in other references, where $J\geq 0$ is the network connectivity parameter. We have avoided this notation to simplify the presentation of the model, so we do not have a parameter J; we just take $S(a,X)\equiv\widetilde{S}(a,JX)$. When using this notation, "weak connectivity" corresponds to small J, and "strong connectivity" corresponds to large J. With appropriate (additional) assumptions on \widetilde{S} , one may show (10) (or a very similar condition to (10)) either when J is small enough, or when J is large enough.

Results on properties 1 and 2 were first given in [9, 10, 26] by using variations of the generalized relative entropy method [23, 27] in the case of instantaneous transmission (4a)–(4b), while a semigroup approach based on Doeblin's theory [28, 29] was given in [21], applicable to both equation (4a)–(4b) and modified models with fatigue proposed in [10]. The same ideas were also used to study a model structured by additional past discharge times in [12] and with a memory term in [13].

Besides the case with instantaneous transmission, exponential convergence with distributed delay has been previously studied by Mischler et al. [24, 30] for weak nonlinearities under regularity assumption such as when the firing coefficient $S \in \text{Lip}_X \ L_a^1$. This result was



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proved through a spectral analysis based on the analysis in [31] for the growth-fragmentation equation.

The goal of our article is to fill some gaps on the convergence to the equilibrium for the elapsed-time model for both distributed and discrete delays under the regime of weak nonlinearities with an alternative method to the spectral analysis previously cited and under simple assumptions for S. Apart from introducing a relatively simple method, we are also able to include some new cases such as the case of algebraic decay of α . In addition, the case with discrete delay, despite being formally a particular case of the distributed delay, should be analyzed separately, since it is a singular case and no explicit proof was given before for this case.

Our approach relies on a comparison principle for integral equations involving the distance to equilibrium of the total activity $|X(t) - X^*|$ in the case of Equation (1a)–(1e) and $|r(t) - r^*|$ in the case of Equation (3a)–(3d). The strategy consists in finding a suitable upper solution of a Volterra-type equation that vanishes when $t \to \infty$ and that allows to bound the quantities $|X(t) - X^*|$ and $|r(t) - r^*|$. Comparisons techniques for other age-structured models have been recently studied in [32] with logistic growth and spatial diffusion.

The advantage of this argument is that we obtain a simpler proof of convergence to equilibrium, whose rate also depends explicitly on the bounds of the kernel α and the delay d in their respective cases. Moreover, we also point out that suitable modifications of the argument based on a perturbation of the linear case stated in Proposition 1 can also deal with the delayed equations (1a)–(1e) and (3a)–(3d), and get the desired property 2 above.

1.1 Main Results of This Article

We now present the results of this paper, highlighting the crucial role played by the size λ of the *spectral gap* of the linear equation (7), with $\bar{r} = r^*$, given in Proposition 1. We will always assume the following:

Hypothesis 1 (Conditions on S) We assume $S: (0, +\infty) \times [0, +\infty) \to [0, +\infty)$ is a bounded measurable function, and Lipschitz with respect to its second variable with Lipschitz constant l:

$$|S(a,r) - S(a,r')| < \ell |r - r'|$$
 for all $a, r, r' > 0$.

We also assume that there exist constants s_0 , $\sigma > 0$ such that

$$S(a,r) > s_0 \mathbb{1}_{\{a > \sigma\}}$$
 for all $a, r > 0$. (11)

Hypothesis 2 (Initial conditions) We assume that n^0 is a nonnegative probability measure on $(0, +\infty)$. For the distributed delay equation (1a)–(1e) we assume that $r^0: (-\infty, 0] \rightarrow [0, +\infty)$ is a bounded function; for the single discrete delay equation (3a)–(3d) we assume that d > 0 and $r^0: [-d, 0] \rightarrow [0, +\infty)$ is a bounded function.

It is also known, in general, [9, 21, 26] that in either weak or strong connectivity regime the nonlinear problems (1a)–(1e) and (3a)–(3d) have a unique probability equilibrium: there exists $\ell_* > 0$ such that if S satisfies Hypothesis 1 with $0 \le \ell \le \ell_*$ then equations (1a)–(1e) and (3a)–(3d) have a unique equilibrium (n^*, r^*) such that n^* is a probability measure. Since our results below are stated for small ℓ one may always assume that $\ell \le \ell_*$, so the fact that there is a unique equilibrium in that case is known. The results presented in this article are



still valid when S satisfies similar Lipschitz estimates involving the integral with respect to a, as it was done for example in [24, 30]. Furthermore, see Remarks 2 and 4 for more details on how to apply our main results in the context of weak and strong regimes.

The following are the main results of this article. Regarding the single discrete delay model we have:

Theorem 1 (Single discrete delay) Assume Hypothesis 1, with ℓ small enough such that there exists a unique steady state (n^*, r^*) of equation (3a)–(3d), and let $\lambda > 0$ be the spectral gap of the linear equation (7), with $\bar{r} = r^*$. Then there exists $\ell_0 > 0$ (depending only on λ) such that for all d > 0 there exist constants $0 < \mu < \lambda$ (depending only on d and d), d0 so that when d1 dependence on initial condition d2 satisfying Hypothesis 2, the solution d3 of equation (3a)–(3d) satisfies

$$||n(t) - n^*||_{TV} \le C K_0 e^{-\mu t},$$

$$|r(t) - r^*| < C K_0 e^{-\mu t}$$
(12)

for all t > 0, where K_0 measures the initial distance to equilibrium in the following sense:

$$K_0 := ||r^0 - r^*||_{\infty} + ||n^0 - n^*||_{TV}.$$

We notice that in this case $||r^0 - r^*||_{\infty}$ denotes the L^{∞} norm in the interval [-d, 0].

The previous theorem informally states that in the weak-connectivity regime, the non-linear model (3a)–(3d) converges to equilibrium at essentially the same rate as the linear system. We can also obtain similar results for the distributed delay model (1a)–(1e), with the important difference that solutions will now converge to equilibrium at (roughly) the slowest of the following rates:

- 1. The rate $e^{-\lambda t}$ of decay to equilibrium of the linear model.
- 2. The decay rate to 0 of the function α .

The following two results make this idea precise:

Theorem 2 (Exponentially distributed delay) Assume Hypothesis 1, with ℓ small enough such that there exists a unique steady state (n^*, r^*) of equation (1a)–(1e), and let $\lambda > 0$ be the spectral gap of the linear equation (7), with $\bar{r} = r^*$. Assume that there exist constants C_{α} , $\beta > 0$ such that

$$\alpha(t) \le C_{\alpha} e^{-\beta t}$$
 for all $t > 0$.

Then, for any $0 < \mu < \min\{\lambda, \beta\}$ there exists $\ell_0 > 0$ depending only on $\|S\|_{\infty}$ and μ such that if $\ell \le \ell_0$, there exists a constant C > 0 (depending only on S, C_{α} and β) such that for any initial condition (n^0, r^0) satisfying Hypothesis 2 the solution (n, r) of equation (1a)–(1e) satisfies

$$||n(t) - n^*||_{TV} \le CK_0e^{-\mu t},$$
 (13)

$$|r(t) - r^*| \le C K_0 e^{-\mu t},$$
 (14)

$$|X(t) - X^*| \le C K_0 e^{-\mu t} \tag{15}$$

for all t > 0, where K_0 measures the initial distance to equilibrium in the following sense:

$$K_0 := \|r^0 - r^*\|_{\infty} + \|n^0 - n^*\|_{TV}.$$



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In this case $||r^0 - r^*||_{\infty}$ denotes the L^{∞} norm on $(-\infty, 0)$. We also point out that $X^* := r^* \int_0^{\infty} \alpha(s) \, ds$ is the total activity at equilibrium.

Regarding algebraic tails we have a similar result, this time with an algebraic speed of convergence:

Theorem 3 (Distributed delay, algebraic tail) Assume Hypothesis 1, with ℓ small enough such that there exists a unique steady state (n^*, r^*) of equation (1a)–(1e), and let $\lambda > 0$ be the spectral gap of the linear equation (7), with $\bar{r} = r^*$. Assume that there exist constants $C_{\alpha} > 0$, $\beta > 1$ such that

$$\alpha(t) \le \frac{C_{\alpha}}{1 + t^{\beta}}.$$

Then there exists $\ell_0 > 0$ depending only on S such that if $\ell \leq \ell_0$, there exists a constant C > 0 (depending only on S, C_α and β) such that for any initial condition (n^0, r^0) satisfying Hypothesis 2 the solution (n, r) of equation (1a)–(1e) satisfies

$$||n(t) - n^*||_{TV} \le \frac{CK_0}{1 + t^{\beta - 1}},$$
 (16)

$$|r(t) - r^*| \le \frac{CK_0}{1 + t^{\beta - 1}},$$
 (17)

$$|X(t) - X^*| \le \frac{CK_0}{1 + t^{\beta - 1}} \tag{18}$$

for all t > 0, where K_0 measures the initial distance to equilibrium in the following sense:

$$K_0 := \|r^0 - r^*\|_{\infty} + \|n^0 - n^*\|_{TV}.$$

This result allows to extend the convergence result in [24, 30] where the kernel α must have a Laplace transform $\widehat{\alpha}(z)$ defined for $\Re(z) > -c$ for some c > 0, i.e. α decays exponentially. Thus, even if α decays like an inverse of a polynomial, it is still possible to have convergence to the equilibrium with explicit rates that depend on the bounds of α .

The proof of the above results is based on a perturbation argument, writing the nonlinear equations as the linear one plus a perturbation term which can be shown to be small, and then using Duhamel's formula to compare with the solution of the linear equation. There are two important ideas to consider in order to carry out this plan: first, it is natural to consider the spectral gap in total variation norm, as the perturbation term is small in this norm (but is not even finite in stronger norms such as L^p); this was used in [21] in order to study the case without delay. Second, the inequalities obtained after using Duhamel's formula are modified versions of Volterra integral equations for which there is no general theory readily available. We give comparison theorems for them, from which one can then obtain the main results.

The rest of the paper is devoted to proving the convergence theorems and offering remarks and perspectives that emerge from them. It is organized as follows: Sect. 2 contains the proof of Theorem 1, while Sect. 3 contains the proofs of Theorems 2 and 3.



2 Model with a Single Discrete Delay: Proof of Theorem 1

This section is devoted to the elapsed time equation with a single discrete delay given in (3a)–(3d):

$$\partial_t n + \partial_a n + S(a, r(t-d))n = 0, \qquad t, a > 0, \tag{19a}$$

$$n(t, a = 0) = r(t) := \int_0^\infty S(a, r(t - d)) n(t, a) \, da, \qquad t > 0.$$
 (19b)

We remind that the steady states (n^*, r^*) in this case are given by:

$$\begin{cases} \partial_a n^* + S(a, r^*) n^* = 0 & a > 0, \\ r^* := n^* (a = 0) = \int_0^\infty S(a, r^*) n^* (a) \, da, \end{cases}$$

where $n^*(a) = r^* e^{-\int_0^a S(a', r^*) da'}$ and $r^* > 0$ satisfies Equation (6).

The aim of this section is to prove Theorem 1. To achieve this, we make use of the following comparison lemma.

Lemma 1 (Comparison lemma with discrete delay) *Consider the constants* d > 0, $c_1 \ge 0$, $c_2 \ge 0$ and the functions $f \in L^{\infty}(0, \infty)$, $u^0 \in L^{\infty}(-d, 0)$. Let $\underline{u} \in L^{\infty}(-d, \infty)$ such that

$$\begin{cases}
\underline{u}(t) \le c_1 \underline{u}(t-d) + c_2 \int_0^t e^{-\lambda(t-s)} \underline{u}(s-d) \, \mathrm{d}s + f(t) & \forall t > 0, \\
\underline{u}(t) \le u^0(t) & \forall t \in (-d,0),
\end{cases} \tag{20}$$

and $\overline{u} \in L^{\infty}(-d, \infty)$ such that

$$\begin{cases}
\overline{u}(t) \ge c_1 \overline{u}(t-d) + c_2 \int_0^t e^{-\lambda(t-s)} \overline{u}(s-d) \, \mathrm{d}s + f(t) & \forall t > 0, \\
\overline{u}(t) \ge u^0(t) & \forall t \in (-d,0),
\end{cases} \tag{21}$$

Then $\underline{u}(t) \leq \overline{u}(t)$ for all t > -d.

In other words \underline{u} and \overline{u} are respectively lower and upper solutions of the delayed Volterra-type equation given by

$$\begin{cases} u(t) = c_1 u(t-d) + c_2 \int_0^t e^{-\lambda(t-s)} u(s-d) \, \mathrm{d}s + f(t) & \forall t > 0, \\ u(t) = u^0(t) & \forall t \in (-d,0), \end{cases}$$
 (22)

and the comparison principle holds.

Proof Observe that $h(t) := \overline{u}(t) - \underline{u}(t)$ satisfies the following inequalities

$$\begin{cases} h(t) \ge c_1 h(t-d) + c_2 \int_0^t e^{-\lambda(t-s)} h(s-d) ds & \forall t > 0, \\ h(t) \ge 0 & \forall t \in (-d, 0). \end{cases}$$

From the first inequality we conclude that $h(t) \ge 0$ for all $t \in (0, d)$ and by iterating over the intervals (kd, (k+1)d) with $k \in \mathbb{N}$, we conclude that $h(t) \ge 0$ for all t > -d.

Now we can proceed with the proof of Theorem 1.



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Proof of Theorem 1 We write the solution of Equation (19a)–(19b) as

$$\partial_t n = L_{r^*}[n] + h$$

where the linear operator L_{r^*} was defined in (8), with $\bar{r} = r^*$, and h is given by

$$\begin{split} h(t,a) &= (S(a,r^*) - S(a,r(t-d)))n(t,a) \\ &+ \delta_0(a) \int_0^\infty (S(a',r(t-d)) - S(a',r^*))n(t,a') \, \mathrm{d}a', \end{split}$$

and by applying Duhamel's formula and Proposition 1, there exists C_0 , $\lambda > 0$ such that the following inequality holds:

$$||n(t) - n^*||_{TV} \le C_0 e^{-\lambda t} ||n^0 - n^*||_{TV} + C_0 \int_0^t e^{-\lambda(t-s)} ||h(s)||_{TV} \, \mathrm{d}s. \tag{23}$$

By using the mass-conservation property (2) of the system, for h we obtain

$$||h(t,\cdot)||_{TV} < 2\ell|r(t-d) - r^*| \quad \forall t > 0,$$
 (24)

where ℓ is the Lipschitz constant of S with respect to r (see Hypothesis 1). Also, from the definition of r(t) (see (19b)) we obtain

$$\begin{split} |r(t) - r^*| &= \left| \int_0^\infty S(a, r(t - d)) n(t, a) \, \mathrm{d}a - \int_0^\infty S(a, r^*) n^*(a) \, \mathrm{d}a \right| \\ &\leq \int_0^\infty |S(a, r(t - d)) - S(a, r^*)| n(t, a) \, \mathrm{d}a + \int_0^\infty S(a, r^*) |n(t, a) - n^*(a)| \, \mathrm{d}a \\ &\leq \ell |r(t - d) - r^*| + \|S\|_\infty \|n(t, a) - n^*(a)\|_{TV}. \end{split}$$

Now using (23) and (24) in the previous equation we get

$$|r(t) - r^*| \le \ell |r(t - d) - r^*| + C_0 ||S||_{\infty} ||n^0 - n^*||_{TV} e^{-\lambda t}$$

$$+ 2C_0 ||S||_{\infty} \ell \int_0^t e^{-\lambda(t - s)} |r(s - d) - r^*| \, \mathrm{d}s.$$

$$(25)$$

We define the constants $C_1 := 2C_0 ||S||_{\infty}$ and $C_2 := C_0 ||S||_{\infty} ||n^0 - n^*||_{TV}$ so that for $u(t) := |r(t) - r^*|$ we get the inequality

$$u(t) \le \ell u(t-d) + C_1 \ell \int_0^t e^{-\lambda(t-s)} u(s-d) \, \mathrm{d}s + C_2 e^{-\lambda t} \quad \forall t \ge 0.$$

The main idea is to apply now the comparison lemma. We look for a constant A, $\mu > 0$ such that we get $u(t) \le Ae^{-\mu t}$ for all t > -d. This means that the function $v(t) := Ae^{-\mu t}$ must satisfy the following inequalities

$$\begin{cases} v(t) \ge \ell v(t-d) + C_1 \ell \int_0^t e^{-\lambda(t-s)} v(s-d) \, \mathrm{d}s + C_2 e^{-\lambda t} & \forall t > 0 \\ v(t) \ge |r^0 - r^*| & \forall t \in (-d, 0), \end{cases}$$



or equivalently in terms of A and μ

$$A\left(1 - \ell e^{\mu d} - C_1 \ell e^{\mu d} \frac{1 - e^{-(\lambda - \mu)t}}{\lambda - \mu}\right) \ge C_2 e^{-(\lambda - \mu)t} \ \forall t > 0$$

$$A \ge e^{\mu t} |r^0(t) - r^*| \qquad \forall t \in (-d, 0).$$
(26)

Observe that (using $e^{-(\lambda-\mu)t} \ge 0$ on the left and $e^{-(\lambda-\mu)t} \le 1$ on the right) a sufficient condition to verify (26) is given by the inequalities

$$A\left(1 - \ell\left(e^{\mu d} + C_1 e^{\mu d} \frac{1}{\lambda - \mu}\right)\right) \ge C_2$$
$$A \ge \sup_{t \in [-d,0]} |r^0(t) - r^*|.$$

Therefore, for $\ell > 0$ satisfying

$$\ell\left(e^{\mu d} + C_1 e^{\mu d} \frac{1}{\lambda - \mu}\right) < 1,$$
 or equivalently $\ell < \frac{e^{-\mu d}(\lambda - \mu)}{\lambda - \mu + C_1},$

and A verifying

$$A > \max \left\{ ||r^0 - r^*||_{\infty}, \ \frac{C_2(\lambda - \mu)}{\lambda - \mu - \ell_0 e^{\mu d} (\lambda - \mu + C_1)} \right\} \qquad \text{with } \mu < \lambda, \text{ and } \ell \le \ell_0,$$

we get that (26) holds and hence v(t) satisfies the desired inequalities. By Lemma 1 we conclude that

$$u(t) = |r(t) - r^*| < Ae^{-\mu t}.$$
(27)

Without loss of generality we can assume $\|n^0 - n^*\|_{TV} + \|r^0 - r^*\|_{\infty} > 0$, so we can choose A of the form $A = \widetilde{C}(S, d, \mu) \left(\|n^0 - n^*\|_{TV} + \|r^0 - r^*\|_{\infty} \right)$ (since C_2 is the only constant we defined which depends on the initial distance $\|n^0 - n^*\|_{TV}$).

We now assert that we can find a bound on ℓ , ℓ_0 , independent of d such that (27) holds for some choice of $\mu > 0$. Indeed, when $d \le 1$ we can choose $\mu = \frac{\lambda}{2}$ and set $\ell_0 := \frac{\lambda \ell^{-\lambda}}{\lambda + 2C_1}$ such that for

$$\ell \le \ell_0 < \frac{\lambda e^{-\frac{\lambda}{2}}}{\lambda + 2C_1}$$

the estimate (27) is verified. Similarly for d > 1, if we take $\mu = \frac{\lambda}{d+1}$ such that for

$$\ell \le \ell_0 < \frac{d\lambda e^{-\frac{d}{d+1}\lambda}}{d\lambda + (d+1)C_1},$$

the same conclusion holds. Finally, from estimates (23) and (24) the exponential convergence of $||n(t) - n^*||_{TV}$ in (12) readily follows.

In light of the proof, we draw attention to the following remarks.

Remark 1 We have proved the existence of a sufficiently small connectivity parameter ℓ_0 such that for any transmission delay d, we have exponential convergence of the system



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towards its unique steady state. Nevertheless, the rate of convergence is influenced by d and, as expected, it decreases as d increases.

An interesting extension would be to jointly study the dependence on the delay d and the spectral gap given λ in Proposition 1. For a given delay d, one would expect that a larger value of λ will allow a larger value of the Lipschitz constant ℓ_0 where the exponential convergence holds. The choice of $\ell_0 = \frac{\lambda e^{-\lambda}}{\lambda + 2C_1}$ obtained in the proof of the theorem is decreasing in terms of $\lambda \gg 1$, suggesting that this bound might be improved.

Remark 2 (Relaxed hypotheses) Our proofs can be adapted to work when the following relaxed condition on S holds, instead of Hypothesis 1:

Hypothesis 3 (Conditions on S) We assume $S: (0, +\infty) \times [0, +\infty) \to [0, +\infty)$ is a bounded measurable function, and let (n^*, r^*) be an equilibrium of the linear equation (7). We assume that S is Lipschitz with respect to r with constant ℓ when $|r - r^*|$ is small enough, that is: there exists $\delta > 0$ such that

$$|S(a,r)-S(a,r')| \le \ell |r-r'|$$
 for all $a > 0$ and all $r, r' \in [r^* - \delta, r^* + \delta]$.

This assumption requires a Lipschitz constant only close to the equilibrium r^* . With this condition, following the proof of Theorem 1, we may obtain convergence to the equilibrium provided that the initial condition is close enough to the equilibrium itself. In this case one does not need to impose that the equilibrium is unique.

3 Model with Distributed Delay: Proof of Theorems 2 and 3

In this section we will consider the elapsed time model with distributed delay given in (1a)–(1e)

$$\partial_t n + \partial_a n + S(a, X(t))n = 0, \qquad t, a > 0, \tag{28a}$$

$$n(t, a = 0) = r(t) := \int_0^\infty S(a, X(t)) n(t, a) da,$$
 $t > 0,$ (28b)

$$X(t) = \int_{-\infty}^{t} \alpha(t - s)r(s) \,\mathrm{d}s. \tag{28c}$$

Remind that in this case the equilibrium distribution (n^*, r^*) solves the system

$$\begin{cases} \partial_a n^* + S(a, X^*) n^* = 0 & a > 0, \\ r^* := n^* (a = 0) = \int_0^\infty S(a, X^*) n^* (a) \, da, \\ X^* = r^* \int_0^\infty \alpha(s) \, ds. \end{cases}$$

where $n^*(a) = r^* e^{-\int_0^a S(a', r^*) da'}$ and $r^* > 0$ satisfies Equation (6).

For the proof of Theorems 2 and 3 we first need the following comparison lemma. For $f, g \in L^{\infty}(0, \infty)$ we use the notation $f * g := \int_0^t f(t-s)g(s) \, ds$.

Lemma 2 Consider the functions $f, k \in L^{\infty}(0, \infty)$ with k nonnegative. Let $\underline{u} \in L^{\infty}(0, \infty)$ such that

$$\underline{u}(t) \le (k * \underline{u})(t) + f(t) \qquad \forall t > 0.$$
(29)



and $\overline{u} \in L^{\infty}(0, \infty)$ such that

$$\overline{u}(t) \ge (k * \overline{u})(t) + f(t) \qquad \forall t > 0.$$
 (30)

Then it holds that $\underline{u}(t) \leq \overline{u}(t)$ for all $t \geq 0$.

In other words \underline{u} and \overline{u} are respectively lower and upper solutions of the Volterra equation given by

$$u(t) = (k * u)(t) + f(t) \quad \forall t > 0,$$
 (31)

and the comparison principle holds.

Proof Observe that $h(t) := \overline{u}(t) - \underline{u}(t)$ satisfies

$$h(t) \ge (k * h)(t)$$
.

For T > 0 we consider $A_1[T] := \inf_{t \in [0,T]} h(t)$ and we have

$$\left(1 - \int_0^T k(s) \, \mathrm{d}s\right) A_1[T] \ge 0.$$

Therefore when we choose T such that

$$T\|k\|_{\infty} < 1,\tag{32}$$

we conclude that $A_1[T] \ge 0$, which means that $\overline{u}(t) \ge \underline{u}(t)$ for all $t \in [0, T]$. Similarly for $t \in [T, 2T]$ we define $A_2[T] := \inf_{t \in [T, 2T]}$ and obtain

$$\left(1 - \int_{T}^{2T} k(s) \, \mathrm{d}s\right) A_2[T] \ge 0.$$

Again, using the uniform bound for T in (32) we have that $A_2[T] \ge 0$, which implies that $\overline{u}(t) \ge \underline{u}(t)$ for all $t \in [T, 2T]$. By iterating this argument, we deduce that $\overline{u}(t) \ge \underline{u}(t)$ for all t > 0.

Now we can prove Theorem 2.

Proof of Theorem 2 As in the proof of Theorem 1, by Duhamel's formula and Proposition 1 there exist C_0 , $\lambda > 0$ such that the following inequality holds

$$||n(t) - n^*||_{TV} \le C_0 e^{-\lambda t} ||n^0 - n^*||_{TV} + C_0 \int_0^t e^{-\lambda(t-s)} ||h(s)||_{TV} \, \mathrm{d}s, \tag{33}$$

where h is given by

$$h(t,a) = (S(a,X^*) - S(a,X(t)))n(t,a) + \delta_0(a) \int_0^\infty (S(a,X(t)) - S(a',X^*))n(t,a') da',$$

thus, using Hypothesis 1, we have the estimate

$$||h(t,\cdot)||_{TV} \le 2\ell|X(t) - X^*|$$
 for all $t > 0$. (34)



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Also, we can estimate $|r(t) - r^*|$ as in the proof of Theorem 1:

$$|r(t) - r^*| = \left| \int_0^\infty S(a, X(t)) n(t, a) \, \mathrm{d}a - \int_0^\infty S(a, X^*) n^*(a) \, \mathrm{d}a \right|$$

$$\leq \int_0^\infty |S(a, X(t)) - S(a, X^*)| n(t, a) \, \mathrm{d}a + \int_0^\infty S(a, X^*) |n(t, a) - n^*(a)| \, \mathrm{d}a$$

$$\leq \ell |X(t) - X^*| + ||S||_\infty ||n(t, a) - n^*(a)||_{TV}. \quad (35)$$

Using now (33) and (34) we obtain

$$|r(t) - r^*| \le \ell |X(t) - X^*| + C_0 ||S||_{\infty} ||n^0 - n^*||_{TV} e^{-\lambda t}$$

$$+ 2C_0 ||S||_{\infty} \ell \int_0^t e^{-\lambda(t-s)} |X(s) - X^*| \, \mathrm{d}s. \quad (36)$$

To simplify the notation define the constants $C_1 := 2C_0 ||S||_{\infty}$ and $C_2 := C_0 ||S||_{\infty} ||n^0 - n^*||_{TV}$.

We seek to estimate $|X(t) - X^*|$, so we define $u(t) := |X(t) - X^*|$, and we obtain

$$\begin{aligned} u(t) &= \left| \int_0^\infty \alpha(s) r(t-s) \, \mathrm{d}s - r^* \int_0^\infty \alpha(s) \, \mathrm{d}s \right| \le \int_0^\infty \alpha(s) |r(t-s) - r^*| \, \mathrm{d}s \\ &= \int_0^t \alpha(t-s) |r(s) - r^*| \, \mathrm{d}s + \int_t^\infty \alpha(s) |r^0(t-s) - r^*| \, \mathrm{d}s \\ &\le \int_0^t \alpha(t-s) |r(s) - r^*| \, \mathrm{d}s + \|r^0 - r^*\|_\infty \int_t^\infty \alpha(s) \, \mathrm{d}s. \end{aligned}$$

Using (36) in the previous expression,

$$u(t) \le ||r^0 - r^*||_{\infty} \int_t^{\infty} \alpha(s) \, \mathrm{d}s$$
$$+ \int_0^t \alpha(t - s) \left(\ell u(s) + C_2 e^{-\lambda s} + C_1 \ell \int_0^s e^{-\lambda(s - s')} u(s') \, \mathrm{d}s' \right) \, \mathrm{d}s.$$

We define

$$g(t) := \|r^0 - r^*\|_{\infty} \int_{t}^{\infty} \alpha(s) \, \mathrm{d}s + C_2 \int_{0}^{t} \alpha(t - s) e^{-\lambda s} \, \mathrm{d}s,$$

so we write the inequality for u(t) as

$$u(t) \leq g(t) + \ell(\alpha * u) + C_1 \ell(\alpha * e^{-\lambda t} * u).$$

Like in the case of a single discrete delay, we aim to apply the comparison lemma. We look for constants $A, \mu > 0$ such that $u(t) \le Ae^{-\mu t}$ for all $t \ge 0$. For this, we would like the function $v(t) := Ae^{-\mu t}$ to satisfy

$$v(t) \ge g(t) + \ell(\alpha * v) + C_1 \ell(\alpha * e^{-\lambda t} * v)$$
 for all $t \ge 0$,



or equivalently in terms of A and μ

$$A \ge g(t)e^{\mu t} + \ell A \int_0^t e^{\mu s} \alpha(s) \, \mathrm{d}s + \ell \frac{AC_1}{\lambda - \mu} \int_0^t e^{\mu s} \alpha(s) (1 - e^{-(\lambda - \mu)(t - s)}) \, \mathrm{d}s$$
for $t \ge 0$. (37)

For $\mu < \min\{\beta, \lambda\}$, we estimate each term in the right-hand side. For the first one,

$$g(t)e^{\mu t} \leq C_3 \frac{C_\alpha}{\beta} e^{-(\beta-\mu)t} + C_2 C_\alpha \frac{e^{-(\beta-\mu)t} - e^{-(\lambda-\mu)t}}{\lambda - \beta} \leq C_\alpha \left(\frac{C_3}{\beta} + \frac{C_2}{|\lambda - \beta|}\right),$$

where we call $C_3 := ||r^0 - r^*||_{\infty}$. For the remaining two terms we have

$$\int_0^t e^{\mu s} \alpha(s) \, \mathrm{d}s \le C_\alpha \frac{1 - e^{-(\beta - \mu)t}}{\beta - \mu} \le \frac{C_\alpha}{\beta - \mu},$$

$$\int_0^t e^{\mu s} \alpha(s) (1 - e^{-(\lambda - \mu)(t - s)}) \, \mathrm{d}s \le \int_0^t e^{\mu s} \alpha(s) \, \mathrm{d}s \le \frac{C_\alpha}{\beta - \mu}.$$

Hence in order to satisfy (37) it is enough to satisfy

$$A \ge C_{\alpha} \left(\frac{C_3}{\beta} + \frac{C_2}{|\lambda - \beta|} \right) + \frac{\ell A C_{\alpha}}{\beta - \mu} \left(1 + \frac{C_1}{\lambda - \mu} \right),$$

that is,

$$A\left(1 - \frac{\ell C_{\alpha}}{\beta - \mu} \left(1 + \frac{C_1}{\lambda - \mu}\right)\right) \ge C_{\alpha} \left(\frac{C_3}{\beta} + \frac{C_2}{|\lambda - \beta|}\right).$$

Therefore if the following inequalities hold

$$\ell < \frac{\beta - \mu}{C_{\alpha}} \frac{\lambda - \mu}{\lambda - \mu + C_{1}},$$

$$A > C_{\alpha} \left(\frac{C_{3}}{\beta} + \frac{C_{2}}{|\lambda - \beta|}\right) \left(\frac{(\beta - \mu)(\lambda - \mu)}{(\beta - \mu)(\lambda - \mu) - \ell C_{\alpha}(\lambda - \mu + C_{1})}\right)$$

we get that A and μ satisfy (37) and thus, due to our comparison result in Lemma 2

$$|X(t) - X^*| < Ae^{-\mu t}$$
 for $t > 0$.

Notice that the dependence on $||r^0 - r^*||_{\infty}$ and $||n^0 - n^*||_{\text{TV}}$ are included in C_3 and C_2 , respectively. The exponential decay of $||n(t) - n^*||_{TV}$ readily follows from (33) and (34), and then exponential decay of $|r(t) - r^*|$ follows from (35).

To prove Theorem 3 regarding the case in which α decays algebraically we will need the following lemma on decay of convolutions:

Lemma 3 Let $f, g \in L^{\infty}(\mathbb{R}^+)$ and a > 0, b > 1 such that $f = O(t^{-a})$ and $g = O(t^{-b})$ when $t \to \infty$. Then for their convolution we have

$$h(t) := \int_0^t f(t - s)g(s) \, \mathrm{d}s = O(t^{-\min\{a, b - 1\}}) \qquad \text{as } t \to \infty.$$



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Proof Observe that $g \in L^1(\mathbb{R}^+)$ since b > 1. Thus there exists two constants $C_1, C_2 > 0$ such that for t large enough we have the following estimate

$$|h(t)| \le \int_0^t |f(t-s)g(s)| \, \mathrm{d}s,$$

$$\le \int_0^{\frac{t}{2}} |f(t-s)g(s)| \, \mathrm{d}s + \int_{\frac{t}{2}}^t |f(t-s)g(s)| \, \mathrm{d}s$$

$$\le C_1 \int_0^{\frac{t}{2}} (t-s)^{-a} |g(s)| \, \mathrm{d}s + C_2 \int_{\frac{t}{2}}^t |f(t-s)| s^{-b} \, \mathrm{d}s$$

$$\le 2^a t^{-a} C_1 ||g||_1 + C_2 ||f||_{\infty} \frac{2^{b-1} - 1}{b-1} t^{-(b-1)},$$

where the last inequality proves the desired result.

With this lemma we prove Theorem 3.

Proof of Theorem 3 We can carry out the same initial steps as in the exponential case. With the same notation, the function $u(t) = |X(t) - X^*|$ satisfies

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$$u(t) \leq g(t) + \ell(\alpha * u) + C_1 \ell(\alpha * e^{-\lambda t} * u),$$

with $g(t) = C_3 \int_t^\infty \alpha(s) ds + C_2 \int_0^t \alpha(t-s)e^{-\lambda s} ds$. We recall that the constants C_1 , C_2 and C_3 were defined by

$$C_1 := 2C_0 \|S\|_{\infty}, \qquad C_2 := C_0 \|S\|_{\infty} \|n^0 - n^*\|_{TV}, \qquad C_3 := \|r^0 - r^*\|_{\infty}.$$

Like the previous result, we aim to apply the comparison lemma. We look for constants $A, \mu > 0$ such that the function $v(t) := \frac{A}{1+t^{\mu}}$ satisfies the inequality

$$v(t) > g(t) + \ell(\alpha * v) + C_1 \ell(\alpha * e^{-\lambda t} * v)$$
 for all $t > 0$,

or equivalently in terms of A and μ ,

$$A \ge g(t)(1+t^{\mu}) + \ell A \int_0^t \frac{1+t^{\mu}}{1+(t-s)^{\mu}} \alpha(s) \, \mathrm{d}s + \ell A C_1 \int_0^t \int_0^s \alpha(t-s) e^{-\lambda(s-s')} \frac{1+t^{\mu}}{1+(s')^{\mu}} \, \mathrm{d}s' \, \mathrm{d}s \quad (38)$$

for all $t \ge 0$. We now estimate each term in the right-hand side. First observe that for the first term of g(t) we have that

$$\int_{t}^{\infty} \alpha(s) \, \mathrm{d}s \le \frac{C_{\alpha,\beta}}{1 + t^{\beta - 1}}$$

for some constant $C_{\alpha,\beta} > 0$ depending on C_{α} and β . Thus, by choosing $\mu = \beta - 1$ and applying Lemma 3, there exists a constant $C_4 > 0$ depending on C_{α} and β such that

$$g(t)(1+t^{\mu}) \le C_3C_4\frac{1+t^{\mu}}{1+t^{\beta-1}} + C_2C_4\frac{1+t^{\mu}}{1+t^{\beta-1}} \le C_4(C_2+C_3)$$



and similarly (possibly taking a larger constant C_4) we get

$$\int_0^t \frac{1+t^{\mu}}{1+(t-s)^{\mu}} \alpha(s) \, \mathrm{d}s \le C_4,$$

$$\int_0^t \int_0^s \alpha(t-s) e^{-\lambda(s-s')} \frac{1+t^{\mu}}{1+s'^{\mu}} \, \mathrm{d}s' \, \mathrm{d}s \le C_4.$$

Therefore in order to satisfy (37) it is enough to satisfy

$$A > C_4(C_2 + C_3) + \ell A C_4(1 + C_1),$$

or equivalently

$$A(1 - \ell C_4(1 + C_1)) > C_4(C_2 + C_3).$$

Hence, if the following inequalities hold

$$\ell < \frac{1}{C_4(1+C_1)}, \qquad A > \frac{C_4(C_2+C_3)}{1-\ell C_4(1+C_1)}.$$

we get that A and μ satisfy (38) and thus

$$|X(t) - X^*| \le \frac{A}{1 + t^{\beta - 1}} \quad \text{for all } t \ge 0.$$

Notice again that the dependence on the initial condition is implicit in C_2 and C_3 . The convergence of $|r(t) - r^*|$ and $||n(t) - n^*||_{TV}$ readily follows from estimates (33), (34) and (35) as in the exponential case, by using Lemma 3 to estimate the integral in (33).

We end the paper with the following two remarks.

Remark 3 The convergence results of Theorems 2 and 3 with α bounded by an exponential function or with algebraic tail, respectively, can be extended for a general α as long as we are able to find a suitable upper solution, which might depend on several parameters and an optimization may be performed.

Remark 4 (Relaxed hypotheses) Analogously to Remark 2, our proofs for the model with distributed delay can be carried out under the relaxed Hypothesis 3 on S, instead of Hypothesis 1. In this case we obtain convergence to the equilibrium in both regimes, provided the initial data is close to the equilibrium in terms of r.

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Declarations

Competing Interests The authors declare that they do not have any conflict of interest.



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