Reliable Storage and Recall of Aperiodic Spatiotemporal Activity Patterns Using Scaffolded Attractors

M. Furqan Afzal and Ali A. Minai, *Senior Member, IEEE*

Abstract—**Spatiotemporal patterns of neural activity have increasingly come to be seen as important for encoding information in the nervous system, motivating the development of various neurocomputational models. In this paper, we present a simple recurrent neural network model motivated by the need to understand the basis of voluntary motor control.**

For a given individual, any specific voluntary movement is ultimately encoded as an aperiodic spatiotemporal pattern of activation across a set of muscles, and presumably in spinal and cortical, motor neurons. Over time, such patterns can become stereotypical for the individual, and determine the "style" of specific movements – e.g., how they walk or write an "A". Experimental studies also indicate that these activity patterns may themselves be constructed as linear combinations of a few fixed spatiotemporal basis patterns of activity called motor synergies. For this to work, it is essential that neural systems be able to represent spatiotemporal activity patterns that are stimulus-specific, aperiodic (i.e., not rhythmic), transient (i.e., lasting only briefly), and robust (i.e., at least somewhat tolerant of errors and noise). The model we describe achieves this by using the dynamics of a recurrent neural network with two classes of primary neurons: Fast neurons that rapidly identify the patterns to be produced based on the stimulus and set up a "scaffolding" for it; and slow neurons that eventually instantiate the relevant spatiotemporal activity pattern. We show that this minimal system exhibits many of the properties needed for the flexible construction of complex, aperiodic movements.

I. INTRODUCTION

The representation of perceptual, cognitive, and behavioral states in the nervous system is based on patterns of activity across populations of neurons in various regions. However, there is a lot of variety within this general framework, with representational mechanisms ranging from feature detectors in the sensory cortices and grid cells in the entorhinal cortex to population codes in the motor system. It is also clear that all representations must be fundamentally dynamical in nature, and even persistent patterns such as the attractors thought to underlie associative memory [1], [2], [3], [4] must, at best, be only metastable [5], [6], [7], [8], [9]. Neurons are known to encode information at multiple levels from single spikes and bursts to modulated patterns of spiking, and theories of large-scale brain function are based increasingly on the assumption of dynamic spatiotemporal activity patterns rather than static feature codes or fixed-point attractors. [10], [11], [12], [13], [14], [15].

M. Furqan Afzal (Email: afzalmn@mail.uc.edu) and Ali A. Minai (Email: Ali.Minai@uc.edu) are both with the Department of Electrical Engineering and Computing Systems, University of Cincinnati, Cincinnati OH 45221

In many cases, the requirement is to produce relatively short (200-300 ms) patterns of activity across a neural population such that specific neural groups within the population become active and inactive at particular phases of the overall pattern. To be useful, such patterns must meet some basic criteria:

1) It should be possible to associate the patterns with specific stimuli, and for these stimuli to reliably elicit the correct patterns.
2) Sufficiently similar stimuli – e.g., noisy versions of a nominal stimulus – should elicit the same response pattern.
3) Significantly different stimuli should elicit significantly different response patterns.
4) The recall of the patterns should be somewhat robust against noise in the system.

It may also be required that the recalled patterns depend not only on the stimulus but also on prior states of the system [14], though this need not always be the case. Ultimately, the goal is for the neural system to learn a specific set of *robust and repeatable transients*, which poses a prima facie dilemma: How can a transient be made robust? In this paper, we demonstrate a very simple model based on a modification of the standard attractor network models used for associative memory [4]. This model uses an approach termed *scaffolded attractors*, where transient spatiotemporal patterns are stabilized by using metastable fixed point attractors as scaffolding. To make the model concrete, we relate it specifically to the problem of modeling voluntary motor tasks such as writing or drawing.

II. BACKGROUND

All movement in vertebrates requires the activation of groups of muscles in specific temporal patterns. This muscle activity is triggered by input from motor neurons in the spinal cord, which are, in turn, driven by afferents from the motor cortex and somatosensory feedback through muscle spindles. This implies the existence of specific spatiotemporal activity patterns in the spinal cord motor pools and the motor cortex. Much of the work on neurocomputational models of motor control has focused on rhythmic movements such as swimming, walking, finger tapping, etc [16], [17], [18], [19], but most voluntary movements involve *aperiodic* and *transient* muscle activity. Thus, the challenge in explaining the underlying control signals is to model how a neural substrate can reliably and robustly generate aperiodic, transient patterns of spatiotemporal activity in response to specific

stimuli. While such activity has been studied at the muscle [20], [21], [22], [23] and cortical [24], [25], [26], [27], [28] levels, modeling the underlying neural dynamics has received less attention.

One important clue to how non-rhythmic voluntary movements may be constructed comes from extensive experimental studies indicating that animals build complex movements through combination of a pre-defined set of canonical patterns of activity across specific muscle groups [29], [20], [21], [22], [23]. These patterns – called *motor synergies* – thus serve as a basis set for the construction of movement [21], [20], [23], [30]. The neural basis of motor synergies remains poorly understood [31], [32], though some models have been proposed [33], [34]. However, it is reasonable to hypothesize that motor synergies correspond to spatiotemporal patterns of activity across motor neurons in the spinal cord and the motor cortex, and that such patterns represent the "natural dynamics" of the neural networks involved. Indeed, it has been proposed that a wide variety of mental functions could be seen as arising from the interaction of such "neural synergies" at multiple hierarchical levels [35], [36]. This resonates with the view of the brain-body system as a complex adaptive system, where complex patterns of perception, cognition and action emerge from the self-organized coordination of modular canonical patterns [37], [10], [19]. Experimental data on the cortical representations of sequential actions [38] and complex canonical actions [28] also suggests the existence of a synergy hierarchy.

The work by Graziano and colleagues [24], [25], [27], [28] is especially relevant to the proposed model. It showed that stimulating localized regions of the motor cortex and several surrounding areas in macaques resulted in the production of stereotypical complex and non-repeating movements such as bringing a hand to the mouth or raising a hand above the head. Since these movements obviously require spatiotemporal patterns of activation in muscles, spinal cord motor neurons and, presumably, motor cortex neurons, it is reasonable to see the process as one where a particular stimulus elicits a transient spatiotemporal activity pattern in a neural population in a repeatable way. This is exactly what the proposed model does. To make this concrete, the modeled system's output is read as a *population code* for movement direction – as is well-known to occur in the motor cortex [39], [40]. Each output neuron in the system is assumed to be tuned to movement in a particular direction. The output is read as a vector combination of neural tuning directions weighted by the activities. As a result, each spatiotemporal pattern produced by the system represents a trajectory in 2-dimensional space, and is visualized as writing (or drawing doodles) on a 2-dimensional surface. This also links the current model to more detailed models of writing and drawing [41], [42].

The view of motor control underlying the model is also related to the issue of "style". Almost every movement in an individual is characterized by distinctive – and often clearly recognizable – details that represent that individual's style,

e.g., a handwriting, a way of walking, specific hand gestures, etc. This is easily explained within the framework of synergies: The motor synergies used by the individual form the basis of their style, and differences between individuals reflect differences in their motor synergy repertoire. Since synergies represent long-lasting, reliably repeatable neural and muscle activity patterns, an individual's style is both consistent and relatively fixed.

While motivated in part by the motor system, the model presented in this paper addresses a more abstract function: How to reliably generate stimulus-dependent, robust and transient spatiotemporal activity patterns in a neural population. This issue too has received some attention, though most of it has focused on the generation of activity sequences, where a neural network goes through a succession of states with previous states generating subsequent ones [43], [44], [45], [46], [47]. The model presented here is concerned with generating more integrated spatiotemporal patterns, where different neurons (or neuron groups) become active at different phases of the overall pattern, and remain active only for a certain period before subsiding. The same neuron or neural group can be activated multiple times within the pattern, and the activity of different neurons can overlap, making it more difficult to see this as a sequence (though that is theoretically possible).

Another approach to understanding spatiotemporal activity patterns in neural systems is that of dynamic neural fields [48], [49]. However, here, the focus is typically on large scale activity patterns in 2-dimensional neural layers, which can be very useful for modeling many cognitive functions. The proposed model focuses on producing aperiodic transients in a neural population. It shares many features with previous models developed for both the production and decoding of spatiotemporal activity patterns [5], [50], [14], [15], but these tend to be more complex – especially in their use of spiking neurons and real-time synaptic modulation. While both these features are biologically important and plausible, our goal is to develop a simpler model that illustrates a principle, and is potentially suitable for use in computational applications and hardware implementations. To fully capture the phenomenology of spatiotemporal dynamics in the nervous system, this model will require significant extensions, which will be addressed in future work.

III. Neural Network Model

A. Model Description

The model described in this paper achieves robust representation of aperiodic transient activity patterns using the dynamics of a one-layer continuous-time recurrent neural network with two classes of primary neurons:

- *Fast neurons*, that rapidly identify the patterns to be produced based on the stimulus and set up a "scaffolding" for it.
- *Slow neurons*, that are gradually activated by the fast neurons and other slow neurons, and instantiate the relevant spatiotemporal activity pattern.

The sets of fast and slow neurons are denoted by FN and SN, respectively. There are n_f fast neurons and n_s slow neurons in the network, giving a total of $n = n_f + n_s$ neurons. The equations governing the activity of a fast neuron i are given by:

$$\frac{dv_i}{dt} = \frac{1}{\tau_i}\left(-qv_i + e\sum_{j\in FN} w_{ij}u_j + f\sum_{k\in SN} w_{ik}u_k - \alpha z_i\right) + I_i \tag{1}$$

$$\frac{dz_i}{dt} = \frac{-z_i}{a_i} + \frac{\sum_{j\in SN} u_j}{b_i} \tag{2}$$

The equations for slow neuron i are:

$$\frac{dv_i}{dt} = \frac{1}{\tau_i}\left(-qv_i + g\sum_{j\in FN} w_{ij}u_j + h\sum_{k\in SN} w_{ik}u_k - \alpha z_i\right) \tag{3}$$

$$\frac{dz_i}{dt} = \frac{-z_i}{a_i} + \frac{u_i}{b_i} \tag{4}$$

The output of neuron i from either class is calculated as:

$$u_i = f(v_i) = \frac{1}{1 + e^{-\beta(v_i - \mu)}} \tag{5}$$

In these equations, v_i represents the activity of neuron i, u_i is a nonlinear transformation of this activity representing the output of neuron i, z_i is a deactivation variable that controls how rapidly a neuron can be activated and how long it can remain active, τ_i is the time constant for the activity dynamics of a particular neuron and q is a gain parameter for v_i. External input, I_i, is provided only to the fast neurons. Though the duration of this input can vary in principle, the simulations in the current work involve providing the input only at the initiation of a trial. Thus, it is used to set the initial state of the fast neurons, after which the network activity evolves autonomously. The network's output is taken to be the output vector of the slow neurons, i.e., the fast neurons do not contribute directly to the system's output. The parameters a_i and b_i are charging and discharging time constants for z_i, respectively, e and f are gain parameters controlling the influence of recurrent inputs from fast and slow neurons, respectively, on fast neuron i, and g and h are the corresponding gain parameters for slow neuron i. The parameter α is a gain for the deactivation of all the neurons after they have fired for a certain amount of time. It should be noted that the total slow neuron activity has an inhibitory effect on fast neurons via the z_i variables of the latter.

The recurrent weights for the network are assumed to be symmetric, and are calculated using a covariance Hebbian learning rule [51], [52] to embed N_A attractor patterns in the network. Each attractor pattern $y^k = [y_1^k \; y_2^k \; ... \; y_n^k]$ specifies an 'active' (1) or 'inactive' (0) state for all the fast and slow neurons. The rule for embedding the attractors is:

$$w_{ij} = \langle (y_i^k - \langle y_i \rangle)(y_j^k - \langle y_j \rangle)\rangle_k \tag{6}$$

where $\langle . \rangle$ represents a sample mean.

It is assumed that the number of fast neurons is significantly less than the number of slow neurons. The main difference between fast and slow neurons is in their response time. Fast neurons have a lower value of τ and respond faster, reaching their equilibrium values quickly in response to an external stimulus. The slow neurons depend on input from the fast neurons for their activity. They have larger and more varied values of τ, which means that they are slower to become activated even if their nominal state in the attractor is active.

When a stimulus is presented briefly to the fast neurons, they respond rapidly, recovering their portion of one of the stored attractors by correcting any errors in the stimulus. This begins to activate slow neurons based on two factors: Whether a particular slow neuron is designated to be active in the current attractor, and its activation time constant. Thus, the activity of the fast neurons acts as a *scaffolding* to activate the appropriate slow neurons at appropriate times. Once a sufficient number of slow neurons are activated, the cumulative inhibition signal from slow to fast neurons turns off the latter, thus removing the scaffolding and allowing the slow neuron activity to develop on its own. The time constants of the deactivation variable and α then control the duration of activity for each slow neuron, generating a unique and repeatable spatiotemporal activity pattern.

IV. SIMULATIONS AND RESULTS

A. Intrinsic Neuronal Behavior

A spatiotemporal activity pattern over a population of neurons ultimately involves controlling the phase and duration of activity for the individual neurons. Thus, before considering the behavior of the network, it is useful to consider how the dynamics of the slow neurons can be modulated by various parameters. To do this, the original equation for neuronal activity (v) is modified in the following way:

$$\frac{dv_i}{dt} = \frac{1}{\tau_i}(-qv_i + \gamma I(t) - \alpha z_i) \tag{7}$$

The recurrent input terms in Eq. (1) and Eq. (3) are replaced by a simple square wave input $\gamma I(t)$, with γ controlling the magnitude of excitation to the neuron. The equations for u and z remain the same as before. The simulations are run for 1000 time steps to demonstrate the effect of varying α and γ on the dynamics of u, v and z when the neuron is stimulated with a square wave pulse of unit height and duration from time step 100 to 400.

Increase in α increases the effect of deactivation and the neuron remains active for less time (Figure 1). With rise in γ, the neuron experiences greater excitation. Thus, it turns on quickly and remains active for a longer time (Figure 2). Thus, in the presence of a simple input, the activation phase and duty cycle of a single neuron can be modulated through several parameters. In a full network, some of these parameters would be modulated by the state of the system or external control inputs, thus creating a flexible and context-dependent mechanism for controlling the phase and duration of activity for each neuron. Since the purpose of the current study is only to demonstrate the basic capabilities

of the model, we keep it simple by using fixed (but possibly random) values for parameters.
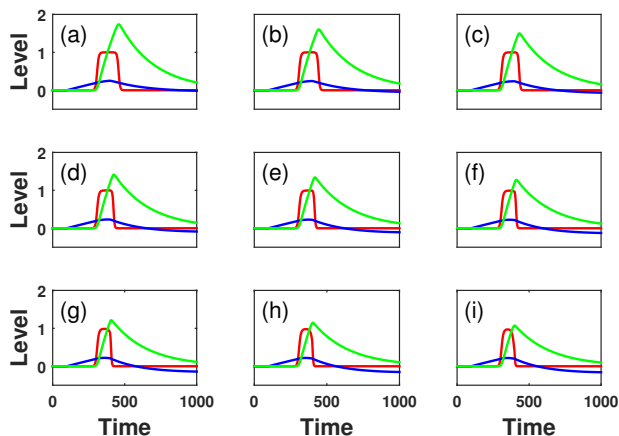

Fig. 1: Single neuron dynamics with α modulation: red, blue and green curves represent u, v and z respectively. (a) $\alpha =$ 1; (b) 1.25; (c) 1.5; (d) 1.75; (e) 2; (f) 2.25; (g) 2.5; (h) 2.75; (i) 3
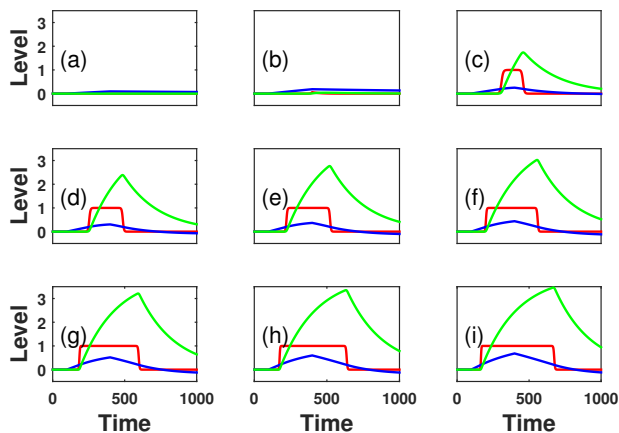

Fig. 2: Single neuron dynamics with γ modulation: red, blue and green curves represent u, v and z respectively. (a) $\gamma =$ 0.66; (b) 1.33; (c) 2; (d) 2.66; (e) 3.33; (f) 4; (g) 4.66; (h) 5.33; (i) 6

B. Network Behavior

The simulations reported in this paper all use networks with $n = 200$ neurons, of which $n_f = 50$ are fast and $n_s = 150$ are slow neurons. The τ value for all fast neurons is set to 1.5, whereas slow neurons have random τ values in the interval [5,15]. The values β and μ in the nonlinear output function $f(\ )$ are set to 40 and 0.2, respectively. The a and b parameters for the fast neurons are set to random values in the interval (0,0.5]. The a and b parameters for the slow neurons are set to random values in the intervals (0,5] and (0,0.5], respectively. Finally, α is set to 1.2 for slow neurons and 1.5 for fast neurons.

The weights between neurons are calculated by a covariance rule as shown in Eq. (6). In this equation, y_i^k represents the value of neuron i in the attractor pattern k.

Five distinct binary-valued attractors, $y^k = [y_1^k \ y_2^k \ ... \ y_n^k]$, $y_j^k \in \{0,1\}$, $k = 1,...,5$, are embedded in the system. Each of these binary patterns can be divided into the pattern for the fast neurons and that for the slow neurons, referred to as the *fast neuron component* (FNC) and *slow neuron component* (SNC), respectively. However, these binary patterns only define *which* neurons are to be active or inactive in each attractor. The *spatiotemporal attractors* arise from the interaction between this specification and the natural dynamics of the network. To obtain these, the network is stimulated with the FNC for each attractor and the resulting spatiotemporal pattern across the slow neurons is observed. This pattern, termed the *ideal spatiotemporal output* (ISO) for each attractor is regarded as the desired output pattern for the corresponding attractors, and is used in assessing the quality of recall. It is denoted as: $x^k(t) = [x_1^k(t) \ x_2^k(t) \ ... \ x_{n_s}^k(t)]$, $x_j^k(t) \in [0,1]$, $k = 1,...,5$. It should be noted that: a) The pattern is defined only over the slow neurons; and b) It is a time-dependent pattern, unlike the corresponding nominal attractor specification. The ISO patterns for the five attractors are shown in Figure 3. As described earlier, the fast neurons turn on quickly for a short duration and then shut off once slow neuronactivity becomes sufficiently strong.

The input to the network is a noisy version of one of the attractors stored in the fast neurons. The noise level in the input is parameterized by a positive value ϕ – termed the *input error* – and is produced by setting the jth component of the input as:

$$I_j = y_j^k - \phi c_j(2y_j^k - 1) \qquad (8)$$

where k denotes the index of the attractor and c_j is a uniform random number between 0 and 1. Thus, 1-bits in the attractor are decremented by random amounts and 0-bits are randomly incremented. The input is applied to the fast neurons by setting their initial states to the corresponding input values. The slow neurons are all initialized to an activity level of 0.

In addition to the input error, the outputs of all neurons are also subject to additive uniform noise at every time step, so that the actual output of neuron j becomes $\hat{u}_j(t) = u_j(t) + \delta_j(t)$, where δ_j is a uniform random number between $-\eta$ and η. Thus, η parameterizes the level of ongoing noise in the system.

The system is evaluated for performance at two levels: a) Whether all those – and only those – slow neurons designated for activity in a target attractor actually become active in the spatiotemporal pattern (albeit at different times); and b) Whether the recalled slow neuron spatiotemporal activity pattern corresponds to the one obtained under conditions of no input error and no noise.

The first of these is evaluated using two metrics: 1) *Sensitivity* – the degree to which all the designated slow
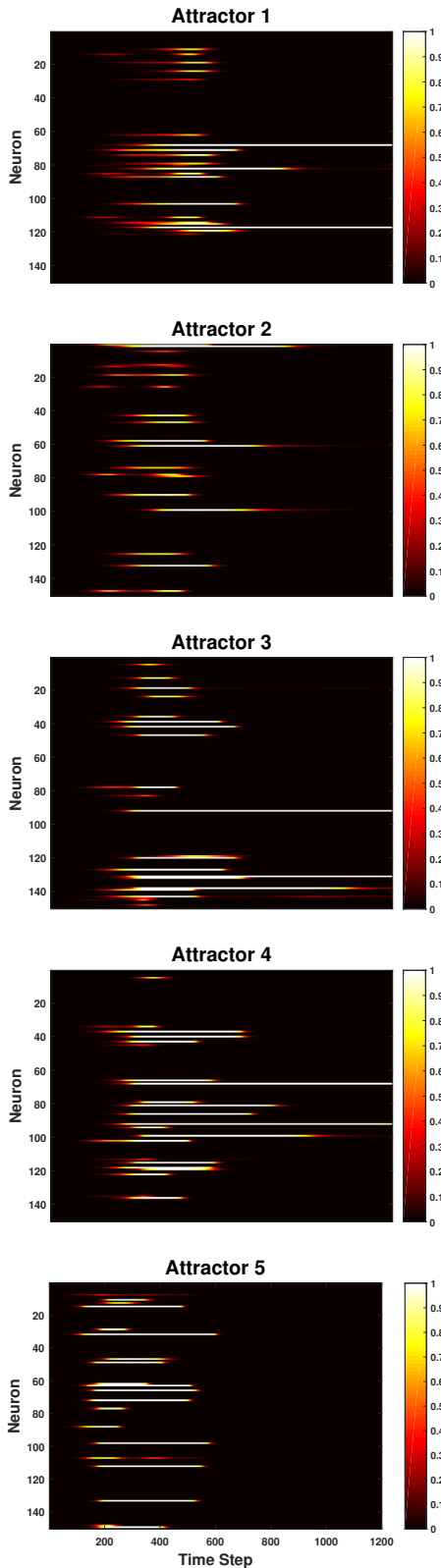
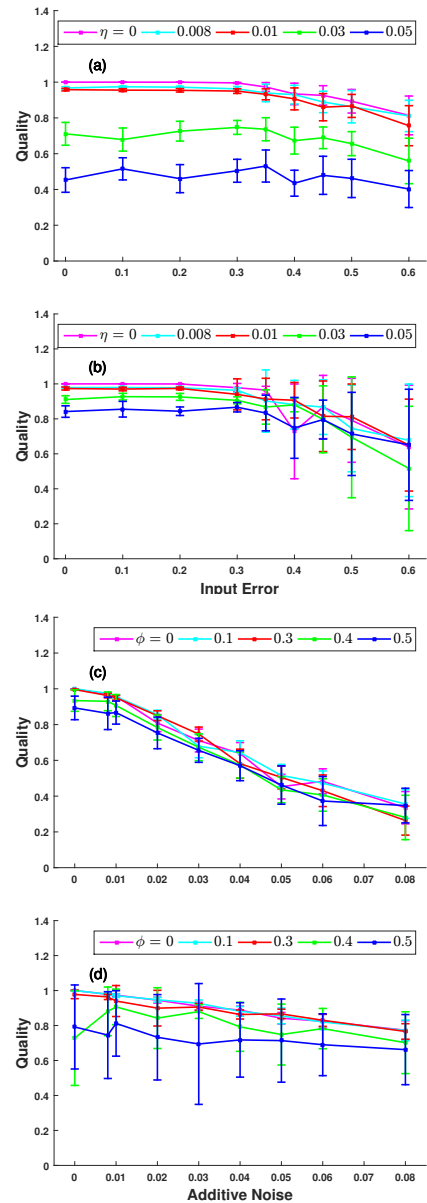Fig. 3: Attractors 1 through 5 in the absence of noise or error.

Fig. 4: (a) Mean recall quality vs input error at different additive noise levels, h=2.5; (b) Mean recall quality vs input error at different additive noise levels, h=12; (c) Mean recall quality vs additive noise at different input error levels, h=2.5; (d) Mean recall quality vs additive noise at different input error levels, h=12. 50 % connectivity in all cases.

neurons actually become active at some point during the spatiotemporal pattern recalled under the error, no noise situation; 2) *Specificity* – the degree to which neurons designated for inactivity remain inactive in the recalled spatiotemporal pattern under no error, no noise conditions. Systematic simulations for various recurrent gain and slow network connectivity values showed that only slow network connectivities greater than 50% and recurrent gains, h, greater than around 2.5 give sensitivity and specificity greater than 0.9. Thus, connectivities of $50 - 100\%$ and two gain
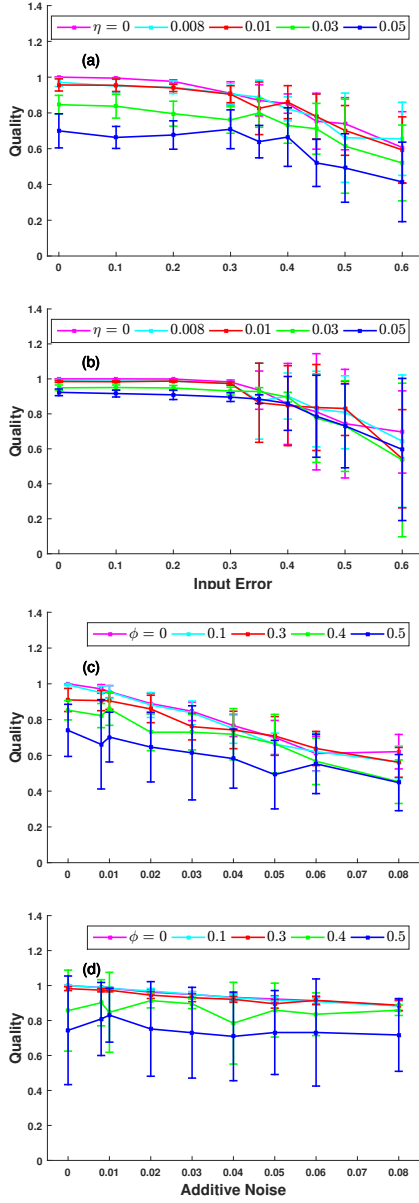
Fig. 5: (a) Mean recall quality vs input error at different additive noise levels, h=2.5; (b) Mean recall quality vs input error at different additive noise levels, h=12; (c) Mean recall quality vs additive noise at different input error levels, h=2.5; (d) Mean recall quality vs additive noise at different input error levels, h=12. 100 % connectivity in all cases.

levels of 2.5 and 12 (signifying low and high gain levels) are chosen for the subsequent recall stability simulations.

The system's recall accuracy is quantified by *mean attractor similarity*, M, which is defined as a measure of the similarity of the recalled activity pattern to the attractor in the presence of different types of noise. It is given by:

$$M = \frac{\sum_i \langle u_i \rangle_t \, r_i}{\sum_i \langle u_i \rangle_t}; \; i \; \in \; SN \qquad (9)$$

Here, r_i gives the Pearson correlation coefficient between $u_i(t)$ and $\hat{u}_i(t)$, where $\hat{u}_i$ denotes the output of neuron i in the noisy case and u_i is its output in the noise-free case. Time t ranges over the entire 1200-step time interval from the point of stimulus application to the end of the cycle. Recall quality is measured only over the slow neurons, since they represent the attractor's output activity pattern. It ranges between -1 and 1, with 1 representing perfect recall including the exact temporal phases, and -1 indicating recall of the complementary pattern.

Both ϕ and η are varied systematically to measure the robustness of the system. Figures 4 and 5 show the mean recall quality for all the attractors plotted against ϕ for different levels of η, for connectivity levels of 50 and 100% and gain values of 2.5 and 12. Each plot is averaged over 15 independent trials. It can be seen that the recall quality improves drastically with a high gain value, and also increases somewhat with increasing connectivity, although this increase is not linear. Both these facts show that attractor dynamics in the slow network plays a significant role in the robustness of the recall. At full connectivity and high gain value, the system has a noise handling capacity of around $5-6\%$ which is quite high. Similarly, the system can tolerate an error level of more than 0.3.
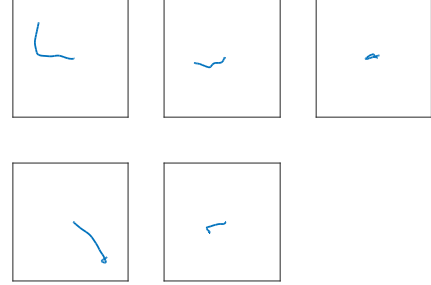

Fig. 6: Doodles generated by the 5 attractors.

C. Visualization through Motor Response

Given the motivation of the model by the motor system, the response patterns generated are visualized by turning them into observable movement trajectories in space. In particular, the activity of the slow neurons is mapped onto the 2-dimensional X-Y plane by considering each neuron, i, as coding movement in a fixed preferred direction, θ_i, which is chosen randomly with a uniform distribution between 0 and 2π. The instantaneous direction of movement coded by a specific pattern of slow neuron activity is given by:

$$X(t) = \sum_{i \in SN} u_i(t) cos\theta_i \qquad (10)$$

$$Y(t) = \sum_{i \in SN} u_i(t) sin\theta_i \qquad (11)$$

The resulting trajectory is seen as a "doodle" generated due to the spatiotemporal activity in the network, and is plot-

ted in the X-Y-plane. Different attractors generate distinct doodles, as shown in Figure 6.

The robustness of the recalled patterns can be evaluated in a concrete way by comparing the doodles generated at various levels of input error, ϕ, and additive noise, η, with those generated in the error- and noise-free case. Figure 7 shows what happens to the doodle for Attractor 1 as ϕ is varied from 0 to 0.6. The figure remains robust through a level of $\phi = 0.3$, but changes dramatically thereafter. Results for changes in η show a similar pattern of robustness up to a threshold level (not shown).
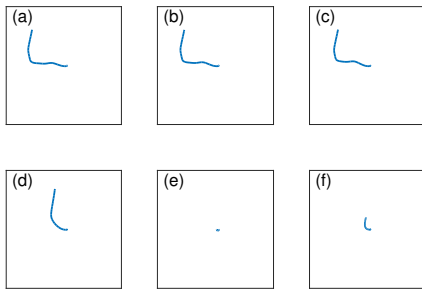

Fig. 7: Change in the doodle for Attractor 1 due to different levels of input error, ϕ: (a) $\phi = 0$; (b) 0.1; (c) 0.2; (d) 0.4; (e) 0.5; (f) 0.6

As discussed earlier, the forms of the spatiotemporal patterns produced by the system can be modified systematically through several parameters. This is especially important in the motor system because minor and systematic variations of movements – such as writing specific characters – is observed in practice, and is often useful. The modulation also provides a potential control mechanism by which trajectories can be modified in predictable ways to avoid obstacles or to satisfy constraints. A global way to modulate the spatiotemporal output in the proposed system is to vary the deactivation gain, α. Figure 8 shows the effect of increasing slow neuron α from a value of 0.8 to 2 in the case of Attractor 1. It is interesting to note that increased deactivation does not cause a drastic change in the resulting doodle's shape, but causes it to lose some of its features gradually.

Other parameters (α,τ,a,b) can be varied systematically – some globally and others in neuron-specific ways – to produce different types of doodles. In particular, we suggest that one or both of the parameters a and b can be modulated in pattern-specific ways.

As discussed earlier, the patterns encoded by the model can be seen as representing a repertoire of canonical *movement primitives* as suggested by experimental studies. Multiple networks encoding a set of such patterns can be triggered in combination to generate patterns that interpolate between these basis movements. Figure 9 shows the doodles drawn by combining the activity patterns of Attractors 4 and 1 in different proportions. Clearly, there is a pattern of interpola-
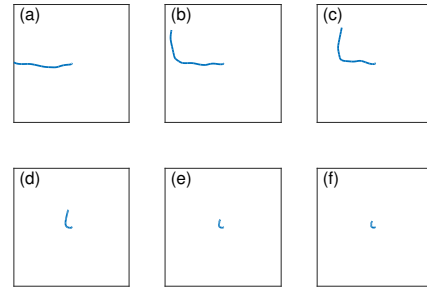

Fig. 8: Modulation of the doodle for Attractor 1 due to different values of deactivation gain, α: (a) $\alpha = 0.8$; (b) 1; (c) 1.2 (nominal case); (d) 1.5; (e) 1.8; (f) 2

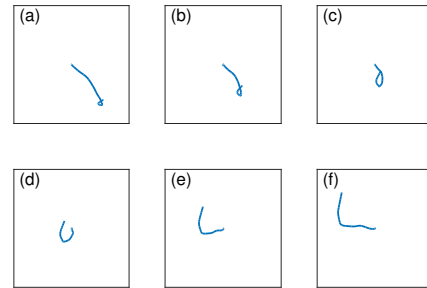tion. Similar results are seen for other combinations, which are not shown for lack of space.

Fig. 9: Interpolation between doodles by the combined activation of Attractors 4 and 1, combined with weights ψ and $1 - \psi$, respectively: (a) $\psi = 1$; (b) 0.8; (c) 0.6; (d) 0.4; (e) 0.2; (f) 0

V. Conclusion

This paper has described a recurrent neural network model that can store spatiotemporal activity patterns and recall them robustly in response to specific stimuli. The patterns can be seen as encoding temporal responses, such as voluntary movements mediated by motor synergies. The utility of the system is demonstrated by mapping its output to doodling movements through population coding. The patterns encoded by the model can be seen as representing a repertoire of canonical movement primitives as suggested by experimental studies. Such movement primitives can be combined to produce more complex or interpolated movements. The patterns can also be modulated systematically through several parameters that can serve as a locus for learning and real-time adaptation. Future work will explore these possibilities, as well as the use of these extended models to understand high-level behaviors such as writing by imitation, and to understand the basis of motor disorders.

References

[1] D. Marr, "Simple memory: a theory for archicortex," *Phil. Trans. Royal Soc. London*, vol. 262, pp. 23–81, 1971.

[2] J. J. Hopfield, "Neural networks and physical systems with emergent collective computational abilities," *Proceedings of the National Academy of Sciences USA*, vol. 79, pp. 2554–2558, 1982.

[3] ——, "Neurons with graded response have collective computational properties like those of two-state neurons," *Proceedings of the National Academy of Sciences USA*, vol. 81, pp. 3088–3092, 1984.

[4] D. Amit, *Modelling Brain Function*. Cambridge, UK: Cambridge University Press, 1989.

[5] M. Rabinovich, A. Volkovskii, P. Lecanda, R. Huerta, H. D. I. Abarbanel, and G. Laurent, "Dynamical encoding by networks of competing neuron groups: winnerless competition," *Physical Review Letters*, vol. 87, pp. 068 102–1, 2001.

[6] A. A. Minai, L. R. Iyer, D. Padur, and S. Doboli, "A dynamic connectionist model of idea generation," in *Proceedings of IJCNN 2009*, 2009, pp. 2109–2116.

[7] L. R. Iyer, S. Doboli, A. A. Minai, V. R. Brown, D. S. Levine, and P. B. Paulus, "Neural dynamics of idea generation and the effects of priming," *Neural Networks*, vol. 22, pp. 674–686, 2009.

[8] N. Marupaka and A. A. Minai, "Connectivity and creativity in semantic neural networks," in *Proceedings of IJCNN 2011*, 2011, pp. 3127–3133.

[9] N. Marupaka, L. R. Iyer, and A. A. Minai, "Connectivity and thought: The influence of semantic network structure in a neurodynamical model of thinking," *Neural Networks*, vol. 32, pp. 147–158, 2012.

[10] J. A. S. Kelso, *Dynamic Patterns: The Self-Organization of Brain and Behavior*. Cambridge, MA: MIT Press, 1995.

[11] F. Varela, J. P. Lachaux, E. Rodriguez, and J. Martinerie, "The brainweb: phase synchronization and large-scale integration," *Nature Reviews Neuroscience*, vol. 2, pp. 229–239, 2001.

[12] A. K. Engel, P. Fries, and W. Singer, "Dynamic predictions: oscillations and synchrony in top-down processing," *Nature Reviews Neuroscience*, vol. 2, pp. 704–716, 2001.

[13] S. L. Bressler and E. Tognoli, "Operational principles of neurocognitive networks," *International Journal of Psychophysiology*, vol. 60, pp. 139–148, 2006.

[14] D. V. Buonomano and W. Maass, "State-dependent computations: Spatiotemporal processing in cortical networks," *Nature Reviews—Neuroscience*, vol. 10, pp. 113–125, 2009.

[15] J. K. Liu and D. V. Buonomano, "Embedding multiple trajectories in simulated recurrent neural networks in a self-organizing manner," *The Journal of Neuroscience*, vol. 29, p. 1317213181, 2009.

[16] H. Haken, J. A. S. Kelso, and H. Bunz, "A theoretical model of phase transitions in human hand movements," *Biological Cybernetics*, vol. 51, pp. 347–356, 1985.

[17] G. Orlovsky, T. Deliagina, and S. Grillner, *Neuronal Control of Locomotion:From Mollusc to Man*. Oxford University Press, Oxford, UK, 1999.

[18] S. Grillner, "Biological pattern generation: the cellular and computational logic of networks in motion," *Neuron*, vol. 52, pp. 751–766, 2006.

[19] A. J. Ijspeert, A. Crespi, D. Ryczko, and J. M. Cabelguen, "From swimming to walking with a salamander robot driven by a spinal cord model," *Science*, vol. 315, pp. 1416–1420, 2007.

[20] A. d'Avella, P. Saltiel, and E. Bizzi, "Combinations of muscle synergies in the construction of natural motor behavior," *Nature Neuroscience*, vol. 6, pp. 300–308, 2003.

[21] M. Tresch, P. Salitel, and E. Bizzi, "The construction of movement by the spinal cord," *Nature Neuroscience*, vol. 2, pp. 162–167, 1999.

[22] E. Bizzi, V. Cheung, A. d'Avella, P. Salitel, and M. Tresch, "Combining modules for movement," *Brain Research Reviews*, vol. 57, pp. 125–133, 2007.

[23] L. Ting and J. Macpherson, "A limited set of muscle synergies for force control during a postural task," *Journal of Neurophysiology*, vol. 93, pp. 609–613, 2005.

[24] T. A. Aflalo and M. S. A. Graziano, "Possible origins of the complex topographic organization of motor cortex: reduction of a multidimensional space onto a two-dimensional array," *Journal of Neuroscience*, vol. 26, pp. 6288–6297, 2006.

[25] M. S. A. Graziano and T. A. Aflalo, "Mapping behavioral repertoire onto the cortex," *Neuron*, vol. 56, pp. 239–251, 2007.

[26] P. Cisek, "Cortical mechanisms of action selection: the affordance competition hypothesis," *Phil. Trans. R. Soc. B*, vol. 362, pp. 1585–1599, 2007.

[27] T. A. Aflalo and M. S. A. Graziano, "Four-dimensional spatial reasoning in humans," *Journal of Experimental Psychology: Human Perception and Performance*, vol. 34, pp. 1066–1077, 2008.

[28] M. Graziano, *The Intelligent Movement Machine: An Ethological Perspective on the Primate Motor System*. Oxford University Press, Oxford, UK, 2009.

[29] F. Mussa-Ivaldi, "A. modular features of motor control and learning," *Curr.Opin. Neurobiol*, vol. 9, pp. 713–717, 1999.

[30] S. Muceli, A. Boye, A. d'Avella, and D. Farina, "identifying representative synergy matrices for describing muscular activation patterns during multidirectional reaching in the horizontal plane," *Journal of Neurophysiology*, vol. 103, pp. 1532–1542, 2010.

[31] M. Tresch and A. Jarc, "The case for and against muscle synergies," *Current Opinion in Neurobiology*, vol. 19, pp. 601–607, 2009.

[32] M. Riley, N. Kuznetsov, and S. Bonnette, "State-, parameter-, and graph-dynamics: Constraints and the distillation of postural control systems," *Science & Motricite*, vol. 74, pp. 5–18, 2011.

[33] K. V. Byadarhaly, M. Perdoor, and A. A. Minai, "A neural model of motor synergies," in *Proceedings of IJCNN 2011*, 2011, pp. 2961–2968.

[34] K. Byadarhaly, M. Perdoor, and A. Minai, "A modular neural model of motor synergies," *Neural Networks*, vol. 32, pp. 96–108, 2012.

[35] A. A. Minai, M. Perdoor, K. V. Byadarhaly, S. Vasa, and L. R. Iyer, "A synergistic view of autonomous cognitive systems," in *Proceedings of IJCNN 2010*, 2010, pp. 498–505.

[36] R. Yuste, J. Maclean, J. Smith, and A. Lanser, "The cortex as a central pattern generator," *Nature Rev. Neurosci.*, vol. 6, pp. 477–483, 2005.

[37] H. Haken, *Synergetics: An Introduction*. Berlin: Springer, 1983.

[38] J. Tanji and E. Hoshi, "Behavioral planning in the prefrontal cortex," *Current Opinion in Neurobiology*, vol. 11, pp. 164–170, 2001.

[39] A. P. Georgopoulos, J. F. Kalaska, R. Caminiti, and J. T. Massey, "On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex," *Journal of Neuroscience*, vol. 2, pp. 1527–1537, 1982.

[40] A. P. Georgopoulos, A. B. Schwarz, and R. E. Kettner, "Neuronal population coding of movement direction," *Science*, vol. 233, pp. 1416–1419, 1986.

[41] D. Bullock, P. Cisek, and S. Grossberg, "Cortical networks for control of voluntary arm movements under variable force conditions," *Cerebral Cortex*, vol. 8, pp. 48–62, 1998.

[42] S. Grossberg and R. W. Paine, "A neural model of cortico-cerebellar interactions during attentive imitation and predictive learning of sequential handwriting movements," *Neural Networks*, vol. 13, pp. 999–1046, 2000.

[43] A. Minai and W. Levy, "Sequence learning in a single trial," in *Proc. World Congress on Neural Networks, San Diego*, vol. Vol. IV, 1993, pp. 176–180.

[44] B. Ans, Y. Coiton, J. P. Gilhodes, and J. L. Velay, "A neural network model for temporal sequence learning and motor programming," *Neural Networks*, vol. 7, pp. 1461–1476, 1994.

[45] R. Huerta and M. Rabinovich, "Reproducible sequence generation in random neural ensembles," *Physical Review Letters*, vol. 93, pp. 238 104–1 238 104–4, 2004.

[46] K. V. Byadarhaly, M. Perdoor, S. Vasa, E. Fernandez, and A. A. Minai, "Learning complex population-coded sequences," in *Proceedings of ICANN 2009*, 2009, pp. 296–305.

[47] S. Vasa, T. Ma, K. V. Byadarhaly, M. Perdoor, and A. A. Minai, "A spiking neural model for the spatial coding of cognitive response sequences," in *Proceedings of ICDL 2011*, 2010, pp. 140–146.

[48] S. Amari, "Dynamics of pattern formation in lateral inhibition type neural fields," *Biological Cybernetics*, vol. 27, pp. 77–87, 1977.

[49] P. C. Bressloff, "Spatiotemporal dynamics of continuum neural fields," *Journal of Physics A: Mathematical and Theoretical*, vol. 45, p. 033001, 2012.

[50] J. D. Rolston, D. A. Wagenaar, and S. M. Potter, "Precisely timed spatiotemporal patterns of neural activity in dissociated cortical cultures," *Neuroscience*, vol. 148, p. 294303, 2007.

[51] P. K. Stanton and T. J. Sejnowski, "Associative long-term depression in the hippocampus induced by hebbian covariance," *Nature*, vol. 339, pp. 215–218, 1989.

[52] A. Minai, "Covariance learning of correlated patterns in competitive networks," *Neural Computation*, vol. 9, pp. 667–681, 1997.