Stationary bumps in networks of spiking neurons

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Abstract

We examine the existence and stability of spatially localized "bumps" of neuronal activity in a network of spiking neurons. Bumps have been proposed in mechanisms

Funahashi *et al.* (1989) . The net ork is bistable ith the bump and the "all–off" state both being stable. Note that the neurons are not intrinsically bistable as in Camperi & Wang (1998) and the bump solutions do not arise from a Turing–Hopf instability like that studied by Bressloff & Coombes (1998) and Bressloff *et al.* (1999), i.e. there is no continuous path in parameter space connecting a bump and the all–off state. A time–stationary solution is one hich corresponds to asynchronous firing of neurons here the firing rate is constant at each spatial point but the rate depends on spatial location. We sho that the activity profile of the bumps of our model are the same as that of a corresponding population rate model.

Ho ever, bumps predicted by the rate model to be stable may in fact be unstable in a model hich includes the spiking dynamics of the neurons. The rate model implicitly assumes asynchronous firing and only considers the dynamics of the firing rate. As the synaptic decay time is increased in the spiking net ork the bump can lose stability as a result of temporal correlation or "partial synchronization" of neurons involved in the bump. If the initial conditions are symmetric then this synchronization causes the input to the neurons to drop belo the threshold required to keep it firing, leading to cessation of oscillation of the neurons and consequently the rest of the bump. Ho ever, for generic initial conditions or ith the inclusion of noise, the bump destabilizes to a traveling ave. For fast enough synapses, the ave cannot exist. If some heterogeneity in the intrinsic properties of the neuron is included then the bump can be "pinned" to a fixed location; the traveling ave does not form and the bump loses stability to the all-off state.

This instability provides a mechanism for the termination of a bump, as ould be required at the end of a memory task (e.g. the delayed saccade task discussed by Colby *et al.* (1995)): if many of the neurons involved in the bump can be caused to fire approximately simultaneously, and the synaptic time scale is short, there ill not be enough input after this coincident firing to sustain activity and the net ork ill s itch to the all-off state.

2 Neuron model

We consider a net ork of N integrate–and–fire neurons hose voltages, v_i, obey the differential equations

$$\frac{dv_i}{dt} = I_i - v_i + \sum_{j,m} \frac{J_{ij}}{N} \alpha(t - t_j^m) - \sum_l \delta(t - t_i^l), \tag{1}$$

here the subscript i indexes the neurons, t_j^m is the mth firing of neuron j, defined by the times that $v_j(t)$ crosses the threshold hich e have set to 1, I_i is the input current applied to neuron i, and $\delta(\cdot)$ is the Dirac delta function, hich resets the voltage to zero. The function $\alpha(t)$ is a post-synaptic current and is nonzero only for $t > 0$. The connection eight bet een neuron i and neuron j is J_{ij}. The sum over m and l extend over the entire firing history of the neurons in the net ork and the sum over j extends over the net ork. Each time the voltage crosses the threshold from belo the neuron is said to "fire". The voltage then immediately resets to $v_i = 0$ and a synaptic pulse $\alpha(t)$ is sent to all connected neurons.

In our examination of bump solutions e ill consider subthreshold input ($I_i < 1$) and a eight matrix that is translationally invariant (i.e. J_{ij} only depends on $|i - j|$). It is of the lateral inhibition form (i.e. locally excitatory but distally inhibitory); this type of connectivity matrix can be sho n to arise from a multi–layer net ork ith both inhibitory and excitatory populations if the inhibition is fast, as sho n by Ermentrout (1998).

We can formally integrate Eq. (1) to obtain the spike response form (Gerstner, 1995; Gerstner *et al.*, 1996; Cho , 1998). This form ill allo us to relate the bump profile for the integrate–and–fire net ork to the profile of a rate model similar to that studied by Amari (1977). Suppose that neuron i has fired in the past at times t_i^l, here $l = 0, -1, -2, \ldots, -\infty$. The neuron most recently fired at t_i^0. We consider the dynamics for $t > t_i^0$. Integrating Eq. (1) yields

$$v_i(t) = I_i(1 - e^{-(t-t_i^0)}) + \sum_{j,m} \frac{J_{ij}}{N} \int_{t_i^0}^{t} e^{s-t} \alpha(s - t_j^m)\, ds, \tag{2}$$

By breaking up the integral in (2) into t o pieces e obtain

$v_i(t) = I_i(1-e$ E Eq E c $-\infty$

The parameter β affects the rate at hich the post–synaptic current decays. Noise is added to the net ork as current pulses to each neuron of the form

$$I_{\mathrm{rand}}(t) = 6(e^{-10t} - e^{-15t})$$

 here $t \geq 0$. The arrival times of these pulses have a Poisson distribution ith mean frequency 0.05 and there is no correlation bet een pulse arrival times for different neurons.

3 Existence of the bump state

We examine the existence of bump solutions to the spike response system described by (4). A bump solution is spatially localized ith spatially dependent average firing rate of the participating neurons. The firing rate is zero outside the bump and rises from zero at the edges to a maximum in the center. The firing times of the neurons are uncorrelated, so the bump is a localized patch of incoherent or asynchronous firing. The state coexists ith the homogeneous non–firing (all–off) state.

It is convenient to define the activity of neuron i as

$$A_i(t) = \sum_l \delta(t - t_i^l), \tag{9}$$

 here the sum over l is over all past firing times. Our activity differs from the population activity of Gerstner (1995) hich considers the activity of an infinite pool of neurons at a given spatial location. We can then re rite the synaptic input (5) in terms of the activity as

$$u_i(t) = \sum_j \frac{J_{ij}}{N} \int_0^\infty \epsilon(s) A_j(t-s)\ ds \tag{10}$$

Consider stationary asynchronous solutions to the spike response equations. Many authors have studied the spatially homogeneous asynchronous state ith various coupling schemes (Abbott and van Vrees ijk, 1993; Treves, 1993; Gerstner, 1995, 1998, 2000). Our approach is similar to that of Gerstner (1995, 1998, 2000). We first re rite the activity as

$$A_i(t) = A_i^0 + \Delta A_i(t), \tag{11}$$

 here

$$A_i^0 = \lim_{\tau\to\infty} \frac{1}{\tau} \int_0^\tau A_i(r) dr. \tag{12}$$

Substituting (9) into (12) then yields $A_i^0 = \lim_{\tau\to\infty} n(\tau)/\tau$, here $n(\tau)$ is the number of times neuron i fired in the time interval τ. Thus, A_i^0 is the mean firing rate of neuron i.

We no insert (11) into (10) to obtain $u_i(t) = u_i^0 + \Delta u_i(t)$ here

$$u_i^0 = \sum_j \frac{J_{ij}}{N} A_j^0, \tag{13}$$

and

$$\Delta u_i(t) = \sum_j \frac{J_{ij}}{N} \int_0^\infty \epsilon(s) \Delta A_j(t-s) ds \tag{14}$$

(recall that $\int_0^\infty \epsilon(s)\, ds = 1$). We define the asynchronous state to be one here $\Delta u_i(t)$ is zero in the limit of infinite net ork size N. In the asynchronous state the input to neuron i is a constant and given by u_i^0. This implies that the firing times of the neurons are uncorrelated. For a finite system, $\Delta u(t)$ ill contribute fluctuations hich scale as $N^{-1/2}$.

We no derive the self-consistent equations for the asynchronous state. Substitute $u_i(t) = u_i^0$ into (4); the local firing period $(A_i^0)^{-1}$ ill be given by

$$v_i((A_i^0)^{-1} + s, s) = 1 = I_i - [I_i + u_i^0]e^{-(A_i^0)^{-1}} + u_i^0. \tag{15}$$

Solving (15) yields

$$A_i^0 = G[u_i^0] \tag{16}$$

 here

$$G[z] = \begin{cases} 0, & z \leq 1 - I \\ -1/\ln\left[\frac{I+z-1}{I+z}\right], & z > 1 - I \end{cases} \tag{17}$$

(A plot of $G[z]$ can be seen in Fig. 2.) This form is similar to the usual neural net ork rate equation, (e.g. Amari, 1977; Kishimoto & Amari, 1979; Hansel & Sompolinsky, 1998; Ermentrout, 1998) except that the gain function e have derived is a result of the intrinsic neuronal dynamics of our model (Gerstner, 1995). Combining (13) and (16) e obtain the condition for a stationary asynchronous solution

$$u_i^0 = \sum_j \frac{J_{ij}}{N} G[u_j^0], \tag{18}$$

For a finite sized system, the time averaged firing rate of the neurons follo s a profile given by $A_j^0 = G[u_j^0]$.

We first consider mean-field solutions to (18). We assume that $u_i^0 = u^0$, $I_i = I$ and $\sum J_{ij}/N = J$ yielding

$$u^0 = JG[u^0] \tag{19}$$

If $I > 1$ (oscillatory neurons), then there are no solutions if J is too large and one solution if J is small enough. For $I < 1$ (excitatory neurons), (19) has one solution at $u_0 = 0$ if J is too small and t o solutions if J is large enough (See Fig. 2, hich sho s the case $J = 2$). These t o states correspond to an 'all-off' state and an 'all-on' state respectively.

3.1 Bump State

In order for a bump to exist, a solution to (18) for u_i^0 must be found such that $u_i^0 + I_i$ is above threshold ($u_i^0 + I_i > 1$) in a localized region of space. We sho example figures of such solutions in Figs. 3 and 4. Amari (1977) and Kishimoto & Amari (1979) proved that such a solution can exist for a class of gain functions $G[z]$. Similar to the mean field solution, e find that for subthreshold input ($I_i < 1$), the all-off state al ays exists and the bump state can exist if the eight function has enough excitation. We ill discuss stability of the bump in Sec. 4. Stability ill be affected by the synaptic time scale, the eight function, the amount of applied current and the size of the net ork. For a finite sized system, e sho in Appendix A that the individual neurons in a bump do not fire ith a fixed spatially dependent period. These finite sized fluctuations act as a source of noise.

As noted by Gerstner (1995, 1998), the spike response model can be connected to classical neural net ork or population rate models (Wilson and Co an, 1972; Amari, 1977; Hopfield, 1984). If e choose $\epsilon(s) = e^{-s}$, hich is true for $\alpha(t) = \delta(t)$, and assume near synchronous firing so that $A_i(t) \simeq G[u_i(t)]$, then by differentiating (10) ith respect to time e obtain:

$$\frac{d}{dt}u_i(t) = -u_i(t) + \sum_j J_{ij}G[u_j(t)] \tag{20}$$

This is the classical neural net ork or population rate model. Amit and Tsodyks (1991), Gerstner (1995) and Shriki *et al.* (

bump, this computation is quite involved. Instead, e infer the conditions for stability of the bump from a stability analysis of the homogeneous asynchronous state of the spike response model and confirm our conjectures ith numerical simulations.

Stability of the bump state has previously been examined in a first order rate model. Amari (1977) and Kishimoto & Amari (1979) found for saturating gain functions, that the stability of the bump in the rate model depended on a relationship bet een the eight function and the applied current. Hansel & Sompolinsky (1998) find the stability constraints for a model ith a simplifi of neurons can be activated by noise, but they cannot persist if β is too large.

We conjecture that the loss of stability in the bump for large β is due to a loss of stability of the asynchronous bump state due to the synchronizing tendency of the neurons ith fast excitatory coupling as is seen in the homogeneous net ork. Integrate-and-fire neurons belong to hat is kno n as Type I or Class I neurons (Hansel *et al.*, 1995; Ermentrout, 1996). It is kno n that for Type I neurons, fast excitation has a synchronizing tendency hereas slo excitation has a desynchronizing tendency (Van Vrees ijk *et al.*, 1994; Gerstner, 1995; Hansel *et al.*, 1995). Cho (

of the fluctuations in the input due to the finite number of neurons and the synchronizing dynamical effect. The termination of the bump as β is increased is not due to this overall decrease in by a corresponding population rate model. Ho ever, hen the synapses occur on a fast time scale, bumps can no longer be sustained in the net ork. They either lose stability to traveling aves or completely s itch off. We also find that heterogeneity or disorder can pin the bumps to a single location and keep them from andering. We conjecture that the loss of stability of the bump is due to partial synchronization bet een the neurons. It is kno n for homogeneous net orks of Type 1 neurons that fast excitatory synapses have a synchronizing tendency. We use this instability to turn off bumps ith a brief excitatory stimulus to partially synchronize the neurons.

For the net ork sizes that e have probed, e have found that bumps can be sustained by synapses ith decay rates as fast as three to four times the firing rate of the fastest neurons in the bump. If e consider neurons in the cortex to be firing at approximately 40 Hz this ould correspond to synaptic decay times of the order of 5 to 10 ms hich is not unreasonable. Results ith conductance-based neurons have found that the synaptic time scale can be sped up to ell ithin the AMPA range and still sustain a bump state (Gutkin *et al.*, 2000). We also find that as the net ork size increases, the bump may tolerate faster synapses. While the stability of the bump depends crucially on the synaptic time scale, the activity profile of the bump depends only on the connection eights and the gain function. Thus, it may be possible to make predictions on the connectivity patterns of experimental cortical systems from the firing rates of the neurons ithin the bump and the firing rate (F-I) curve of individual neurons.

If these recurrent bumps are involved in orking memory tasks then our results lead to some experimental predictions. For example if it is possible to pharmacologically speed up the excitatory excitations in the cortex, bump formation and hence orking memory may be perturbed. A brief applied stimulus applied to the cortical area here the orking memory is thought to be held may also disrupt a orking memory task.

Among other authors ho have produced similar ork are Hansel & Sompolinsky (1998), Bressloff *et al.* (1999) and Compte *et al.* (1999). Hansel & Sompolinsky (1998) consider a rate model similar to that studied by Amari (1977) and Kishimoto & Amari (1979), using a piece–ise linear gain function (our $G[z]$) and retaining only the first t o Fourier components of the eight function J, hich allo s them to make analytic predictions about the transitions bet een different types of behavior. They also sho the existence of a bump in a net ork of conductance–based model neurons and sho that bumps can follo ing moving spatially–localized current stimulations, a feature that may be relevant for head–direction systems such as those studied by Redish *at al.* (1996) and Zhang (1996).

Bressloff & Coombes (1998) and Bressloff *et al.* (1999) study pattern formation in a net ork of coupled integrate–and–fire neurons, but their systems consider suprathreshold input ($I_i > 1$) so that the all–off state is not a solution. They find that by increasing the coupling eight bet een neurons the spatially–uniform synchronized state (all neurons behave identically) becomes unstable through a Turing–Hopf bifurcation, leading to spatial patterns similar to those sho n in Fig. 4. They find bistability bet een a bump and a spatially–uniform synchronized state, hereas e find bistability bet een a bump and the all–off state. This difference is crucial if the system is to be thought of as modeling orking memory as investigated by, among others, Colby *et al.* (1995) and Funahashi *et al.* (1989).

Compte *et al.* (1999), have demonstrated the existence of a bump attractor in a t o-layer net ork of excitatory and inhibitory integrate–and–fire neurons. Their net ork involves strong excitation and inhibition in a balanced state. It is possible that a corresponding rate model could be found for this net ork to obtain the shape of the profile. They ere also able to s itch the bump off and on ith an excitatory stimulus. Ho ever, it is believed that their s itching off mechanism is due to the inhib

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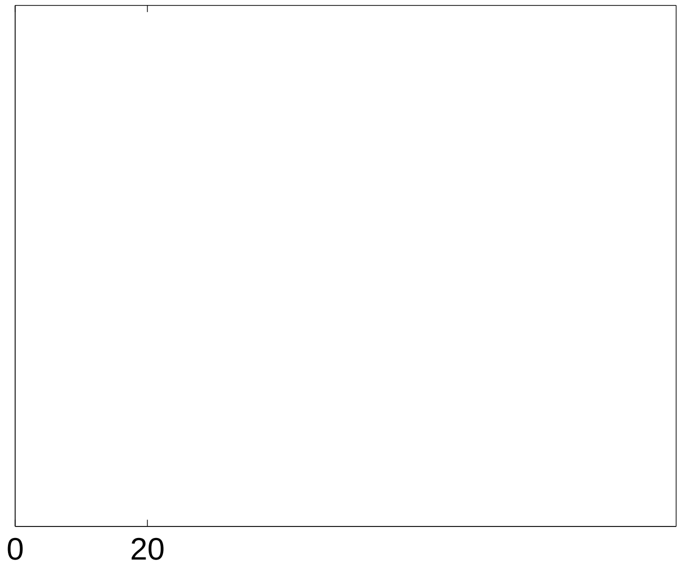
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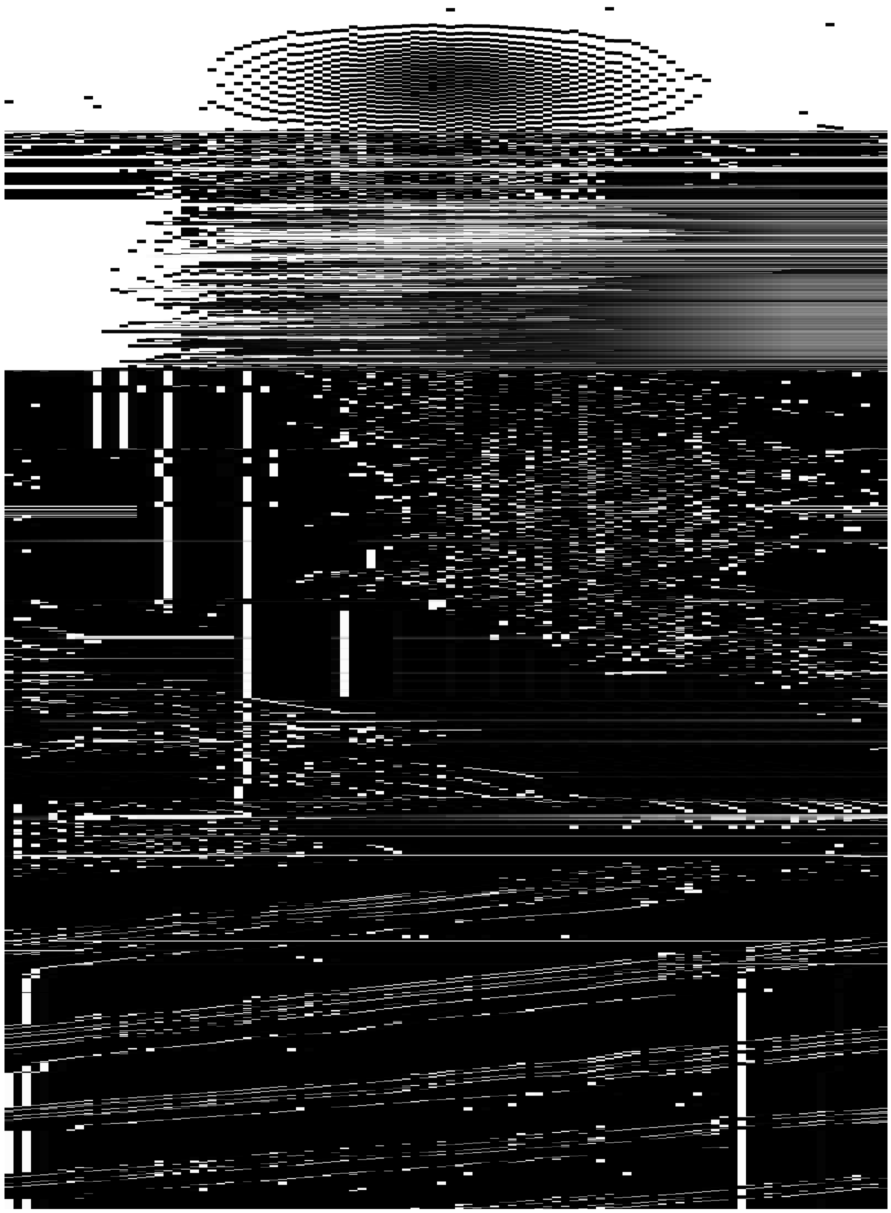

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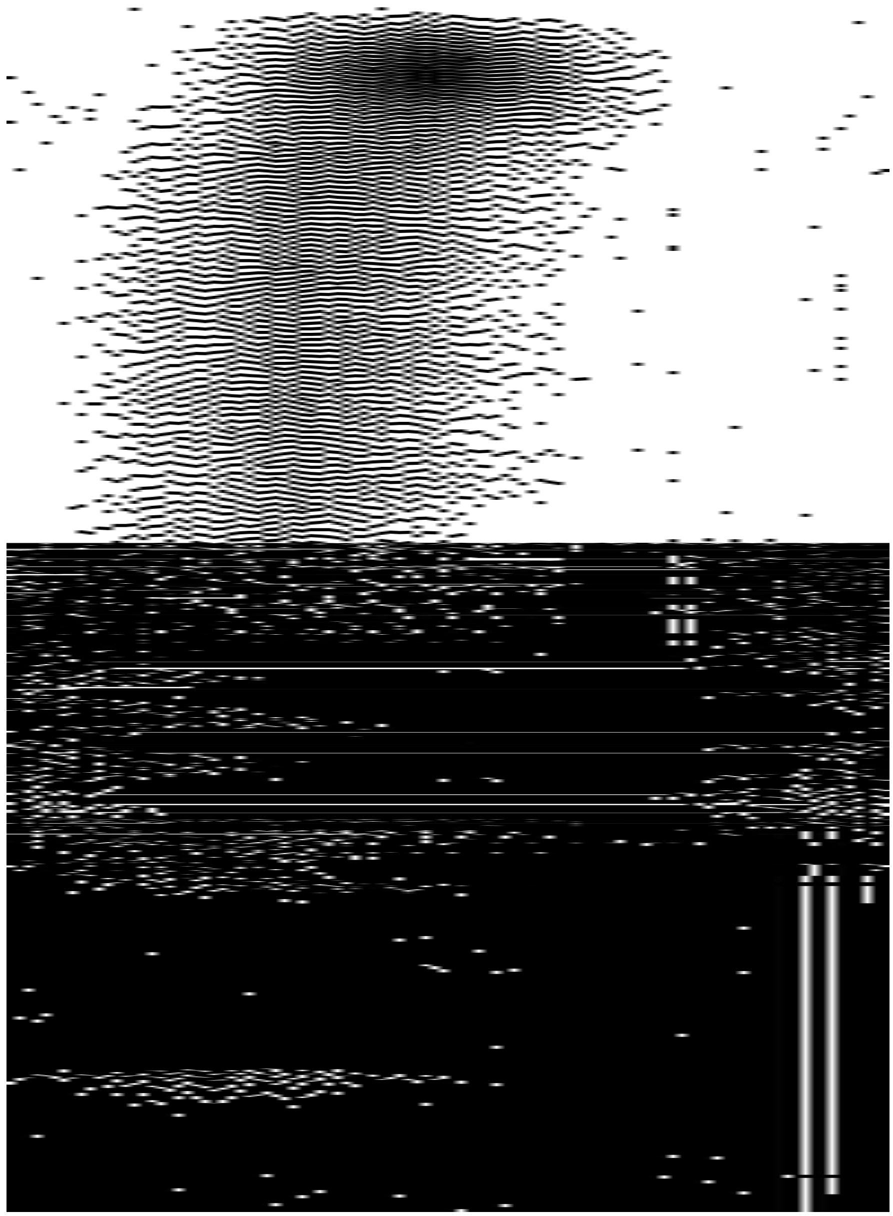

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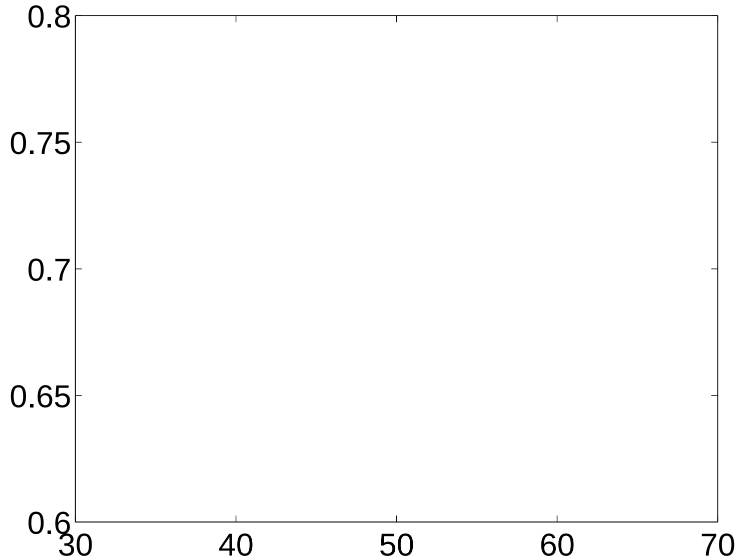
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