Neural Fields with Distributed Transmission Speeds and Long-Range Feedback Delays

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Abstract. We introduce distributed axonal transmission speeds and a long-range constant feedback loop into the standard neural field model. We analyze the stability of spatially homogeneous equilibrium solutions for general connectivity kernels. By studying reduced models based on the assumption of small delays, we determine the effects of the delays on the stability and bifurcations. We show in a reduced model that delayed excitatory feedback generally facilitates stationary bifurcations and Turing patterns, while suppressing the bifurcation of periodic solutions and traveling waves. The reverse conclusion holds for inhibitory feedback. In case of oscillatory bifurcations, the variance of the distributed propagation and feedback delays affects the frequency of periodic solutions and the phase speed of traveling waves. Moreover, we give a nonlinear analysis of traveling fronts and find that distributed transmission speeds can maximize the front speed.

Key words. synaptic networks, nonlocal interaction, distributed delays, spatio-temporal patterns, traveling fronts

AMS subject classifications. 34K99, 37N25, 92C20

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1. Introduction. Several models of coupled neurons have recently attracted much attention, including topological neural networks [25, 34, 42, 47, 55] and networks involving spatial structures [1, 6, 18, 23, 27, 31, 59, 61]. This paper considers the latter networks describing a continuous synaptically coupled neural field extended in space, whose dynamics are governed by an integro-differential equation. We expand this classical model by incorporating two novel elements suggested by experimental evidence, namely a distribution of signal transmission speeds within the field, and a long-range feedback term involving distributed time delays. These elements constitute two sources of temporal delays with different character and have significant consequences for the dynamics of the neural ensemble. The present work studies their effects on the dynamics through the stability of equilibria, the bifurcations leading to spatial patterns and oscillations, and the analysis of traveling fronts. The measured activity of the neural system indicates that such spatio-temporal dynamics are intimately related to various brain functions and cognition. We mention the space-time instabilities during several types of hallucinations [5] and epileptic seizures [40, 41], the stimulus-evoked traveling waves in turtle visual cortex [48], and the evoked traveling pulses in somatosensory brain slices [46].

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The mathematical analysis is thus an important step in understanding the relation between neural processes and the model parameters.

The spatial structure in most cortical areas is not known in detail; therefore, the spatial field is usually assumed to be homogeneous, with an underlying arbitrary spatial connectivity. On the other hand, the temporal structure of neural activity is well studied. Multiple time scales are present in real neural areas, which may originate from the delayed impulse response of chemical synapses [20], the finite axonal speed [44], or the presence of feedback loops [56]. To be more specific, finite axonal transmission speed results in a space-dependent delay between two distant locations; i.e., the neural field shows retarded interaction. Moreover, experimental studies reveal not a single axonal speed but statistically distributed speeds in cortico-cortical connections in rats [44] and in intracortical connections in visual cortex of cats and monkeys [7, 16]. In all studies, the histogram of axonal speeds follows a gamma-distribution with maxima between 5 m/s and 12 m/s in rats and at about 0.2 m/s in the cat and monkey brain (Figure 1). To our best knowledge, such distributions of propagation speeds have not been considered yet in dynamical neural models.

In addition, feedback loops play an important role in real neural processing [53]. For instance, detailed studies of interhemispheric connections [17], connections of the visual areas of different functional order [8, 43], and reciprocal thalamic connections [14, 45, 57] indicate interareal feedback loops. In sum, most experimental findings indicate a network of interacting neural areas [52], which allows the brain to accomplish complex tasks, such as motor
coordination or visual feature binding [54]. Due to this network structure, some theoretical studies examined the effects of delayed self-interaction and the interactions of different neural areas [32]. In this context, a well-known example is corticothalamic feedback connections [45], which have been modeled recently by a simple constant feedback delay [49, 51]. The present work extends these previous studies by introducing arbitrary nonlocal feedback kernels; in other words, we consider the case in which the distance between the initial and the final spatial locations of the loop obeys an arbitrary probability density distribution. Furthermore, the time delays in the loop are also described by a general distribution function.

In the following sections, we study the stability of equilibrium solutions of neural fields subject to two sources of temporal delays, namely the transmission delays and the delays in the nonlocal feedback loops. These two delay types turn out to have quite different characters, which are reflected in their dynamical effects. Our aim is to draw general conclusions about the dynamics of the model without reference to specific choices of the connectivity, transmission speed, or feedback delay distributions. The model is introduced in section 2, and the stability of spatially homogeneous equilibria is analyzed in section 3 for arbitrary kernels. In section 4 we introduce approximate models under the assumption of large but finite axonal speeds and small feedback delays. Based on such a model, in section 4.2 we are able to give further details of the effects of the delays on stability and bifurcations. The theoretical analysis is supplemented by numerical simulations in section 5 for some commonly used choices of the connectivity and delay distribution functions. Section 6 treats traveling fronts. The discussion in section 7 closes the work.

2. Distributed speeds and nonlocal feedback. This section aims to motivate the model equation [2, 30]. A detailed review of the derivation of the basic model can be found in, e.g., [6, 28]. Here we additionally introduce the distribution of transmission speeds and the delayed long-range feedback loop.

An essential ingredient of neural activity is the input-output behavior of synapses which convert incoming pulses to postsynaptic potentials. In the coarse-grained population model, at time $t$ and some point $x$ in the field, ensembles of excitatory $(e)$ and inhibitory $(i)$ chemical synapses respond to incoming pulse activity $P_{e,i}(x, t)$ by temporal convolution with some impulse response function $h(t)$. Specifically,

\begin{equation}
V_{e,i}(x, t) = g_{e,i} \int_{-\infty}^{t} h(t - t') P_{e,i}(x, t') dt'
= g_{e,i}I \circ P_{e,i}(x, t),
\end{equation}

where $g_{e,i}$ denotes the efficacy of excitatory and inhibitory synapses, $I$ is the integral operator, and $V_{e,i}$ denotes the excitatory and inhibitory postsynaptic potential. The presynaptic pulse activity $P_{e,i}(x, t)$ originates from the somatic pulse activity $P_{k}^{e}(x, t)$ of distant neural ensembles of neuron type $k$ and is given by

\begin{equation}
P_{e,i}(x, t) = g_{0} \int_{0}^{\infty} g(v) \int_{\Omega} K_{e,i}(x - x') P_{k}^{e}(x', t - \frac{|x - x'|}{v}) dx' dv
+ \bar{\mu}_{e,i} \int_{0}^{\infty} f(\tau) \int_{\Omega} F_{e,i}(x - x') P_{k}^{e}(x', t - \tau) dx' d\tau + E_{e,i}(x, t).
\end{equation}
Here, \( \Omega \) represents a spatial domain, which is taken to be the real line in this paper. The kernels \( K_e(x) \) and \( K_i(x) \) represent the spatial distributions for excitatory and inhibitory synaptic connections, respectively, while \( F_e(x) \) and \( F_i(x) \) give the distributions of excitatory and inhibitory long-range delayed feedback connections, respectively. The factors \( \bar{\mu}_e, \bar{\mu}_i \) weight the corresponding feedback connections, and \( g_0 > 0 \) weights the interareal contribution towards the delayed feedback distribution. Moreover, the somatic conversion of the effective membrane potential \( V = V_e - V_i \) to ensemble pulse activity \( P^s \) can be modeled by a sigmoidal function \( P^s_k(x, t) = S(V(x, t) - V_0) \) with the mean firing threshold \( V_0 \) [21, 28]. The present model does not distinguish different neuron types and thus presumes \( P^s \) and the external input \( E = E_e - E_i \). The kernels \( K, F : \mathbb{R} \rightarrow \mathbb{R}^+ \) is differentiable and monotone increasing. The terms \( E_e \) and \( E_i \) represent the external stimuli terminating at excitatory and inhibitory synapses, respectively. Equation (2.2) incorporates several realistic mechanisms as sources of time delays in the neural field, including the signal propagation delays within the field and the delays in the long-range feedback loop. The finite speed \( v \) of signal propagation within the field gives rise to distance-dependent delays; such delays have been discussed in some recent studies [10, 13, 30, 32, 46]. As a novel aspect, in this paper we relax the constraint of a single transmission speed \( v \) and consider more naturally a distribution function of speeds \( g(v) \). As mentioned in the introduction, the motivation for distributed transmission speeds originates from experimental findings. In addition, we take into account the feedback delays \( \tau \) in the feedback loop, whose distribution is given by the function \( f \). In contrast to the transmission speeds, only a few details on the distribution of feedback delays are known from experiments; we mention the corticothalamic feedback delay [14], the feedback delay between visual areas V1 and V2 in monkeys [24], and the delayed inhibitory response in the retina of the horseshoe crab *Limulus polyphemus* [26]. The distribution functions \( g \) and \( f \) are probability densities on \([0, \infty)\), i.e., nonnegative functions satisfying

\[
\int_0^\infty g(v) \, dv = \int_0^\infty f(\tau) \, d\tau = 1.
\]

Combining (2.1) and (2.2), we find the equation

\[
V(x, t) = \int_{-\infty}^t h(t - t') \left[ \bar{\alpha} \int_0^\infty g(v) \int_{-\infty}^\infty K(z) S(V(x + z, t' - |z|/v)) \, dz \, dv 
+ \bar{\beta} \int_0^\infty f(\tau) \int_{-\infty}^\infty F(z) S(V(x + z, t' - \tau)) \, dz \, d\tau + E(x, t') \right] \, dt'
\]

with \( K = a_e K_e - a_i K_i, F = \mu_e F_e - \mu_i F_i, a_{e,i} = g_0 g_{e,i}, \mu_{e,i} = g_{e,i} \bar{\mu}_{e,i} \) and the external input \( E = E_e - E_i \). The kernels \( K, F : \mathbb{R} \rightarrow \mathbb{R} \) are continuous, integrable, and even; that is, \( K(-z) = K(z), F(-z) = F(z) \) for all \( z \in \mathbb{R} \). They can have different signs for small and large values of \( |z| \), showing different local and lateral contributions of excitation and inhibition. Furthermore, with the help of the nonnegative scaling factors \( \bar{\alpha} \) and \( \bar{\beta} \), they can be assumed to satisfy the normalization conditions

\[
\int_{-\infty}^\infty |K(z)| \, dz = \int_{-\infty}^\infty |F(z)| \, dz = 1.
\]
By introducing a temporal differentiation operator $L = \mathcal{T}^{-1}$, where $Lh(t) = \delta(t)$ and $\delta$ is the Dirac delta function, (2.4) can be written as an integro-differential equation. Thus, $h$ plays the role of the Green’s function corresponding to $L$. In this way we obtain our main equation

$$L \left( \frac{\partial}{\partial t} \right) V(x, t) = \bar{\alpha} \int_{-\infty}^{\infty} g(v) \int_{-\infty}^{\infty} K(z) \delta(V(x + z, t - |z|/v)) \, dz \, dv$$

$$+ \bar{\beta} \int_{0}^{\infty} f(\tau) \int_{-\infty}^{\infty} F(z) \delta(V(x + z, t - \tau)) \, dz \, d\tau + E(x, t).$$

(2.6)

As an example for Green’s function $h$, we mention the form suggested by experiments [15], namely $h(t) = (\exp(-t/T_1) - \exp(-t/T_2))/(T_1 - T_2)$ with synaptic time constants $T_1, T_2 > 0$. Letting $T_1 \to T_2 = T$ yields the well-studied case $h(t) = t \exp(-t/T)/T$ (see, e.g., [50]), corresponding to a second order differentiation operator with time scale $T$. We shall consider this case in sections 4.2 and 5, as well as a first order operator in section 6. However, the general formulation will be given for an arbitrary order operator $L$, often with the assumption that $L$ is stable, i.e., that all its characteristic values have negative real parts.

We close this section with several comments about the model (2.6). To begin with, the unbounded spatial domain $(-\infty, \infty)$ is physically unrealistic; however, it gives a good approximation when boundary effects are negligible inside the domain. Our results also hold when the domain is a circle, corresponding to a bounded region with periodic boundary conditions, and we use the circle as the spatial domain when we do numerical simulations in section 5. Since an unbounded domain is merely a mathematical convenience, the kernels $K$ and $F$ will typically have compact support, especially when they are experimentally determined, although the model allows arbitrary kernels defined on $(-\infty, \infty)$. In a similar vein, it may be more desirable to formulate the model in terms of $v^{-1}$ instead of $v$, because the probability density for $v^{-1}$ will have a compact support. Moreover, in terms of $v^{-1}$ it makes sense to discuss the perturbation of the distribution about the Dirac delta at zero, corresponding to instantaneous information transmission. We keep $v$ in (2.6) mainly because it allows slightly more intuitive and less cumbersome notation, and because the experimental measurements of the distribution are given in terms of $v$. Similarly, the probability density $f$ for the feedback delays will have compact support, making all delays in (2.6) bounded. In summary, the unbounded spatial and temporal domains appearing in the model are mostly for convenience of notation and reduce to finite ranges for physically reasonable choices of distributions. A main point of interest is the different nature of the two delay types in the two terms on the right-hand side of (2.6), which we study in the subsequent sections.

3. Equilibrium solutions. In this section we consider the basics of a stability analysis for spatially uniform equilibria of the model (2.6). The material here is essentially a brief version of sections 2 and 3 of [2], with the purpose of indicating the differences introduced by distributed speeds and nonlocal feedback.

For a constant input $E(x, t) \equiv E^*$, a spatially uniform equilibrium solution $V(x, t) \equiv V^*$ of (2.6) satisfies $V^* = \kappa S(V^*) + E^*$, where

$$\kappa = \bar{\alpha} \int_{-\infty}^{\infty} K(z) \, dz + \bar{\beta} \int_{-\infty}^{\infty} F(z) \, dz.$$
It is easy to see that if $S$ is a continuous and increasing function (such as a sigmoid) and $\kappa \leq 0$, then $V^*$ is unique for any $E^* \in \mathbb{R}$, whereas if $\kappa > 0$, then there may be multiple equilibria $V^*$ [2]. The stability of the equilibrium solution $V^*$ is determined by the linear variational equation

$$ L \left( \frac{\partial}{\partial t} \right) u(x, t) = \alpha \int_0^\infty g(v) \int_{-\infty}^\infty K(z) u(x + z, t - |z|/v) \, dz \, dv $$

$$ + \beta \int_0^\infty f(\tau) \int_{-\infty}^\infty F(z) u(x + z, t - \tau) \, dz \, d\tau, $$

(3.1)

where $u(x, t) = V(x, t) - V^*$ and

$$ \alpha = \tilde{\alpha} S'(V^*) \geq 0, \quad \beta = \tilde{\beta} S'(V^*) \geq 0. $$

(3.2)

Note that the values of $\alpha$ and $\beta$ depend implicitly on the external input $E^*$ through the value of $V^*$. Using the ansatz $u(x, t) = e^{\lambda t} e^{ikx}$ in (3.1), where $\lambda \in \mathbb{C}$ and $k \in \mathbb{R}$, we obtain the dispersion relation between the temporal and spatial modes as

$$ L(\lambda) = \alpha \int_0^\infty g(v) \int_{-\infty}^\infty K(z) \exp(-\lambda |z|/v) \exp(-ikz) \, dz \, dv $$

$$ + \beta \int_0^\infty f(\tau) e^{-\lambda \tau} \int_{-\infty}^\infty F(z) \exp(-ikz) \, dz. $$

(3.3)

Notice that the last term in (3.3) factors as the product of the Laplace transform of $f$ and the Fourier transform of $F$. By contrast, such a factorization does not arise for the term multiplying $\alpha$. This difference accounts for the different character of the two delay sources, whose effects are further studied in section 4.2. For now we make some elementary observations regarding the stability of the equilibrium solution. When the characteristic values of the operator $L$ have negative real parts, the zero solution of (3.1) is stable for $\alpha = \beta = 0$. It follows that $V^*$ is stable for small $\alpha, \beta$, as quantified by the next theorem.

**Theorem 3.1.** Suppose that $L$ is a stable polynomial. If

$$ \alpha + \beta < \min_{\omega \in \mathbb{R}} |L(i\omega)|, $$

(3.4)

then $V^*$ is asymptotically stable. In particular, if $L(\lambda) = \lambda + \rho$, $\rho > 0$, then the condition

$$ \alpha + \beta < \rho $$

(3.5)

is sufficient for the asymptotic stability of $V^*$. If $L(\gamma) = \lambda^2 + \gamma \lambda + \rho$ with $\gamma, \rho > 0$, then $V^*$ is asymptotically stable, provided that the condition

$$ \frac{\gamma^2}{2} > \rho - \sqrt{\rho^2 - (\alpha + \beta)^2} $$

(3.6)

holds in addition to (3.5).
Proof. In the ansatz \( u(x,t) = e^{\lambda t} e^{ikx} \) let \( \lambda = \sigma + i\omega \), where \( \sigma \) and \( \omega \) are real numbers. We will prove that \( \sigma < 0 \) if (3.4) holds. Suppose by way of contradiction that (3.4) holds but \( \sigma \geq 0 \). From the dispersion relation (3.3),

\[
|L(\sigma + i\omega)| = \left| \alpha \int g(v) \int_{-\infty}^{\infty} K(z) \exp(-i(\sigma |z|/v) \exp(-ikz) \, dz \, dv \\
+ \beta \int_{0}^{\infty} f(\tau) \exp(-i(\sigma \tau) \, d\tau \int_{-\infty}^{\infty} F(z) \exp(-ikz) \, dz \right|
\]

\[
\leq \alpha \int g(v) \int_{-\infty}^{\infty} |K(z)| \exp(-\sigma |z|/v) \, dz \, dv + \beta \int_{0}^{\infty} f(\tau) \int_{-\infty}^{\infty} |F(z)| \, dz \\
\leq \alpha \int_{-\infty}^{\infty} |K(z)| \, dz + \beta \int |F(z)| \, dz
\]

(3.7)

\[
= \alpha + \beta,
\]

where we have used (2.3) and (2.5). On the other hand, by Lemma 2.2 in [2],

\[
|L(i\omega)| \leq |L(\sigma + i\omega)|
\]

for all \( \sigma \geq 0 \) and \( \omega \in \mathbb{R} \), which together with (3.7) implies

\[
|L(i\omega)| \leq \alpha + \beta.
\]

This, however, contradicts (3.4). Thus \( \sigma > 0 \), and the first statement of the theorem is proved. The remainder is similar to the proof of Theorem 2.1 in [2].

The change of stability as the parameters \( \alpha, \beta \) are increased beyond the quantity given in (3.4) is characterized by the existence of an eigenvalue \( \lambda = i\omega, \omega \in \mathbb{R} \). The dispersion relation (3.3) then implies that

\[
L(i\omega) = \alpha \int_{0}^{\infty} g(v) \int_{-\infty}^{\infty} K(z) \exp(-i(kz + \omega |z|/v)) \, dz \, dv \\
+ \beta \int_{0}^{\infty} f(\tau) e^{-i\omega \tau} d\tau \int_{-\infty}^{\infty} F(z) \exp(-ikz) \, dz.
\]

(3.8)

The bifurcating solutions near such critical cases can be qualitatively classified as stationary or oscillatory, depending on whether \( \omega = 0 \) or \( \omega \neq 0 \), respectively, and as spatially homogeneous or inhomogeneous, depending on whether \( k = 0 \) or \( k \neq 0 \), respectively, as summarized in Table 1.

<table>
<thead>
<tr>
<th>Homogeneous ((k = 0))</th>
<th>Stationary ((\omega = 0))</th>
<th>Oscillatory ((\omega \neq 0))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatially constant equilibrium</td>
<td>Global oscillations</td>
<td></td>
</tr>
<tr>
<td>Inhomogeneous ((k \neq 0))</td>
<td>Spatial patterns</td>
<td>Traveling waves</td>
</tr>
</tbody>
</table>

Table 1

Classification of possible local bifurcations of equilibria.
For stationary bifurcations which are spatially homogeneous \(( \omega = k = 0 )\), the bifurcating solution is also an equilibrium. From (3.8), this case occurs when

\[
L(0) = \alpha \int_{-\infty}^{\infty} K(z) \, dz + \beta \int_{-\infty}^{\infty} F(z) \, dz.
\]

Suppose \( L(0) > 0 \). If \( \beta = 0 \), (3.9) can be satisfied only when \( \int_{-\infty}^{\infty} K(z) \, dz > 0 \), that is, when the connectivity is dominantly excitatory. On the other hand, if \( \beta > 0 \), such a bifurcation can occur even with inhibitory connectivity kernels, provided that \( \int_{-\infty}^{\infty} F(z) \, dz > 0 \). Hence, excitatory nonlocal feedback can induce this type of bifurcation even when inhibitory connections dominate the field. Conversely, inhibitory feedback can prevent this bifurcation from occurring.

The stationary bifurcations which are spatially inhomogeneous \(( \omega = 0 \) and \( k \neq 0 \)) yield spatial patterns, also called Turing modes. The condition for their appearance is given by (3.8) as

\[
L(0) = \alpha \int_{-\infty}^{\infty} K(z) \exp(-ikz) \, dz + \beta \int_{-\infty}^{\infty} F(z) \exp(-ikz) \, dz
\]

\[
= \alpha \hat{K}(k) + \beta \hat{F}(k), \quad k \neq 0,
\]

where \( \hat{K} \) and \( \hat{F} \) denote the Fourier transforms of \( K \) and \( F \), respectively. Reasoning as in the above paragraph, we conclude that excitatory nonlocal feedback can induce stationary bifurcations and patterns, whereas inhibitory feedback can stabilize the equilibrium against such bifurcations.

By (3.9) and (3.10), stationary bifurcations are independent of the propagation speeds and the feedback delays, as well as the temporal differentiation operator \( L \) (except through \( L(0) \)). The oscillatory bifurcations, however, are very much influenced by the delays and may even be absent if delay effects are small. Indeed, in terms of the mean feedback delay \( E[\tau] = \int_0^\infty \tau f(\tau) \, d\tau \) and the mean propagation delay \( \tau_p \), defined by

\[
\tau_p = \int_0^\infty \frac{g(v)}{v} \, dv \int_{-\infty}^{\infty} |zK(z)| \, dz
\]

(3.11)

(where the first integral is the mean value of \( v^{-1} \) and \( \xi \) is a characteristic interaction distance within the field), the following estimate can be derived.

**Theorem 3.2.** Suppose \( L(\lambda) = \eta \lambda^2 + \gamma \lambda + \rho \), where \( \eta > 0 \) and \( \gamma, \rho \in \mathbb{R} \). If

\[
\alpha \tau_p + \beta E[\tau] < |\gamma|,
\]

then (3.1) has no solutions of the form \( u(x, t) = \exp(i(\omega t + kx)) \) with \( \omega \) real and nonzero.

**Proof.** From (3.8),

\[
L(\lambda) = \alpha \int_0^\infty g(v) \int_{-\infty}^{\infty} K(z) \exp(-\lambda |z|/v) \cos kz \, dz \, dv
\]

\[
+ \beta \int_0^\infty f(\tau) e^{-\lambda \tau} \, d\tau \int_{-\infty}^{\infty} F(z) \cos(kz) \, dz
\]
since the functions $F(z)$ and $K(z) \exp(-\lambda |z|/v)$ are even in $z$. The imaginary part of the above expression at the value $\lambda = i\omega$ is

$$\text{Im} L(i\omega) = -\alpha \int_0^\infty \int_{-\infty}^\infty g(v)K(z) \sin(\omega |z|/v) \cos(kz) \, dz$$

$$- \beta \int_0^\infty f(\tau) \sin(\omega \tau) \, d\tau \int_{-\infty}^\infty F(z) \cos(kz) \, dz. \quad (3.13)$$

If $L(\lambda) = \eta \lambda^2 + \gamma \lambda + \rho$, then $\text{Im} L(i\omega) = \gamma \omega$, and comparing the magnitudes in (3.13) gives

$$|\gamma \omega| \leq \alpha \int_0^\infty \int_{-\infty}^\infty g(v)|K(z)| \sin(\omega z/v) \, dz \, dv + \beta \int_0^\infty f(\tau) |\sin(\omega \tau)| \, d\tau \int_{-\infty}^\infty |F(z)| \, dz$$

$$\leq \alpha \int_0^\infty \int_{-\infty}^\infty g(v)|K(z)\omega z/v| \, dz \, dv + \beta |\omega| \int_0^\infty \tau f(\tau) \, d\tau,$$

where we have used the normalization (2.5) and the estimate $|\sin(x)| \leq |x|$, $x \in \mathbb{R}$. If $\omega \neq 0$, then $\omega$ may be canceled to yield

$$|\gamma| \leq \alpha \int_0^\infty \frac{g(v)}{v} \, dv \int_{-\infty}^\infty |zK(z)| \, dz + \beta \int_0^\infty \tau f(\tau) \, d\tau = \alpha \tau_p + \beta E[\tau].$$

This, however, contradicts the assumption (3.12). Hence $\omega = 0$, which now proves the theorem.

We note that the mean propagation delay $\tau_p$ can be estimated for cortico-cortical connections in humans \cite{35, 58}, and we find $\bar{v} \approx 8 \text{ ms}^{-1}$, $\xi \approx 0.10 \text{ m}$, leading to $\tau_p \approx 12 \text{ ms}$. Similarly, for the corticothalamic loop in humans $E[\tau] \approx 120 \text{ ms}$ \cite{14}, while the feedback loop between V1 and V2 exhibits $E[\tau] \approx 2 \text{ ms}$ \cite{24}. Such estimates together with Theorem 3.2 give a practical means of determining the possibility of oscillatory bifurcations of spatially uniform equilibria. The importance of oscillatory bifurcations stems from the prevalence of oscillatory activity in neural systems. For instance, a spatially homogeneous and oscillatory bifurcation ($\omega \neq 0$ and $k = 0$) corresponds to spatially uniform, or synchronous, oscillations, whereas the spatially inhomogeneous case ($\omega \neq 0$ and $k \neq 0$) corresponds to traveling waves, with wave speed given by $\omega/k$. The analysis of these bifurcations by solving (3.8), however, is not straightforward. Obtaining general results without making specific assumptions about the kernels is particularly difficult. In the next section we will use an approximation scheme to draw qualitative conclusions for general classes of connectivity and feedback kernels and delay distributions. Based on this analysis, we will show in section 4.2 that the stabilizing effect of inhibitory connectivity and feedback against stationary bifurcations is accompanied by their tendency to induce oscillatory bifurcations when delays are present. Similarly, excitatory feedback, which can induce stationary bifurcations, can also prevent oscillatory bifurcations. We are thus able to connect the effects of field connectivity and nonlocal feedback with the effects of delays.

4. Reduced models. We now investigate the bifurcations of equilibria in reference to the two novel aspects of the neural field introduced in section 2—namely, distributed propagation speeds and feedback delays. Our aim is to obtain an analytical understanding of the general
dynamical features of the model, without recourse to specific forms for the connectivity and feedback kernels as well as speed and delay distributions. To make the problem tractable under such generalities, we study an approximate model for which stability and bifurcations can be analytically calculated and the effects of delays can be determined. Based on this analysis, we make qualitative predictions and obtain parameter values which serve as the starting point for numerical investigation of the full model. We return to the original model in section 5 to numerically verify the predictions for particular choices of kernels.

4.1. Series approximation. To investigate the stability and bifurcations of the equilibrium solution, we introduce the power series expansions

\[
\begin{align*}
u(x + z, t - |z|/v) &= \sum_{m=0}^{\infty} \left( -\frac{|z|}{v} \right)^m \frac{\partial^m}{\partial t^m} u(x + z, t), \\
u(x + z, t - \tau) &= \sum_{m=0}^{\infty} \left( -\frac{\tau}{m!} \right)^m \frac{\partial^m}{\partial t^m} u(x + z, t)
\end{align*}
\]

into the linearized equation (3.1) and obtain

\[
L \left( \frac{\partial}{\partial t} \right) u(x, t) = \alpha \int_{-\infty}^{\infty} \sum_{m=0}^{\infty} \frac{(-1)^m E[v^{-m}]}{m!} |z|^m K(z) \frac{\partial^m}{\partial t^m} u(x + z, t) \, dz
+ \beta \int_{-\infty}^{\infty} \sum_{m=0}^{\infty} \frac{(-1)^m E[\tau^{-m}]}{m!} F(z) \frac{\partial^m}{\partial t^m} u(x + z, t) \, dz,
\]

(4.1)

where \(E[\tau^m] = \int_0^\infty \tau^m f(\tau) \, d\tau\) and \(E[v^{-m}] = \int_0^\infty v^{-m} g(v) \, dv\) are the expected values of \(\tau^m\) and \(v^{-m}\), respectively. Now consider the case when the above equation can be well approximated by using the first \(N+1\) terms of the infinite series. This assumption is justified when the delays arising from signal propagation and nonlocal feedback are not too large and their distributions are sufficiently concentrated near their mean values, and when the connection kernel \(K\) decays sufficiently fast away from the origin [2]. For example, \(K\) is typically of exponential order; that is, there exist positive constants \(\kappa_1\) and \(\kappa_2\) such that

\[|K(z)| \leq \kappa_1 \exp(-\kappa_2 |z|), \quad z \in \mathbb{R}.
\]

Then, using the fact that \(K\) is even,

\[
\frac{1}{m!} \int_{-\infty}^{\infty} |z|^m K(z) \, dz \leq \frac{2\kappa_1}{m!} \int_{0}^{\infty} z^m \exp(-\kappa_2 z) \, dz
= 2\kappa_1 \kappa_2^{-(m+1)} \Gamma(m + 1) = 2\kappa_1 \kappa_2^{-(m+1)}.
\]

So if \(\kappa_2 > 1\), the contribution of the terms \(|z|^m K(z)/m!\) to the integral in (4.1) becomes negligible for large \(m\).
We thus have the reduced model for the neural field near the equilibrium solution

$$L \left( \frac{\partial}{\partial t} \right) u(x, t) = \alpha \int_{-\infty}^{\infty} \sum_{m=0}^{N} \frac{(-1)^m E[v^{-m}]}{m!} |z|^m K(z) \frac{\partial^m}{\partial t^m} u(x + z, t) \, dz$$

$$+ \beta \int_{-\infty}^{\infty} \sum_{m=0}^{N} \frac{(-1)^m E[\tau^{-m}]}{m!} F(z) \frac{\partial^m}{\partial t^m} u(x + z, t) \, dz.$$  

(4.2)

The corresponding dispersion relation has the form

$$L(\lambda) = \sum_{m=0}^{N} \frac{(-1)^m \lambda^m}{m!} \left( \alpha E[v^{-m}] \hat{K}_m(k) + \beta E[\tau^{-m}] \hat{F}(k) \right),$$

where

$$\hat{K}_m(k) = \int_{-\infty}^{\infty} |z|^m K(z) e^{-ikz} \, dz$$

denotes the Fourier transforms of the moments of $K$. We also use the usual notation $\hat{K}$ for $\hat{K}_0$. All the transforms $\hat{K}_m$ as well as $\hat{F}$ are real-valued since the kernels $K$ and $F$ are even functions. The next theorem gives conditions for the stability of the zero solution of (4.2).

Recall that the leading principal minors of a $q \times q$ real matrix $A = [a_{ij}]$ are the $q$ real numbers

$$a_{11}, \det \left( \begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array} \right), \det \left( \begin{array}{ccc} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{array} \right), \ldots, \det(A).$$

**Theorem 4.1.** Let $L(\lambda) = \sum_{m=0}^{n} l_m \lambda^m$, and suppose that the pair $(\lambda, k)$ satisfies (4.3). Let

$$c_m(k) = l_m - b_m(k),$$

where

$$b_m(k) = \begin{cases} \frac{(-1)^m}{m!} \left( \alpha E[v^{-m}] \hat{K}_m(k) + \beta E[\tau^{-m}] \hat{F}(k) \right), & m = 0, 1, \ldots, N, \\ 0, & m > N. \end{cases}$$

Let

$$q = \max \{ m : c_m(k) \neq 0 \},$$

and define the $q \times q$ real matrix

$$Q(k) = \text{sign}(c_q) \cdot \begin{pmatrix} c_{q-1} & c_q & 0 & \cdots & 0 \\ c_{q-3} & c_{q-2} & c_{q-1} & \cdots & 0 \\ c_{q-5} & c_{q-4} & c_{q-3} & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & c_1 & c_0 \end{pmatrix}. $$
Then \( \Re \lambda \geq 0 \) if and only if some leading principal minor of \( Q(k) \) is nonpositive. Consequently, the zero solution of (4.2) is asymptotically stable if and only if all leading principal minors of \( Q(k) \) are positive for all \( k \).

**Proof.** The relation (4.3) can be viewed as a \( q \)th order polynomial equation in \( \lambda \), where the coefficients depend on \( k \). We thus write (4.3) as

\[
p_k(\lambda) = \sum_{m=0}^{q} c_m(k)\lambda^m = 0,
\]

where \( c_m(k) \) are as in the statement of the theorem. The stability of \( p_k(\lambda) \) is given by the Routh–Hurwitz criteria, which can be expressed as the leading principal minors of \( Q(k) \) being positive; see, e.g., [3].

Theorem 4.1 allows us to determine the temporal stability of the spatial mode corresponding to a particular wave number \( k \). In this way, it is possible to systematically investigate the bifurcation structure and its dependence on the parameters. As an application, we next analyze a special case where the stability and bifurcations can be completely characterized and a detailed description of the effects of delays can be given.

4.2. Effects of delays in a second order model. The reduced model (4.2) with \( N = 0 \) is equivalent to neglecting all delays in the original field model. Taking \( N = 1 \), on the other hand, gives an equation that depends only on the mean values of the delays and not on their distributions. Hence, the lowest order model which exhibits the effects of distributed speeds and feedback delays is obtained with \( N = 2 \). We now consider the case \( N = 2 \) in some detail to gain insight into the effects of speed and delay distributions. For definiteness, we focus on the second order temporal differential operator

\[
(4.4) \quad L \left( \frac{\partial}{\partial t} \right) = \frac{\partial^2}{\partial t^2} + \gamma \frac{\partial}{\partial t} + \rho, \quad \gamma, \rho > 0,
\]

which has been considered by several authors in models of neural field dynamics, e.g., [6, 28, 30, 50, 60]. As we will make use of the approximation scheme introduced above, the results here hold for sufficiently large transmission speeds. The analysis is based on the following result, which essentially follows from Theorem 4.1.

**Theorem 4.2.** Consider (4.2) with \( N = 2 \) and \( L \) given by (4.4). Then the following hold:

1. (stability) Let \( (\lambda, k) \) be a solution of the dispersion relation (4.3) such that

\[
(4.5) \quad \alpha E[v^{-2}]\hat{K}_2(k) + \beta E[\tau^2]\hat{F}(k) < 2.
\]

Then \( \Re(\lambda) < 0 \) if and only if the conditions

\[
(4.6) \quad \rho - \alpha \hat{K}(k) - \beta \hat{F}(k) > 0
\]

and

\[
(4.7) \quad \gamma + \alpha E[v^{-1}]\hat{K}_1(k) + \beta E[\tau]\hat{F}(k) > 0
\]

are satisfied. The conclusion remains valid if all inequalities in (4.5)–(4.7) are simultaneously reversed. When \( \alpha E[v^{-2}]\hat{K}_2(k) + \beta E[\tau^2]\hat{F}(k) = 2 \), \( \Re(\lambda) < 0 \) if and only if the left-hand sides of (4.6) and (4.7) have the same (nonzero) sign.
2. (stationary bifurcations) The pair \((\lambda, k)\) with \(\lambda = 0\) satisfies (4.3) if and only if
\[
\rho - \alpha \hat{K}(k) - \beta \hat{F}(k) = 0. \tag{4.8}
\]

3. (oscillatory bifurcations) The pair \((\lambda, k)\) with \(\lambda = i\omega, \omega \in \mathbb{R}\{0\}\), satisfies (4.3) if and only if
\[
\gamma + \alpha E[v^{-1}]\hat{K}_1(k) + \beta E[\tau] \hat{F}(k) = 0 \tag{4.9}
\]
and
\[
\omega^2 = \frac{\rho - \alpha \hat{K}(k) + \beta \hat{F}(k)}{2 - \alpha E[v^{-2}]\hat{K}_2(k) - \beta E[\tau^2] \hat{F}(k)} > 0. \tag{4.10}
\]

**Proof.** With \(N = 2\) and \(L\) as given in the statement of the theorem, (4.3) is a quadratic equation in \(\lambda:\)
\[
p_k(\lambda) = c_2(k)\lambda^2 + c_1(k)\lambda + c_0(k) = 0, \tag{4.11}
\]
where
\[
c_0(k) = \rho - \alpha \hat{K}(k) - \beta \hat{F}(k),
\]
\[
c_1(k) = \gamma + \alpha E[v^{-1}]\hat{K}_1(k) + \beta E[\tau] \hat{F}(k),
\]
\[
c_2(k) = 1 - \frac{1}{2} \alpha E[v^{-2}]\hat{K}_2(k) - \frac{1}{2} \beta E[\tau^2] \hat{F}(k).
\]

It is easy to see that, in case \(c_2(k) \neq 0\), the roots of \(p_k\) have negative real parts if and only if all the coefficients \(c_m(k)\) are nonzero and have the same sign. Furthermore, \(p(0) = 0\) if and only if \(c_0(k) = 0\), and \(p(i\omega) = 0\) if and only if \(c_1(k) = 0\) and \(\omega^2 = c_0(k)/c_2(k) > 0\). In case \(c_2(k) = 0\), \(p_k\) has the unique root \(\lambda = -c_0(k)/c_1(k)\).

We note that Theorem 4.2 actually holds without the assumption that \(\gamma\) and \(\rho\) are positive.

When \(\alpha = \beta = 0\) (corresponding to the “uncoupled” dynamics), the equilibrium solution is asymptotically stable since \(\gamma\) and \(\rho\) are positive in (4.4). By (4.6) and (4.7), stability persists for sufficiently small \(\alpha, \beta\), in agreement with Theorem 3.1. As \(\alpha\) or \(\beta\) is further increased, stability can be lost through a stationary or oscillatory bifurcation, characterized by the conditions (4.8) and (4.9)–(4.10), respectively. Note that the stationary bifurcation condition (4.8) depends only on the connectivity kernels and not on the delays. Furthermore, in case of instantaneous signal transmission, \(E[\tau] = E[v^{-1}] = 0\), and by (4.9) oscillatory bifurcations cannot occur, which agrees with Theorem 3.2. For nonzero delays both types of bifurcations become possible. In case of small delays, one can assume that (4.5) holds throughout some parameter range. Then studying the validity of conditions (4.6) and (4.7) while increasing \(\alpha\) or \(\beta\) from zero yields an important result: the condition that is first violated determines the type of bifurcation that actually occurs, i.e., whether a stationary or oscillatory bifurcation takes place, as either (4.8) or (4.9) is satisfied. We now give a qualitative account of the effects of delays on these bifurcations. Under the assumption of small delays as stated in section 4, the conclusions drawn will also hold for the full model (2.6) at nearby parameter values. Numerical solution of (2.6) will be used in section 5 to confirm the results for specific choices of kernels.
Figure 2. Schematic diagram of the competition between stationary and oscillatory bifurcations. The curves $\phi_1$ and $\phi_2$ denote the first and the second terms inside the braces in (4.12). As the bifurcation parameter $\alpha$ is increased from zero, the horizontal line $1/\alpha$ becomes tangent to one of the curves. The tangency with $\phi_1$ is equivalent to a stationary bifurcation, while the tangency with $\phi_2$ is equivalent to an oscillatory bifurcation. Since these tangencies depend only on the maxima of the curves, located at $k_1$ and $k_2$, respectively, the type of bifurcation can be determined by comparing $\phi_1(k_1)$ and $\phi_2(k_2)$.

Propagation delays. We first focus on the effect of propagation delays by setting $\beta = 0$, i.e., by ignoring the contribution of feedback. From (4.8) and (4.9) we have the conditions

$$\frac{1}{\alpha} = \frac{\hat{K}(k)}{\rho}$$

and

$$\frac{1}{\alpha} = -\frac{E[v^{-1}]\hat{K}_1(k)}{\gamma}$$

for stationary and oscillatory bifurcations, respectively. As $\alpha$ is increased from zero, the horizontal line $1/\alpha$ can become tangent to the graph of $\hat{K}(k)/\rho$ or $-\hat{K}_1(k)E[v^{-1}]/\gamma$, at some value $k = k^*$. Whichever tangency occurs first (i.e., for the smaller value of $\alpha$) determines the type of bifurcation as the equilibrium solution loses its stability. In other words, $k^*$ denotes the point where the function

$$\phi(k) := \max \left\{ \frac{\hat{K}(k)}{\rho}, -\frac{E[v^{-1}]\hat{K}_1(k)}{\gamma} \right\}$$

(4.12)

assumes its maximum, which exists if $\phi$ is not strictly negative, and is generically unique. If $\phi(k^*) = \hat{K}(k^*)/\rho$, then the bifurcation is stationary; otherwise it is oscillatory (see Figure 2 for a schematic picture). Hence, higher values of $E[v^{-1}]$ (slower signal propagation) will facilitate
oscillatory bifurcations by increasing the magnitude of the second term inside the braces in (4.12), provided that $\hat{K}_1$ is not a nonnegative function. The oscillation frequency of such bifurcations is given by (4.10) as

$$(\omega^*)^2 = \frac{\rho - \alpha \hat{K}(k^*)}{2 - \alpha E[v^{-2}]\hat{K}_2(k^*)}.$$ 

Furthermore, the bifurcating solution is spatially homogeneous if and only if $k^* = 0$. If $k^* \neq 0$, then $\omega^*/k^*$ is the phase speed of the traveling waves that bifurcate. Thus, the main effect of propagation delays is on oscillatory bifurcations. However, this effect is intimately related to the connectivity kernel through $\hat{K}_1$. Note that even if $K$ is sign definite, such as a purely excitatory or purely inhibitory connection, $\hat{K}_1$ can in general take both positive and negative values.

As noted in [2], if a sufficiently general class of kernels is considered, the maximum of $\phi$ in (4.12) is likely to occur at some nonzero $k$ rather than at the precise value $k = 0$. Consequently, one expects to see traveling waves (respectively, Turing patterns) when signal propagation is slow (respectively, fast), as the dominant mode of bifurcation in the absence of the feedback term.¹

**Feedback delays.** We now include the effect of feedback delays by allowing $\beta$ to be nonzero. Similar to above, the wave number $k^*$ of the bifurcating solution is the point where the function

$$(4.13) \quad \Phi(k) = \max \left\{ \frac{\alpha \hat{K}(k) + \beta \hat{F}(k)}{\rho}, \frac{-\alpha E[v^{-1}]\hat{K}_1(k) - \beta E[\tau]\hat{F}(k)}{\gamma} \right\}$$

assumes its maximum value. The type of bifurcation is again determined by the relative magnitudes of the two terms inside the braces, which can be studied by plotting them on the same graph. Thus, when $\hat{F}$ is a positive function (which is typical for most common forms of excitatory feedback), the first term increases while the second one decreases for increasing $\beta$. We conclude that the presence of excitatory feedback connections generally facilitates stationary bifurcations and suppresses oscillatory ones if $E[\tau]$ is nonzero. The reverse conclusion holds for inhibitory feedback connections. The feedback connections thus show a definite preference on the type of bifurcations, given by the sign of $\hat{F}$. Furthermore, their effect on oscillatory bifurcations increases with the mean feedback delay $E[\tau]$.

A particular observation which may have significance in applications concerns the case when the feedback connections are highly nonlocal, that is, the kernel $F$ has a large variance. It is a well-known fact from Fourier theory that the corresponding transform $\hat{F}$ then has a small variance and thus is highly concentrated near the origin. It follows that increasing $\beta$ from zero will cause $\Phi$ to have its maximum near $k^* = 0$; in fact, if $k$ is restricted to discrete values (e.g., when the spatial domain is a circle), then the maximum will occur at $k^* = 0$. Consequently, nonlocal feedback which has a sufficiently large spatial range tends to enhance spatially homogeneous bifurcations, which are stationary if $\hat{F}$ is a positive function or

¹Of course, in applications which dictate a specific form for the connectivities, this expectation may not always be realized.
oscillatory if $\hat{F}$ is negative and $E[\tau]$ is sufficiently large. This is in contrast with the case $\beta = 0$ noted above, where spatially inhomogeneous bifurcations might be the more likely scenario.

**Distributed delays and speeds.** Finally, we consider the effects of distributed transmission speeds and feedback delays on the bifurcations. To this end, we keep the mean values $E[\tau]$ and $E[v^{-1}]$ fixed and increase the variances $\text{Var}[\tau]$ and $\text{Var}[v^{-1}]$, assuming (4.5) throughout as before. It then follows from the conditions (4.6) and (4.7) that the stability of the equilibrium solution is unaffected by the variances, and the bifurcations occur at the same parameter values. This is also apparent from the above analysis, which shows that the wave number $k^*$, in particular, does not depend on $\text{Var}[\tau]$ or $\text{Var}[v^{-1}]$. The main effect of the variances is on the frequency $\omega^*$ of oscillatory bifurcations. By (4.10),

$$
(\omega^*)^2 = \frac{\rho - \alpha \hat{K}(k^*) + \beta \hat{F}(k^*)}{2 - \alpha \hat{K}_2(k^*)(\text{Var}[v^{-1}] + E^2[v^{-1}]) - \beta \hat{F}(k^*)(\text{Var}[\tau] + E^2[\tau])}.
$$

Suppose that the variance $\text{Var}[\tau]$ is changed while the mean value $E[\tau]$ is kept fixed. If $\hat{F}(k^*)$ is positive (resp., negative), then $\omega^*$ will increase (resp., decrease) with increasing variance of the feedback delays $\tau$. In case of bifurcating traveling waves, an increase in $\omega^*$ corresponds to an increase in the speed $\omega^*/k^*$ of the waves, since $k^*$ is unaffected by the variance of delays and speeds. Thus, increasing the variance of delays will typically increase the frequency of bifurcating oscillatory solutions or the speed of traveling waves for excitatory feedback connections and decrease it for inhibitory feedback connections. Similarly, if $\hat{K}_2(k^*)$ is positive (resp., negative), then $\omega^*$ will increase (resp., decrease) with increasing variance $\text{Var}[v^{-1}]$ of propagation speeds. Figure 7 in section 5 illustrates the dependence of the wave speed on the variance of the propagation speed for a particular choice of connectivity and transmission speed distribution.

**5. Numerical results.** In this section we present simulation results confirming the analysis of previous sections with specific choices for the connectivities and transmission speed distributions. For numerical calculations we take the spatial domain $\Omega$ to be the circle with circumference $C$ (or equivalently the interval $[0, C]$ with periodic boundary conditions) and assume that the feedback connections are uniformly distributed over this domain (global feedback). Thus,

$$
F(z) \equiv \frac{1}{C}, \quad \int_0^C F(z) \, dz = 1,
$$

with the Fourier transform

$$
\hat{F}(k) = \begin{cases} 
1 & \text{if } k = 0, \\
0 & \text{if } k = \frac{2\pi n}{C}, \ n \in \mathbb{Z};
\end{cases}
$$

thus, we denote $\hat{F}(k) = \delta(k)$. We further assume that $L$ is the second order operator (4.4) and take $\rho = L(0) = 1$.

In this setting, the condition (3.9) for temporally stationary and spatially homogeneous bifurcation takes the form

$$
1 - \beta = \alpha \int_{-\infty}^\infty K(z) \, dz.
$$
The condition (3.10) for Turing patterns also simplifies to
\[ 1 = \alpha \hat{K}(k), \quad k \neq 0, \]
which depends only on the distribution \( K \) of intra-areal connections. We choose \( K \) to be
\[ K(z) = \frac{a_e}{2} e^{-|z|} - \frac{a_i}{2} re^{-r|z|}, \tag{5.1} \]
where \( r \) denotes the relation of excitatory and inhibitory spatial ranges and \( a_e \) and \( a_i \) represent excitatory and inhibitory synaptic weights [30]. For instance, in case of a single propagation speed and \( r > a_e/a_i \), the neural field exhibits local inhibition and lateral excitation and thus facilitates traveling waves [30].

5.1. Feedback delays. We now present simulation results displaying the role of global feedback delay. We apply an explicit Euler-forward algorithm for the time integration, which stores past activity according to the distance-dependent propagation delays and the feedback delays. The initial conditions are chosen randomly from a uniform distribution; however, see figure captions for more details. At each temporal iteration step, both spatial integrals in (2.6) have to be computed. In previous studies, we applied modified Riemannian sums [2, 30], which need a large number of spatial grid points to obtain small numerical errors. More advanced integration rules take into account the kernel properties. Here we use the VEGAS algorithm [22, 39], which is a Monte-Carlo integration algorithm in combination with importance sampling. In principle, the algorithm samples points from the probability function to be integrated, so that the points are concentrated in the regions that make the largest contribution to the integral. This approach can be applied to (2.6), as the function \( S \) is bounded and the kernels define the contribution to the integral. In the simulations, 2000 calls are applied for a single Monte-Carlo integration. The integration is repeated five times, and the average result is considered. Other variants of Monte-Carlo integration algorithms, such as plain Monte-Carlo or the MISER algorithm [22], showed worse performance. We remark that our criteria for the best algorithm have been the speed and the error at computing the norm of both connectivity kernels. The final parameters allow the computation of the kernel norms to an error of \( 10^{-5} \). Since (2.6) necessitates integral computations for each value of \( x \), we discretize the spatial domain into \( N \) intervals, i.e., \( x_n = Cn/N \) with \( n = 0, \ldots, N \). The sigmoidal transfer function has been chosen to be the logistic function \( S(V) = 10/(1 + \exp(-1.8(V - 3.0))) \).

According to section 4.2, global inhibitory feedback with delays can destabilize the equilibrium solution and induce periodic oscillations. In the simulation, we applied a single feedback delay with \( f(\tau) = \delta(\tau - \tau_0) \), i.e., \( E[\tau] = \tau_0 \) and \( \text{Var}[\tau] = 0 \), and chose a single transmission speed, i.e., \( g(v) = \delta(v - v_0) \). The function \( \Phi \) given in (4.12) now has the form
\[ \Phi(k) = \max \left\{ \alpha \hat{K}(k) + \beta \delta(k) / \rho, -\alpha \hat{K}_1(k)/v_0 - \beta \tau_0 \delta(k) / \gamma \right\}, \]
and will have a maximum at \( k^* = 0 \) if \( \beta \) and \( \tau_0 \) are sufficiently large. Therefore, as the equilibrium loses its stability, spatially constant oscillations emerge. Decreasing either \( \beta \) or \( \tau_0 \) will decrease the effect of global feedback, and the maximum of \( \Phi \) might jump to some \( k^* \neq 0 \), yielding a spatially nonhomogeneous bifurcation. Figure 3 illustrates a jump from constant
oscillations to traveling waves induced by changing the inhibitory feedback.

Figure 4 reveals further feedback effects on the stability of neural fields. For inhibitory feedback and vanishing feedback delay time $\tau_0$, there is a stationary Turing bifurcation for certain parameters (Figure 4, left panel). That is, the first term in (4.13) is larger than the second one. Now increasing the delay time $\tau_0$ makes the second term exceed the first term (since $\beta < 0$), which destabilizes the field towards an oscillatory bifurcation. Hence, by the special choice of the feedback kernel, global oscillations occur (Figure 4, right panel).

5.2. Distributed propagation speeds. Motivated by experimental findings [7, 16, 44] (see Figure 1), we model the distribution of propagation speeds by the (truncated) gamma family of densities

$$g(v) = \begin{cases} \frac{N_p q^p v^{p-1}}{\Gamma(p)} \exp(-v/q) & \text{if } v \in (v_l, v_h), \\ 0 & \text{otherwise}, \end{cases}$$

(5.2)
with parameters $p > 2$ and $q > 0$. The constant $N_{p,q}$ arises from the normalization condition (2.3) if one stipulates that $g$ should be zero outside some interval $v \in (v_l, v_h)$, where $v_l$ and $v_h$ are physiologically dictated lower and upper bounds for the possible propagation speeds. In the limit as $v_l \to 0$ and $v_h \to \infty$ one obtains the usual gamma density with $N_{p,q} = 1$. The maximum of $g(v)$ (i.e., the mode of the distribution) occurs at $v_m = q(p - 1)$. Figure 5 shows the shape of the (untruncated) distribution for various $p$ and some fixed value of $v_m$. Furthermore,

$$E[v^{-1}] = \frac{N_{p,q}}{N_{p-1,q}} \frac{1}{q(p-1)} = \frac{N_{p,q}}{N_{p-1,q}} \frac{1}{v_m},$$

$$E[v^{-2}] = \frac{N_{p,q}}{N_{p-2,q}} \frac{p-1}{p-2} \frac{1}{v_m^2},$$

$$\text{Var}[v^{-1}] = \frac{N_{p,q}}{v_m^2 N_{p-2,q} N_{p-1,q} (p-2)} \left( \frac{N_{p-1,q}^2 (p-1)}{N_{p,q} N_{p-2,q} (p-2)} \right).$$

Figure 6 shows the dependence of $E[1/v^2]$ and $\text{Var}[v^{-1}]$ on $v_m$ and $p$. For a fixed value of $v_m$, a fast decay to a constant value is observed by increasing $p$.

With this choice of $g$, we determine the phase speed $\omega/k$ of bifurcating waves from (4.14), where for simplicity we neglect feedback effects by setting $\beta = 0$. In Figure 7 the resulting phase speed is plotted with respect to the parameters $v_m$ and $p$ of the gamma-distribution. The phase speed is seen to be lower than $v_m$ for all $p$, which affirms causality, and shows accordance to previous results obtained for single transmission speeds [2, 10, 30]. Furthermore, for lower values of $p$ (broader speed distribution) the phase speed is smaller, an effect which is more significant at lower values of $p$. For the chosen parameter set, we calculate $\tilde{K}_2(k^*) < 0$; so, as mentioned in section 4.2, a broader transmission speed distribution yields a lower phase speed for traveling waves.
6. Traveling fronts. We now give an analysis of the effects of distributed propagation speeds and feedback delays on traveling fronts. Here, we take the function $S$ in (2.6) to be the Heaviside function $\Theta$ with a fixed firing threshold $u_0$. In addition, we take the external input $E$ to be zero, which introduces no loss of generality since a constant external input amounts to
shifting the firing threshold.\textsuperscript{2} For definiteness, we consider a first order temporal differential operator

\begin{equation}
L \left( \frac{\partial}{\partial t} \right) = \frac{\partial}{\partial t} + 1.
\end{equation}

Then the evolution equation (2.6) reads

\begin{equation}
\frac{\partial V(x, t)}{\partial t} = -V(x, t) + \int_0^\infty g(v) \int_{-\infty}^\infty K(x-y) \Theta(V(y, t - |x-y|/v) - u_0) dy dv
\end{equation}

\begin{equation}
+ \int_0^\infty f(\tau) \int_{-\infty}^\infty F(x-y) \Theta(V(y, t - \tau) - u_0) dy d\tau,
\end{equation}

where for simplicity of notation we have subsumed the scaling factors $\bar{\alpha}$ and $\bar{\beta}$ into the definitions of $K$ and $F$, respectively.

### 6.1. The stationary front solution

We switch to a frame moving with speed $c$ by the change of variables $V(x, t) = \bar{u}(x - ct) = \bar{u}(z)$, which transforms (6.2) into

\begin{equation}
\frac{d\bar{u}(z)}{dz} = \frac{1}{c} \bar{u}(x, t) - \frac{1}{c} \int_0^\infty g(v) \int_{-\infty}^\infty K(y) \Theta \left( u \left( z - y + \frac{c|y|}{v} \right) - u_0 \right) dy dv
\end{equation}

\begin{equation}
- \frac{1}{c} \int_0^\infty f(\tau) \int_{-\infty}^\infty F(y) \Theta(u(z - y + c\tau) - u_0) dy d\tau.
\end{equation}

The boundary conditions are set to $\lim_{z \to -\infty} \bar{u}(z) = u_\infty > 0$, $\lim_{z \to -\infty} \bar{u}(z) = 0$, and $\bar{u}(0) = u_0$, with $0 < u_0 < u_\infty$. A simple calculation yields $u_\infty = \eta_1 + \eta_2$, where $\eta_1 = \int_{-\infty}^\infty K(x) dx$ and $\eta_2 = \int_{-\infty}^\infty F(x) dx$. Then we obtain

\begin{equation}
z \geq 0 : \frac{d\bar{u}(z)}{dz} = \frac{1}{c} \bar{u}(z)
\end{equation}

\begin{equation}
z < 0 : \frac{d\bar{u}(z)}{dz} = \frac{1}{c} \bar{u}(z) - \frac{1}{c} \int_{v_k}^{v_h} g(v) \int_{\gamma_\pm z}^\infty K(y) dy dv - \frac{1}{c} \int_0^\infty f(\tau) \int_{x+ct}^\infty F(y) dy d\tau,
\end{equation}

with $\gamma_\pm = v/(v \pm c)$. It is not hard to check that (6.4) has finite solutions for $z \to \infty$, provided that

\begin{equation}
u_0 = \frac{\eta_1}{2} + \eta_2 - R(c\tau)
\end{equation}

\begin{equation}
- \int_0^\infty e^{-z'/c} E_g \left[ \gamma_- K(\gamma_- z') \right] dz' - \int_0^\infty e^{-z'/c} E_f \left[ F(z' + c\tau) \right] dz'
\end{equation}

holds with the antiderivative $R(x)$ of $F(x)$, i.e., $dR(x)/dx = F(x)$. Here we have used the expectation operators $E_g$ and $E_f$ with respect to the densities $g$ and $f$, namely

\begin{equation}
E_g[r] = \int_0^\infty g(v) r(v) dv, \quad E_f[r] = \int_0^\infty f(\tau) r(\tau) d\tau.
\end{equation}

\textsuperscript{2}A nonconstant input may yield additional effects, whose study would exceed the aim of the present work.
Figure 8. The traveling front speed $c$ for excitatory fields and vanishing feedback, plotted with respect to the parameters $v_m$ and $p$ of the transmission speed distribution. Further parameters are $a_e = 4$, $a_i = 0$, $u_0 = 0.01$, $v_l = 2$, $v_h = 50$, and $q = v_m/(p - 1)$.

The traveling front solution can now be explicitly calculated as

$$z \geq 0 : \tilde{u}(z) = \eta_1 + \eta_2 - E_g[W(\gamma - z)] - E_f[R(z + c\tau)]$$

$$- \int_{z}^{\infty} e^{(z - z')/c} E_g[\gamma - K(\gamma - z')] dz' - \int_{z}^{\infty} e^{(z - z')/c} E_f[F(z' + c\tau)] dz',$$

$$z < 0 : \tilde{u}(z) = \eta_1 + \eta_2 - E_g[W(\gamma + z)] - E_f[R(z + c\tau)]$$

$$- \int_{z}^{0} e^{(z - z')/c} E_g[\gamma + K(\gamma + z')] dz' - \int_{0}^{\infty} e^{(z - z')/c} E_g[\gamma + K(\gamma + z')] dz'$$

$$- \int_{0}^{\infty} e^{(z - z')/c} E_f[F(z' + c\tau)] dz',$$

where $W(x)$ is the antiderivative of $K(x)$, i.e., $dW(x)/dx = K(x)$.

Equation (6.5) implicitly defines the front speed $c$ in terms of the kernels $K$ and $F$, the threshold $u_0$, the transmission speed distribution $g(v)$, and the feedback delay distribution $f(\tau)$. To illustrate the dependence of the front speed on distributed delays, Figure 8 presents the solutions of (6.5) for the synaptic excitatory kernel taken from (5.1) and various speed distributions (5.2) for vanishing feedback delay. The relation of $c$ and $v_m$ shows accordance to previous results for single propagation speeds [27, 46]. In addition, for low values of $v_m$ an increase in the speed distribution width, i.e., a decrease of $p$, yields an increase in the front speed. In contrast, large values of $v_m$ yield a decreasing front speed for an increase of the speed distribution width, similar to the observations of sections 4.2 and 5 obtained under the assumption of large propagation speeds. Hence, the shape of the transmission speed distributions affects the front speed. A subtler effect is discovered when the front speed is plotted against the variance instead of the parameter $p$ (Figure 9). It is seen that the front speed can...
be maximized by a positive variance of speed distributions. This might indicate an interesting biological principle for maximizing signal propagation in fields of nonlocal interaction.

6.2. Stability of fronts. Considering small deviations $s(x - ct, t) = u(x, t) - \bar{u}(x - ct)$ from the stationary solution, (6.2) yields, in linear order in $s$, 

$$
-c \frac{\partial s(z,t)}{\partial z} + \frac{\partial s(z,t)}{\partial t} = -s(z,t) + \int_{-\infty}^{\infty} K(y) E_g \left[ \delta \left( \bar{u} \left( z - y + \frac{c|y|}{v} \right) - u_0 \right) s \left( z - y + \frac{c|y|}{v}, t - \frac{|y|}{v} \right) \right] dy
$$

(6.8) 

$$
+ \int_{-\infty}^{\infty} F(y) E_f \left[ \delta(\bar{u}(z - y + ct) - u_0) s(z - y + ct, t - \tau) \right] dy,
$$

where $\delta(x)$ denotes the Dirac delta distribution. Subsequently, we obtain 

$$
z > 0 : -c \frac{\partial s(z,t)}{\partial z} + \frac{\partial s(z,t)}{\partial t} = -s(z,t)
$$

(6.9) 

$$
+ E_g \left[ \frac{\gamma - K(\gamma - z)}{|\bar{u}'(0)|} s \left( 0, t - \frac{z}{v - c} \right) \right] + E_f \left[ \frac{F(z + ct)}{|\bar{u}'(0)|} s(0, t - \tau) \right],
$$

$$
z < 0 : -c \frac{\partial s(z,t)}{\partial z} + \frac{\partial s(z,t)}{\partial t} = -s(z,t)
$$

(6.10) 

$$
+ E_g \left[ \frac{\gamma + K(\gamma + z)}{|\bar{u}'(0)|} s \left( 0, t + \frac{z}{v + c} \right) \right] + E_f \left[ \frac{F(z + ct)}{|\bar{u}'(0)|} s(0, t - \tau) \right],
$$

with $\bar{u}'(0) = \partial \bar{u}/\partial z$ computed at $z = 0$. We observe that $s(z,t)$ is continuous but not continuously differentiable at $z = 0$, which results from the applied Heaviside function $\Theta$. 

Figure 9. The traveling front speed $c$ plotted against the mode $v_m$ and the variance $\text{Var}[1/v]$ of the speed distribution for excitatory fields and vanishing feedback. Parameter values are $a_e = 4$, $a_i = 0$, $u_0 = 0.01$, $v_l = 2$, $v_h = 50$, and $q = v_m/(p - 1)$.
Now inserting the ansatz \( s(z,t) = \phi(z)e^{\lambda t} \), we find

\[
\begin{align*}
    z > 0 : \quad & \frac{\partial \phi(z)}{\partial z} = \frac{1 + \lambda}{c} \phi(z) \\
    & \quad - E_g \left\{ \frac{\gamma_- K(\gamma_- z)}{|\hat{u}'(0)|c} e^{-z\lambda/(v-c)} \right\} \phi(0) - E_f \left\{ \frac{F(z + c\tau)}{|\hat{u}'(0)|c} e^{-\lambda \tau} \right\} \phi(0), \\
    z < 0 : \quad & \frac{\partial \phi(z)}{\partial z} = \frac{1 + \lambda}{c} \phi(z) \\
    & \quad - E_g \left\{ \frac{\gamma_+ K(\gamma_+ z)}{|\hat{u}'(0)|c} e^{z\lambda/(v+c)} \right\} \phi(0) - E_f \left\{ \frac{F(z + c\tau)}{|\hat{u}'(0)|c} e^{-\lambda \tau} \right\} \phi(0),
\end{align*}
\]

whose solutions are

\[
\begin{align*}
    z > 0 : \quad & \phi(z) = \phi(0)e^{(1+\lambda)z/c} \left( 1 - \frac{1}{|\hat{u}'(0)|c} \int_{0}^{z} E_g \left\{ \gamma_- e^{-z'(\gamma_- \lambda/v+(1+\lambda)/c)} F(z') \right\} dz' \right) \\
    & \quad - \frac{1}{|\hat{u}'(0)|c} \int_{0}^{z} E_f \left\{ e^{-\lambda \tau} e^{-z'(1+\lambda)/c} F(z' + c\tau) \right\} dz', \\
    z < 0 : \quad & \phi(z) = \phi(0)e^{(1+\lambda)z/c} \left( 1 + \frac{1}{|\hat{u}'(0)|c} \int_{0}^{0} E_g \left\{ \gamma_+ e^{-z'(\gamma_+ \lambda/v+(1+\lambda)/c)} K(z) \right\} dz' \right) \\
    & \quad + \frac{1}{|\hat{u}'(0)|c} \int_{0}^{0} E_f \left\{ e^{-\lambda \tau} e^{-z'(1+\lambda)/c} F(z' + c\tau) \right\} dz'.
\end{align*}
\]

(6.11) (6.12)

Here, we used the continuity of \( \phi(z) \) at \( z = 0 \), i.e., \( \lim_{z \to +0} \phi(z) = \lim_{z \to -0} \phi(z) = \phi(0) \).

Equations (6.11) and (6.12) are equivalent to the solutions found in [12] for traveling fronts involving a single transmission speed and without the constant feedback delay.

It can be seen that finite solutions \( \phi(z) \) exist for \( z \to \infty \), provided that the equation

\[
0 = 1 - \frac{1}{|\hat{u}'(0)|c} E_g \left[ L_0 \left( \frac{1 + \lambda}{c} - \frac{1}{v} \right) \right] \\
- \frac{1}{|\hat{u}'(0)|c} E_f \left[ e^{-\lambda \tau} \int_{0}^{\infty} e^{-z'(1+\lambda)/c} F(z' + c\tau) dz' \right]
\]

holds for \( \text{Re}(\lambda) > -1 \), while the solutions \( \phi(z) \) are finite for \( z \to -\infty \) if

\[
|\hat{u}'(0)|c = -E_g \left[ L_0 \left( -\frac{1 + \lambda}{c} - \frac{1}{v} \right) \right] - E_f \left[ e^{-\lambda \tau} \int_{0}^{\infty} e^{-z'(1+\lambda)/c} F(z' - c\tau) dz' \right]
\]

holds for \( \text{Re}(\lambda) \leq -1 \). Here, the symmetry of both kernels has been used implicitly. The equations (6.13) and (6.14) determine \( \lambda \) implicitly. We observe that \( \lambda = 0 \) represents a solution of (6.13), which reflects the translation symmetry of the moving fronts. Since (6.13) may yield \( \text{Re}(\lambda) > 0 \), it represents a stability condition of the stationary front. The foregoing analysis is equivalent to the method of Evans functions for nonlocal interactions [12, 33, 62], which has been used to obtain a single implicit condition, namely the Evans function, for determining the stability of the field in the absence of speed distributions and feedback delays.

A numerical simulation of the evolution equation (6.2) is presented in Figure 10. The
Figure 10. The simulated traveling front for excitatory fields, distributed transmission speeds, and vanishing feedback delay. Parameter values are $a_e = 1$, $a_i = 0$, $r = 0.5$, $u_0 = 0.1$, $v_m = 4$, $v_l = 2.5$, $v_h = 6$, $p = 3.15$, and $c = 1.97$.

Initial conditions are chosen as $V(x) = \bar{u}(x) + \Gamma(x)$, where $\Gamma(x) \in [-0.05, 0.05]$ is a uniformly distributed random variable and $\bar{u}(x)$ is given by (6.6)-(6.7). It turns out that the random activity is damped out, and the solution converges to the stationary front. In other words, the stationary front $\bar{u}(x)$ is stable for the chosen parameter values.

7. Conclusion. We have introduced transmission speed distributions and a nonlocal feedback loop with distributed delays into the standard neural field model, and studied the stability and bifurcations of spatially homogeneous equilibrium solutions, as well as traveling fronts. As expected, the relation between the connectivities and delays plays an important role in the analysis of bifurcations. We have investigated this relation for general field connectivities and feedback kernels as well as speed and feedback delay distributions. The results have significance in the context of understanding the basic mechanisms of neural activity, since distributed delays and speeds arise naturally in real neural systems. To the best of our knowledge, these effects have been neglected in the literature until now. For the numerical solution of the field equation, we have introduced a Monte-Carlo approach. In contrast to conventional integration procedures such as the trapezoidal rule [46], this approach allows the computation of the interaction integral with a divergent kernel. The numerical results illustrate the effects of nonlocal feedback and the corresponding delays, and confirm the analytical findings. Finally, we have examined stationary traveling fronts involving distributed speeds and feedback delays.

One of the highlights of the presented analysis is the different nature of the two delay sources, namely, the delays caused by the finite speed of signal transmission in the field, and the delays in the long-range feedback loop. The former delays vary continuously, depending on the distance between locations, and so are always distributed, even for a single transmission speed. This continuous dependence on distance interacts in a nontrivial way with the connectivity
kernel. On the other hand, the delays in the feedback loop have a simpler dependence on the feedback connectivity. The difference is made clear by the particular way the terms enter the dispersion relation (3.3). To overcome the analytical difficulties, we have considered in section 4 the case when the delays are not too large, and studied approximate models based on series expansion. The difference of the two delay types is still apparent in reduced models at all orders. For instance, the statement of Theorem 4.1 involves higher moments $\hat{K}_m$ of the field connectivity kernel, showing their intimate relation with the speed distribution, whereas the feedback terms contribute only by a simple Fourier transform $\hat{F}$. One can see the physical effects in a second-order approximate model studied in section 4.2. Because the feedback connectivity enters (4.13) only through $\hat{F}$ in both terms, its role essentially depends simply on the relative magnitudes of $\alpha$ and $\beta$, i.e., the relative strengths of field and feedback connectivities. In contrast, the field connectivity $K$ appears through $\hat{K}$ in the first term and $\hat{K}_1$ in the second. Since $\hat{K}_1$ emphasizes the role of distant interaction more, the role of the involved propagation delays is accentuated, which can facilitate oscillatory bifurcations. Based on similar arguments involving Fourier transforms, we have concluded that feedback connections with large variance tend to induce spatially homogeneous bifurcations, whereas general field connectivity kernels might favor spatially inhomogeneous bifurcations.

The presented study shows that distributed propagation speeds and feedback delays affect the speed of bifurcating waves and traveling fronts. The quantitative changes can be significant for sufficiently broad distributions; otherwise, they may be relatively small. The precise effects depend on the parameters of a particular biological application, which we do not further pursue here. More interestingly, one can observe qualitative changes by the introduction of distributions, such as obtaining a maximum front speed at a positive variance of the transmission speed distribution. (Whether this represents a biological optimization principle is a tempting conjecture beyond the purpose of the present paper.) Moreover, the stability analysis of stationary fronts involving distributed propagation speeds and feedback delays yields a stability condition, which represents the Evans function of the system.

The present work studies only a limited range of dynamical behavior. Nevertheless, the effects of delays are much richer in this setting of spatially extended systems with nonlocal interaction than in simple feedback systems with distributed delays considered in, e.g., [4]. Further research can be expected to discover other interesting features in more global dynamics away from equilibria, for instance, in the evoked response of the field as studied in [29], when distributed speeds and feedback loops are introduced into the model. Moreover, the existence and stability study of bumps [9, 38], spirals [36], or breathers [11, 19] in case of distributed propagation speeds and nonlocal feedback delays promises a wide range of novel phenomena and will yield new insight into neural information processing.

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