



environments (Eckert and Zeil, 2001). Flying predators must accurately track and predict the movement of prey animals along the ground to plan their pursuits and strikes (Kane and Zamani, 2014), while flocking and herding animals anticipate and rapidly respond to the movements of their neighbors to avoid collisions and stay together (Nagy et al., 2010; Torney et al., 2018). Often, conspecifics or objects are only intermittently seen by animals, requiring their velocity and position estimates to be made during the occlusion periods (O'Reilly et al., 2008). Such abilities suggest a normative account of the *apparent motion illusion* in which successive stationary flashes at different locations are perceived as a single moving object hidden from view between flashes (Ramachandran and Anstis, 1986). Voltage sensitive dye recordings from awake fixating monkeys observing such stimuli reveal an interaction of neural activity waves with external inputs suggesting early visual cortical activity helps represent perception of a moving object and its velocity (Chemla et al., 2019). This study also proposed a detailed computational model in which a suppressive wave of activity is generated by the second of two flashes, either explaining away the ambiguity of the first flash as possibly another object or representing the two flashes as a single moving object.

Here, we analyze a neural field description of the apparent motion illusion that relies on the entrainment of traveling activity wave solutions to a sequence of transient and localized stimulations. Neural fields model neuronal networks as a continuous and spatially-extended excitable medium described by nonlinear integro-differential equations allowing for direct analysis using methods adapted from nonlinear partial differential equations, such as reaction diffusion models (Bresslo, 2011). Such a framework is ideal as it allows analytical treatments of the local network mechanisms underlying emergent spatiotemporal patterned activity (Huang et al., 2004; Goulet & Ermentrout, 2011) and stimulus-behavior relationships commonly recorded in cognitive tasks (Bresslo & Webber, 2012; Kilpatrick, 2018; Erlhagen & Schöner, 2002). Traveling wave solutions can be identified explicitly in many instances (Pinto & Ermentrout, 2001; Coombes, 2005), as can their response to non-trivial stimuli (Folias & Bresslo, 2005; Ermentrout et al., 2010; Si, 1977). Our model incorporates a physiologically realistic form of negative feedback as short term synaptic depression, leading to an attenuation at the back of waves, producing traveling pulses (Kilpatrick & Bresslo, 2010c). We will solve for traveling waves and identify their response to flashing stimuli, interpreting the resulting dynamics as a stimulus motion percept. Such an approach allows for explicit and dynamical characterization of the conditions required to promote the apparent motion illusion across a range of potential stimulus types.

Our perturbative approach to studying how traveling waves respond to transient or weak stimuli specifically estimates how

a wave's position changes in response to inputs. Linear asymptotics and even weakly nonlinear analysis have been used previously to understand how perturbations in synaptic connectivity, input, or model parameters shape waves and patterns in neural field equations (Bresslo et al., 2003; Venkov et al., 2007; Bresslo, 2001; Coombes, 2005; Amari, 1977). Perturbative theories describing how waves transform inputs and synaptic weight heterogeneities into changes in position and speed have been used as a model of idiothetic position (i.e., where an animal is or what direction they are heading) (Zhang, 1996; Xie et al., 2002; Burak & Fiete, 2009). Weak inputs alter the dynamics enough to displace wave positions without substantially disrupting their shape, allowing for an accurate linear input-response theory (Kilpatrick & Ermentrout, 2012). Since our model incorporates nonlinear negative feedback, care must be taken in performing the asymptotic calculations to characterize the response to inputs (Kilpatrick & Bresslo, 2010d). In addition, we can study the differential effects of inputs to their

& Webber, 2012). We will move beyond these prior studies to consider the effects of transient and persistent inputs upon waves in networks subject to synaptic depression, and consider how such a model can represent visual motion encoding. Specifically, we consider the following integro-differential equation system:

Here, $u(x, t)$ and $q(x, t)$ denote the average normal-

continuity and appropriate boundary conditions depending on the direction ($\text{sign}(c)$) of travel. Before analyzing the case of moving fronts ($c \neq 0$), we examine the degenerate case of a standing wave solution with speed $c = 0$. In this case, Eq. (3b) reduces to a stationary equation, we have $\xi = x$, and the profile of synaptic efficacy is given by

Substituting into Eq. (3a), we see

so for a normalized ($\int_{\mathbb{R}} w(x) dx = 1$) and even ($w(-x) = w(x)$) weight function, we have $U(0) = \frac{1}{2}$, implying standing fronts only arise for a specific choice of the depression rate $\beta = \frac{1}{2\theta} - 1$ which perfectly balances the tendency of the active region to invade inactive regions with the rate of activity decay (Ermentrout and McLeod, 1993).

For forward moving fronts ($c > 0$), we solve Eq. (3b) with the boundary conditions $\lim_{\xi \rightarrow \infty} Q$

The self-consistency inequality ensuring the active region remains superthreshold then requires $\lim_{\xi \rightarrow -\infty} U(\xi) = \gamma > \theta$ or $1/(1 + \gamma) > \theta$ implying $\gamma < (1 - \theta)/\theta$. Decreasing γ below θ truncates the wave speed branches due to a global bifurcation resulting from the inability of the active region to self-sustain. Profiles are plotted in Fig. 1C, D.

On the other hand, if we assume $c < 0$ (retreating fronts), we can similarly find solutions for which the quiescent region invades the active region. We again solve Eq. (3b), with the same boundary conditions, but now having $c < 0$ implies

Again we substitute into Eq. (3a), enforce boundedness and the threshold condition $U(0) = \theta$. After integrating, we find a condition determining the speed of the front

and a formula for the activity variable of form

Speeds are plotted in Fig. 1A, B and example profile in Fig. 1E. Such fronts exist for sufficiently strong depression as bounded by the standing front condition $\gamma > (1 - 2\theta)/(2\theta)$ or $\gamma < 2$, but not too strong ($\gamma < (1 - \theta)/\theta$ or $\gamma > 2$). The speed formula above, corresponding to the red curve in Fig. 1A, shows that as $\gamma \rightarrow +\infty$ the front speed $c \rightarrow -\infty$, resulting in an infinitely rapidly retreating front corresponding to a quiescent state $U \equiv 0$. Retreating fronts can thus be annihilated by excessively strong synaptic depression. On the other hand, as $\gamma \rightarrow 2^-$, the speed c of retreat of the front decreases to zero, leading the stable branch of regressive fronts to join the unstable branch of advancing fronts in a saddle-node bifurcation.

The analysis presented in Fig. 1 builds on that of Kilpatrick and Bresslo (2010b) by examining the covariation of front speeds and bifurcations with the strength and timescale of adaptation, especially identifying the important role of regressive fronts in the bifurcation picture. Since spike rate adaptation is not included the model presented here, we have

piecewise linear equation. Enforcing the boundary conditions $\lim_{\xi \rightarrow \pm\infty} Q(\xi) = 1$, we obtain the solution

Substituting back into Eq. (6b), we find

which can be solved piecewise up to free constants that can be identified by enforcing continuity, boundedness, and boundary conditions. Notice in the limit

of different speeds. To derive an approximate equation for the time-dependent evolution of the wave position $\varepsilon\zeta(t)$ relative to the coordinate frame $\xi = x - ct$

This analysis would be easy to repeat for a retreating front. Based on our observations here, we expect that global stimuli would cause the front to push outward, so positive stimuli delay rather than advance the position of the front relative to the wave coordinate frame.

Taking the limit of no synaptic depression $\gamma \rightarrow 1^-$, we see we recover

$$\lim_{\gamma \rightarrow 1^-} t = \frac{c+1}{2} H(t - t_0) = \frac{H(t - t_0)}{2},$$

which was derived previously in Kilpatrick and Ermentrout (2012). Note well that because we are not considering persistent stimuli here, the dependence upon ξ on the right-hand-side of Eq. (13) does not come into effect and so it is straightforward to solve the equation by integration. As noted, spatially global stimuli perturb waves in ways that are not always well captured by linear theory, but more spatially localized stimuli have a more modest effect on wave position, which can also be captured well by our linear theory as we now show.

4.3 Pulse wave response

Traveling front solutions are unaffected by activity (I_u) perturbations behind their leading edge ($\xi < 0$) as demonstrated above. On the other hand, traveling pulses have both a front and back which can be perturbed by weak inputs. Moreover, spatially localized inputs that may model the position of a visual object interact with wave position in ways that depend on their width as well as strength. To better understand the dynamics of such interactions as a means of building a theory of visual object tracking, we begin by deriving the nullspace of the adjoint operator in the case of a traveling pulse. Taking a Heaviside nonlinearity in Eq. (12) we find

$$\begin{aligned} -\frac{1}{c} \frac{d}{d\xi} + \frac{d}{d\xi} = & \delta(\xi) \frac{(0)}{|v'(0)|} \cdot \left[\int_{\mathbb{R}} v(\xi - y) v(y) dy - \beta v(0) \right] \\ & + \delta(\xi + \Delta) \frac{(-\Delta)}{|v'(-\Delta)|} \cdot \left[\int_{\mathbb{R}} v(\xi + \Delta - y) v(y) dy - \beta v(-\Delta) \right], \end{aligned} \quad (16a)$$

$$c\tau_q \frac{dp}{d\xi} + p = [H(\xi + \Delta) - H(\xi)] \cdot \left[\int_{\mathbb{R}} w(\xi - y) v(y) dy - \beta p(\xi) \right], \quad (16b)$$

where again the right-hand-side of Eq. (16a) is singularized due to the derivative of the step nonlinearities $f(U(\xi) - \theta) = H(\xi + \Delta) - H(\xi)$ such that

$$\begin{aligned} \delta(\xi + \Delta) - \delta(\xi) &= \frac{d}{d\xi} [H(\xi + \Delta) - H(\xi)] \\ &= \frac{d}{d\xi} H(U(\xi) - \theta) = H'(U(\xi) - \theta) U'(\xi). \end{aligned}$$

Eq. (16a) has the form $c v'(\xi) + v(\xi) = A \delta(\xi) + B \delta(\xi + \Delta)$ suggesting the following ansatz $v(\xi) = \frac{1}{c} [A_0 H(\xi) e^{-\xi/c} + A_{-\Delta} H(\xi + \Delta) e^{-(\xi + \Delta)/c}]$ whose coefficients satisfy $7.28997868 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 10 \ 496.155303955 \ 7130 \text{GS127231.fim}$

Ignoring the trivial solution $A_0 = A_{-\Delta} = 0$ and fixing the first entry $A_0 = 1$, we may solve this singular equation by satisfying the second equation to find

so by defining $A_{-\Delta}$ as in Eq. (20) and $A = \begin{pmatrix} 1 \\ A_{-\Delta} \end{pmatrix}$, we find the one-dimensional nullspace of \mathcal{L}^* is spanned by $(v(\xi), p(\xi))^T$ where

To study the impact of spatially localized and temporally pulsatile stimuli on traveling pulses, we again use Eq. (13) to formulate an approximation to the phase advance of the pulse from an abrupt input at a single point in time,

Integrating against both perturbations of the neural activity of amplitude \bar{I}_u and synaptic efficacy of amplitude \bar{I}_q variables, we adjust the position x_0 of the stimulus relative to the pulse and see the approximation agrees well with numerical simulations (Fig. 4

that move at a fixed *natural* wavespeed. A wave's leading edge is interpreted as the visually encoded position of a moving object. When objects move at speeds other than the natural wavespeed, external stimulation must be able to shift the phase and/or increase the speed of the wave to appropriately encode

Consider the effect the input has upon the front at different displacements. When the front of the stimulus is ahead of the front's leading edge, but the active region of Eq. (26) still contains the front ($x_c t \in [0, x]$), only the part of the stimulus ahead of the front will be filtered by the adjoint nullspace, the same as before. Thus, only the portion of the stimulus ahead of or containing the leading edge of the front has any effect on the location of the leading edge of the pulse. Either a fixed point is reached, or the lag becomes larger than the width of the square stimulus and the impact of the stimulus on the front weakens further. We expect the front will then lose the opportunity to entrain to the stimulus at this point, implying entrainment generally must occur before the entire stimulus slips ahead of the leading edge. When solving for the corresponding fixed point of Eq. (24), this generates the stricter entrainment condition

Stability of the fixed point described by Eq. (25) can be determined in the same way as before showing it is stable.

Boundaries on entrainment for traveling pulses are determined similarly, except that the activity nullspace term has the form

$$y^* = \Delta_x - c \log \left[\frac{\varepsilon}{K + \varepsilon} \cdot \frac{e^{T_{\text{on}}} - e^{-\varepsilon T_{\text{on}}/K}}{e^{-\Delta_c T/c} - e^{-\varepsilon T_{\text{on}}/K}} \right]. \quad (30)$$

The denominator of the argument in the logarithm above is positive, and the solution is defined if $\Delta_c < \varepsilon \frac{T_{\text{on}}}{T} \frac{c}{K}$. Linearizing the map Eq. (29) and plugging in the solution Eq. (30), we find its stability is determined by the single eigenvalue $\lambda = \exp \left[\frac{\Delta_c T}{c} - \frac{T_{\text{on}}}{K} \right]$, so $\lambda \in (0, 1)$ if $\Delta_c < \varepsilon \frac{T_{\text{on}}}{T} \frac{c}{K}$, which implies that the fixed point defining periodic entrainment is stable whenever it exists.

Our theory is consistent with the result of numerical simulations of the response of traveling waves to periodic, moving, and flashing stimuli. Flashing stimuli that are sufficiently strong and that travel at a speed that is not too much faster than the natural wavespeed will entrain the traveling wave (Fig. 6A). Tracking the leading edges of these flash-forced traveling pulses reveals that the stimulus speeds up the wave while it is on, and the pulse speed relaxes to its natural value between flashes. Over time, the average speed of the forced solution matches that of the average speed $c + \Delta_c$ of the forcing stimulus. On the other hand, if (a) the distance traveled with each hop between flashes is too large or (b) the stimulus is too weak or short, then the pulse will not be sped up enough during the on phase of the period. As a result, the pulse will eventually lag further and further behind the forcing stimulus as time goes on (Fig. 6B). The combined necessity of having a forcing stimulus whose speed difference is not too large (Δ_c), whose magnitude is not too weak (ε), or whose on phase is not too short (T_{on}) is all contained in the entrainment boundary inequality $\Delta_c < \varepsilon \frac{T_{\text{on}}}{T} \frac{c}{K}$. Indeed,

we see that this boundary well approximates the boundary we can determine from numerical simulations (Fig. 6C).

Thus we find that the entrainment of neural activity waves in a model of sensory cortex can be described by a relatively accessible theory. Akin to results from past work on phase response theory, we find that stimuli whose speed is

The planar version of Eq. (1) involves convolving the integral over \mathbb{R}^2 , requiring radially symmetric weights $w(x - y) = w(r)$

direction (Pang et al., 2020) of waves. These response properties reflect a highly dynamic and spatiotemporal form of input processing in sensory cortices (Ermentrout & Kleinfeld, 2001; Muller et al., 2018). Disentangling the role of synaptic network architecture in spatiotemporal processing thus requires the analysis of dynamic and mechanistic neural network models that capture cortical complexity while still

fully capture the diversity of static and dynamic models of synaptic transmission and understand how these contribute to the filtering properties of traveling waves. Similar analyses could also be applied to planar neural field models, building

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