



A compositionality machine realized by a hierarchic architecture of synfire chains

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The composition of complex behavior is thought to rely on the concurrent and sequential activation of simpler action components, or primitives. Systems of synfire chains have previously been proposed to account for either the simultaneous or the sequential aspects of compositionality; however, the compatibility of the two aspects has so far not been addressed. Moreover, the simultaneous activation of primitives has up until now only been investigated in the context of reactive computations, i.e., the perception of stimuli. In this study we demonstrate how a hierarchical organization of synfire chains is capable of generating both aspects of compositionality for proactive computations such as the generation of complex and ongoing action. To this end, we develop a network model consisting of two layers of synfire chains. Using simple drawing strokes as a visualization of abstract primitives, we map the feed-forward activity of the upper level synfire chains to motion in two-dimensional space. Our model is capable of producing drawing strokes that are combinations of primitive strokes by binding together the corresponding chains. Moreover, when the lower layer of the network is constructed in a closed-loop fashion, drawing strokes are generated sequentially. The generated pattern can be random or deterministic, depending on the connection pattern between the lower level chains. We propose quantitative measures for simultaneity and sequentiality, revealing a wide parameter range in which both aspects are fulfilled. Finally, we investigate the spiking activity of our model to propose candidate signatures of synfire chain computation in measurements of neural activity during action execution.

Keywords: compositionality, synfire chains, movement primitives, simulation

1 INTRODUCTION

How is a complex object perceived when it is encountered for the first time? Although it is possible that the brain develops new categories for each new object, it is more likely that it breaks the complex object down into simpler objects and their component features such as shape and color. Thus, when a new object is encountered, it is analyzed according to its primitives and the collection of active primitives forms the complex object (e.g., Tanaka, 2003). The concept of creating complex objects out of the sum of their parts is known as compositionality.

The principle of compositionality as stated above is not restricted to reactive computations such as the comprehension of perceptions, it can also be applied to proactive computations, for example planning and executing complex motor programs on the basis of an underlying hierarchy of motion primitives. Evidence for the existence of movement primitives has been found in several studies, either on the actuator/kinematic/dynamic or on the neural level. Direction specificity of neural coding has been demonstrated by Georgopoulos et al. (1982) and can be regarded as the most elementary neural realization of primitives. Mussa-Ivaldi et al. (1994) showed that spinal stimulation of a frog did not produce uniform leg movement. Instead, the stimulated area represented a static “force field” acting on the leg, dragging the foot to a fixed

position. Surprisingly, two force fields superimpose linearly when stimulated together. Furthermore, if an internal model is assumed, human reaching movements can be separated into primitives showing Gaussian (Thoroughman and Shadmehr, 2000) or log-Gaussian (Plamondon, 1995) speed profiles. Likewise, random scribbling from monkeys can be broken into unit segments (Soechting and Terzuolo, 1987) and appears to be composed from a small number of parabolas (Polyakov et al., 2009a,b). The presence of motor primitives is especially prominent during learning of new movements (Sosnik et al., 2004) or recovery from stroke (Rohrer et al., 2002).

The above studies reveal two aspects to the compositionality of complex behavior. The first aspect is that primitives provide a basic set of behaviors whose simultaneous combination yield the final action. We refer to this aspect as simultaneity. Secondly, primitives can be arranged in a series. We will refer to this as sequentiality. Whereas some compositional systems only require one of these computational features, others, most notably motor control, require both.

The question of how such compositional systems are realized in the neural substrate is an unresolved issue. Undoubtedly, aspects of movement can be inferred on the basis of firing rates (e.g., Georgopoulos et al., 1982). An alternative proposition is that information is encoded in the precise time of occurrence of an

action potential. A number of studies have revealed the occurrence of precise spike timing (Eckhorn et al., 1988; Gray and Singer, 1989; Abeles et al., 1993; Prut et al., 1998; Pulvermüller and Shtyrov, 2009) with respect to critical features of experimental protocols, which strongly suggests temporal coding. These strategies are not mutually exclusive; Masuda (2006) demonstrated how the two formulations can coexist.

The mechanism behind the formation of such fine temporal structure is still unknown. A single post-synaptic potential (PSP) is relatively small compared to the range of membrane potential fluctuations and therefore not very likely to elicit a spike (Abeles, 1982; Matsumura et al., 1996; Hasenstaub et al., 2005). However, reliable post-synaptic action potential generation can be triggered by a near-synchronous pulse of a pre-synaptic population (“just-enough, just-in-time”; Douglas and Martin, 2007; Anderson and Martin, 2009). If applied inductively, this insight leads to the concept of a volley of synchronous activity propagating along a structure known as a synfire chain (Abeles, 1991). In its simplest formulation, a synfire chain is a feed-forward subnetwork consisting of a row of neuron groups in which each neuron in a group projects to the neurons in the following group (see **Figure 1**). The propagation of pulse packets in synfire chains has been shown to be stable under quite general conditions (Diesmann et al., 1999; Gewaltig et al., 2001).

Although the synfire concept was originally developed to account for precise firing patterns in the brain, there is as yet no unequivocal proof that they exist. The main evidence in favor of the hypothesis is that the repeating spatiotemporal firing patterns that a synfire chain would generate can be measured during experiments (Abeles et al., 1993; Prut et al., 1998; Baker et al., 2001; Kohn and Smith, 2005; Shmiel et al., 2005, 2006; Long et al., 2010), and have even been shown to re-occur after several minutes (Ikegaya et al., 2004). In awake animals precise firing patterns are related to behavior, but are usually not tightly time locked to any known external event. Other studies have used surrogate or shuffled spike data to challenge these results, suggesting that such patterns occur by chance rather than as a result of an underlying feed-forward structure (Oram et al., 1999; Baker and Lemon, 2000; Mokeichev et al., 2007). These studies have in turn been criticized on the basis

of the underlying null hypothesis (Date et al., 1999; Abeles and Gat, 2001) or the nature of the surrogate data. Abeles and Gat (2001) and Gerstein (2004) argue that the surrogates used to challenge the synfire hypothesis introduced excess structure into the artificial spike trains, whereas Ikegaya et al. (2008) contends that the detection algorithm used in the respective earlier studies was not sufficiently sensitive. Contributing to the ongoing debate on the existence of precise firing or feed-forward networks is outside the scope of the current manuscript. In the following, we therefore assume their existence as a useful working hypothesis.

Bienenstock (1995) conjectured that perception or recall of entities and actions or relations between them are based on the co-operative action of many synfire chains. In this hypothesis, each primitive is realized by a synfire chain, and a specific object can be represented by a particular composition of the underlying primitive chains. This requires some degree of interaction between synfire chains in order to determine which primitives are involved in the composition. Bienenstock (1995) speculated that this interaction is mediated by weak inter-connections between the chains, as illustrated in **Figures 2A,B**. Thus, if stimulated at approximately the same time, chains can aggregate their traveling waves to form one front (see **Figure 2C**). This mechanism is referred to as synfire binding. It has been demonstrated that synfire binding can indeed occur (Arnoldi and Brauer, 1996) and that it is a feasible mechanism to compose complex objects out of multiple perceptual primitives (Abeles et al., 2004). Those networks can reliably discriminate between different triple-pulses. Unlike attractor networks, the resultant network states are transiently active followed by a return to steady low-rate background activity.

The sequential aspect of compositionality has also been attributed to activity in an appropriate architecture of synfire chains. The concatenation of syllables in birdsong has been proposed to result from the consecutive activation of synfire chains, each representing one syllable (Hahnloser et al., 2002; Li and Greenside, 2006; Kozhevnikov and Fee, 2007; Jin et al., 2007; Jin, 2009; Hanuschkin et al., 2010a). Thus, a bird song is realized by a particular sequence of primitives. A song syntax can be realized by the connectivity between the chains representing individual syllables: if syllable A can be followed by a repetition of A or by syllable B, the final group

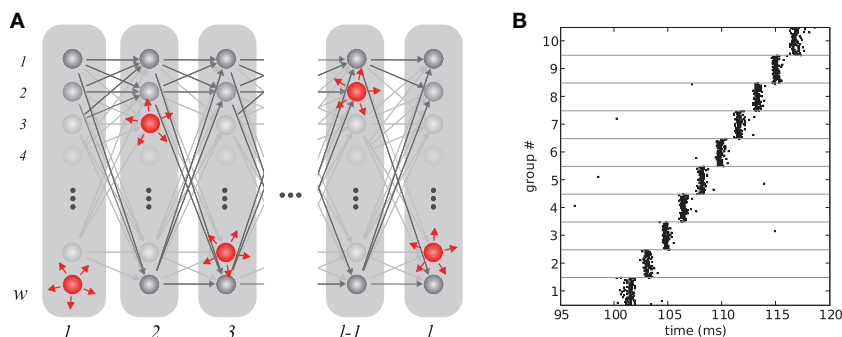
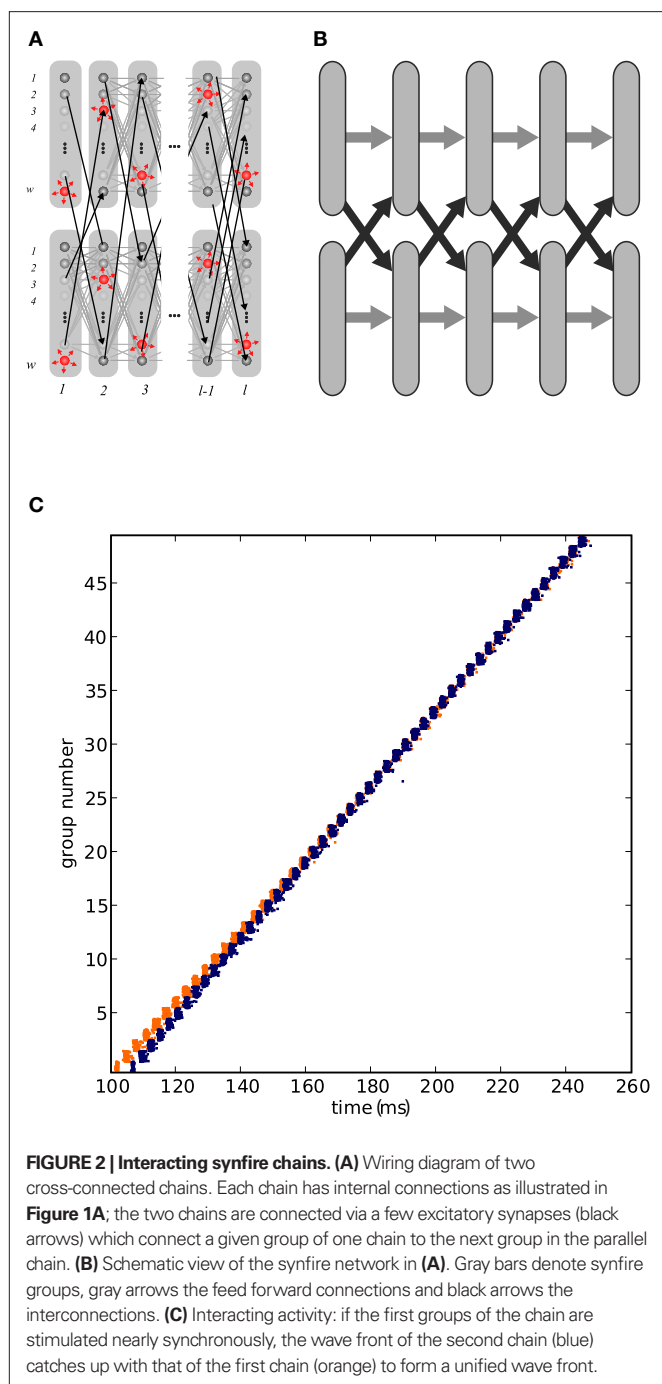


FIGURE 1 | A simple synfire chain. (A) Wiring diagram of a synfire chain. Excitatory neurons in each group (gray discs) have feed-forward connections to all neurons in the next group (gray arrows); in this version of the synfire chain model, inhibitory neurons in each group (red discs) project to random neurons in

the entire network to create a global inhibition. **(B)** Synfire activity. If the first group is sufficiently stimulated, a volley of activity propagates through the chain. Each dot represents the spike time of a neuron; horizontal lines separate the spikes of consecutive neuron groups.



of the synfire chain representing A is connected in a feed-forward fashion to the initial groups of chains A and B. Similarly, a network of interconnected synfire chains can account for key experimental findings in free monkey scribbling with respect to cortical activity and the statistics of the generated trajectories (Hanuschkin et al., 2010b).

So far, modeling studies have investigated the simultaneous and sequential aspects of compositionality in isolation. However, it has yet to be shown that synfire chains can provide the substrate for compositional systems requiring both computational features, such as motor control. It is not clear that the aspects can be combined, as

the models described above that exhibit simultaneity or sequentiality rely on entirely different mechanisms: simultaneity is realized by synfire chain binding, whereas sequentiality is realized by the propagation of activity from the end of one chain to the beginning of the other. It is therefore not obvious that the computational features are compatible either in terms of network architecture or in terms of parameters. Here, we demonstrate that both types of computation can indeed be carried out in a single network model. The resulting behavior exhibits both simultaneous and sequential combination of primitives and is considerably richer than that generated by previous models based on synfire chains. The discovery that the two types of computation are complementary provides support for the hypothesis that synfire chains constitute a key element of neural computation.

In Sec. 3.1 we develop a two-layer network of synfire chains. To illustrate the computational features of our model, we map the feed-forward activity in each of the upper level chains to simple drawing strokes in four different directions. We first show that synfire chain binding allows simultaneous execution of primitives, resulting in composite drawing strokes. Secondly, in Sec. 3.2 we demonstrate that if the lower level chains are constructed in a closed-loop manner, the motion is no longer bounded by synfire chain termination. In this case, the model generates an ongoing sequence of individual and composite drawing strokes. The patterns generated by the network can be either random or deterministic, depending on the connectivity at the seam of the lower level loops. In Sec. 3.3 we investigate the behavior of the network as a function of the inhibition in the upper and lower levels and determine a range of parameters for which the criteria of simultaneity and sequentiality are satisfactorily fulfilled. Finally, in Sec. 3.4 we investigate the spiking activity of our model during the generation of complex behavior and propose candidate signatures for synfire chain activity in massively parallel recordings of spike trains and mass signals.

Preliminary results have been published in abstract form (Schrader et al., 2007).

2 MATERIALS AND METHODS

2.1 SYNFIRE BINDING AND COMPETITION

As demonstrated by Arnoldi and Brauer (1996), synfire binding occurs when two or more cross-connected synfire chains synchronize their traveling pulses after a near-synchronous stimulation (see **Figure 2**). If the two chains are stimulated within a sufficiently short interval, the chain which is stimulated later (the lagging chain) speeds up its propagation of pulses until the activity is synchronized in corresponding groups of the chains. The binding mechanism can be fully described by a wave theoretical approach (Hayon et al., 2005). The detection of the binding state can be realized by a third synfire chain, as is demonstrated in **Figure 3A**. The upper level chain can only be activated if the activity of the lower level chains is sufficiently synchronized. **Figure 3B** shows the activity in the chains associated with the detection of binding states. At 100 ms the inter-stimulus interval is only 10 ms, so the two lower level chains bind and activate the upper level chain. The inter-stimulus interval of 30 ms at 400 ms is too great; no binding takes place and the increase in global inhibition due to both lower level chains being active even causes one of the chains to fail in this example. Abeles et al. (2004) showed that this basic hierarchy of chains is sufficient to

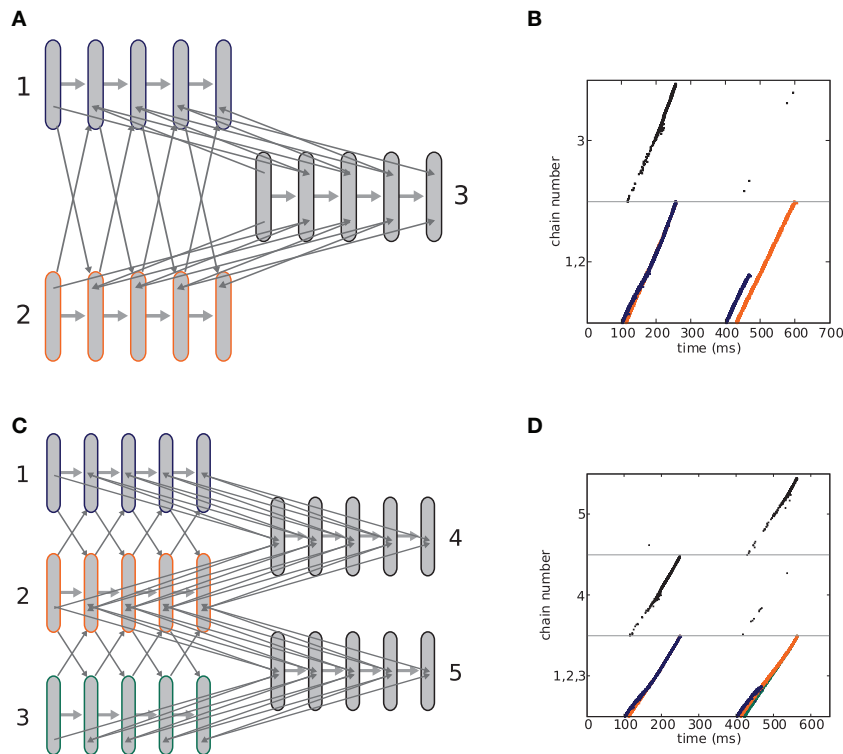


FIGURE 3 | Detection and discrimination of binding states in networks of synfire chains. (A) Simple three-chain network. Each pair of chains (1,2), (1,3), and (2,3) are interconnected as shown in **Figure 2A**. The upper level chain (3, black) serves as a readout chain to detect the binding of the lower level chains (1, blue; 2, orange). **(B)** Detection of binding in the three-chain network in **(A)**, coloring of spike time markers in the lower panel indicates chain membership of neuron. The two lower level chains are stimulated at $t_1 = 100$ and $t_2 = 110$ ms. The chains bind and activate the third chain. The lower level chains are stimulated again at $t_1 = 400$ and $t_2 = 430$ ms. In this case, the chains do not

bind as the stimulus interval of 30 ms is too large. **(C)** Five-chain network. Here, three chains (1, blue; 2, orange; 3, green) constitute the lower level chains and two upper level chains (4–5, black) serve as readout chains. Interconnections are indicated by gray arrows. **(D)** As in **(B)**, but for the five-chain network shown in **(C)**. Chains 1 and 2 are stimulated at $t_1 = 100$ and $t_2 = 115$ ms. They bind together and activate the upper level chain 4. All three lower level chains are stimulated again at $t_1 = 400$, $t_2 = 415$, and $t_3 = 420$ ms. In this case chains 2 and 3 bind, as they have the smallest inter-stimulus interval. Their binding causes the activation of upper level chain 5.

model compositionality: the lower level chains represent primitive features and the upper level chain represents the composite object. The representation of the composite object is only active if the component features are detected near-synchronously.

In addition to binding primitive features, a second property necessary for the computation of compositionality is competition. To prevent the representation of one nonsensical “mega object,” which corresponds in the network model to too many chains binding together, only the most relevant detected features should be bound. In a network of chains, this can be easily realized by the presence of inhibitory neurons. In the small networks studied here, it is sufficient to include inhibitory neurons in the feed-forward structures that project non-specifically to other neurons in the same layer of the hierarchical network (see **Figure 1A**). When chains bind together, the resultant synchronous inhibition prevents further chains from joining the binding state. The activity in a five-chain network (**Figure 3C**) associated with competition between binding states is shown in **Figure 3D**. At around 100 ms the lower level chains 1 and 2 are stimulated with an inter-stimulus interval of 15 ms, which is short enough to allow the chains to bind and thus activate the upper level chain 4. At around 400 ms chains 1 and 2 are once again stimulated with an inter-stimulus interval of 15 ms,

however the shorter inter-stimulus interval of 5 ms between chains 2 and 3 allows those two to bind instead. The synchronous inhibition in chains 2 and 3 prevents chain 1 from joining the binding state. Consequently, only the upper level chain 5 is activated. This dynamics is equivalent to a competition between possible bindings which is biased toward those subsets of features that occur with a higher degree of synchrony; a bias toward binding subsets of features that are detected earlier has also previously been demonstrated (Abeles et al., 2004).

In the current paper, we assume homogeneous layer-specific inhibition, with synaptic strength empirically adjusted such that at most two upper level chains can be simultaneously active (see **Table 2**). For more complex networks, the specificity and heterogeneity of inhibitory projections are likely to be crucial factors affecting the network’s computational properties.

2.2 MAPPING ACTIVITY TO ACTIONS

Abeles et al. (2004) demonstrated that a hierarchical network of synfire chains can detect near-synchronous stimuli and discriminate between different subsets, i.e., that it can compute compositionality of perception. Therefore the purpose of the upper level chains was simply to act as binary indicators of lower level binding states.

The feed-forward dynamics of the response to lower level binding was not further considered. Here, we focus on the ability of such networks to generate actions. In particular, we want to illustrate the capabilities of a synfire chain network to generate both the sequential and simultaneous aspects of compositionality. To this end, we choose a task that is on the one hand as simple as possible (in terms of the number of primitives) and on the other hand easy to visualize. We map the activity of four upper level chains to simple drawing strokes. The mapping of activity to drawing actions facilitates particularly easy visualization of the computational features of the network, i.e., it is immediately apparent to the eye when two strokes have been superimposed or when one follows another. However, the choice of drawing strokes is not intended to suggest an account of movement generation, which would require a much more sophisticated model. Indeed, any set of combinable actions could have been chosen.

To generate the drawing strokes, we consider the neurons in a given upper level chain j to have a preferred direction, characterized by its unit velocity \mathbf{p}_j (see Georgopoulos et al., 1982). The net drawing velocity generated by a network is determined by summing over the activity of all the upper level chains:

$$\dot{\mathbf{x}}(t) = \sum_j \sum_k w_k a_j^k(t) \mathbf{p}_j \quad (1)$$

where $a_j^k(t)$ is the activity of the k th group in the j th chain as expressed by a population histogram with a bin size of $h = 5$ ms and w_k is the weight of the contribution of the k th group in a chain. This bin size is the finest sampling interval possible without resolving the individual contributions of the synfire groups. For this study, we consider only a uniform velocity profile, $w_k = w$. The movement trajectory is then obtained by integrating the population vector $\dot{\mathbf{x}}(t)$ using the initial condition $\mathbf{x}(0) = (0,0)$ for each trial. No further smoothing of the neuronal activity or trajectory is carried out.

2.3 MEASURES FOR SIMULTANEITY AND SEQUENTIALITY

We define two measures to quantify the extent to which the network model realizes the simultaneous and sequential aspects of compositionality. In the full model, activation occurs in rounds due to the cyclical architecture of the lower level chains. In each round of activation either 0, one, or more than one upper level chain is active.

First, we consider the activity $a_{j,i}$ of a single upper level chain j , where i indicates the round of activation. We set $a_{j,i}$ to 0 if the chain is not actively propagating a volley of action potentials (i.e., it responds with fewer than 2 spikes per synfire group). We define the relative contribution $a'_{j,i} = a_{j,i} / \sum_x a_{x,i}$ of a chain j to the overall chain activity during round i . Note that, due to variable propagation times, i does not correspond to absolute time. The measure of simultaneity for network activity is then defined as the average maximal activities over all rounds,

$$p_{\text{sim}} = \frac{1}{N} \sum_{i=1}^N \max(a'_{j,i}), \quad (2)$$

where N is the total number of rounds in which at least one upper level chain was active, i.e., $a_{j,i} > 0$ for at least one j . We further define the measure of sequentiality p_{seq} to be the proportion of rounds of activation in which at least one upper level chain is active.

2.4 NUMERICAL SIMULATIONS

We performed numerical simulations of networks of synfire chains. Simulations were performed with NEST revision 8733 (see www.nest-initiative.org and Gewaltig and Diesmann, 2007) using a computational step size of 0.1 ms. This software is capable of simulating large-scale networks by means of distributed computing (Morrison et al., 2005). All simulations were performed on an AMD Opteron Dual Core SMP machine with four processors running Linux. To allow other researchers to perform their own experiments, at the time of publication we are making a module available for download at the NEST Initiative website containing all relevant scripts.

2.4.1 Neuron model

The model used in this study is a current-based leaky integrate-and-fire (IAF) point neuron (Tuckwell, 1988). Its membrane potential V is described by a linear differential equation

$$\frac{dV}{dt} = -\frac{1}{\tau_m} V + \frac{1}{C_m} I_{\text{syn}}(t) \quad (3)$$

where τ_m is the membrane time constant, C_m is the membrane capacitance and I_{syn} the synaptic current. If the membrane potential exceeds a fixed threshold θ , a spike is emitted and the potential is immediately set to its reset value V_{reset} . During the subsequent refractory period τ_{ref} the membrane potential is clamped at V_{reset} . A single post-synaptic current (PSC) is modeled as an α -function (Jack et al., 1983):

$$I_{\alpha}(t) = \frac{e}{\tau_{\alpha}} t e^{-t/\tau_{\alpha}} \quad (4)$$

where τ_{α} is the rise time. The total synaptic current I_{syn} is then

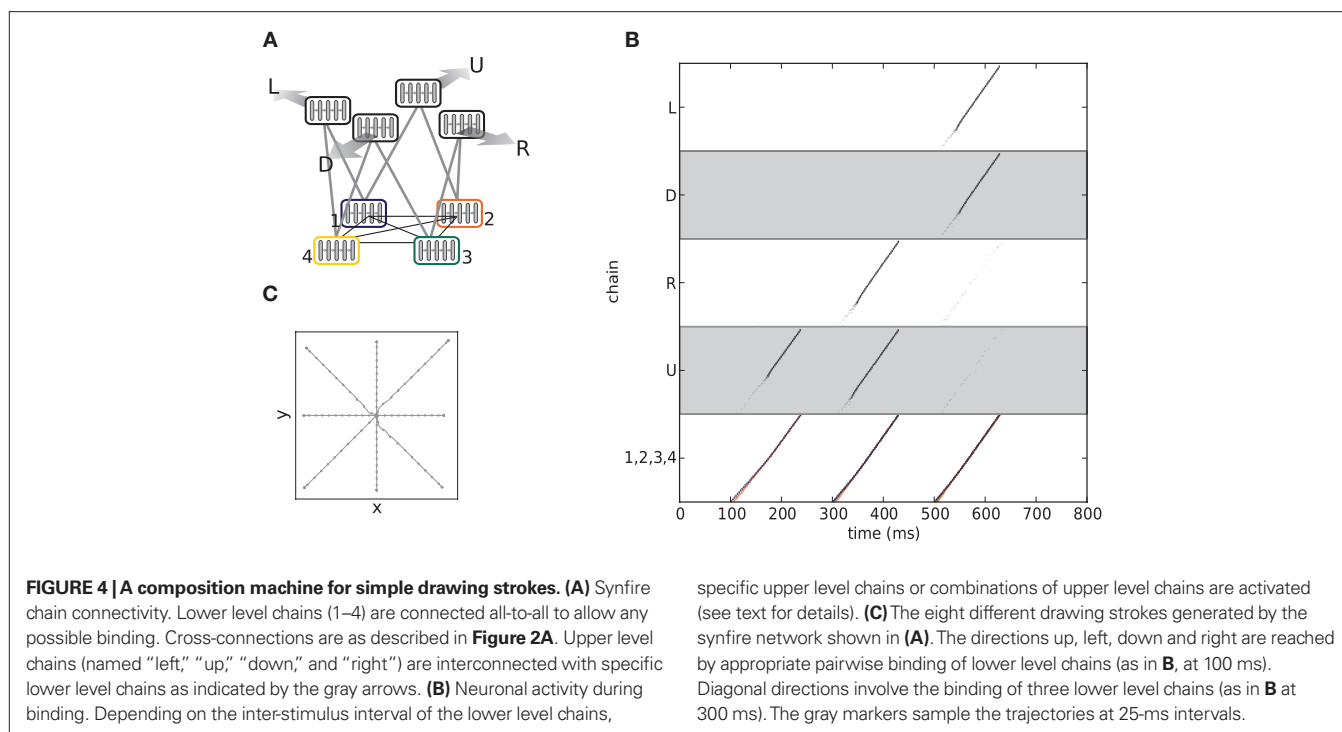
$$I_{\text{syn}} = \sum_i \sum_{s \in S_i} J_i I_{\alpha}(t - s - d) \quad (5)$$

where i runs over all pre-synaptic neurons and s over the set of all spike times S_i of a pre-synaptic neuron i . J is the peak value of the PSC and d the synaptic delay. As the passive membrane potential of the integrate-and-fire neuron is a linear system, Eq. 3 can be solved numerically without approximation (Rotter and Diesmann, 1999; Plesser and Diesmann, 2009). The neuronal parameters used in this study are given in **Table 2**.

3 RESULTS

3.1 SIMULTANEOUS COMPOSITION OF PRIMITIVES

In this section we show that the binding and competition properties exhibited by hierarchic networks of synfire chains (Sec. 2.1) are sufficient to enable the composition of actions from simpler actions. We construct a two layer network of synfire chains, illustrated in **Figure 4A**. Each synfire chain is internally connected according to the feed-forward connectivity described in Abeles et al. (2004) and illustrated in **Figure 2A**, i.e., containing both excitatory neurons (100) which constitute the feed-forward connections and globally projecting inhibitory neurons (25) to introduce a competition between possible bindings. Unlike the five chain network shown in **Figure 3C**, in our model the strength of the inhibition is adjusted to allow as many as three lower level chains to simultaneously enter a binding state. Each upper level chain is activated by the binding of the two specific



lower level chains with which it is interconnected. The lower level chains have all-to-all cross-connections to allow all combinations of binding, but not all pairs of lower level chains can activate an upper level chain. Interconnections are realized such that each excitatory neuron in group i of one chain has a small number of synapses to neurons in group $i + 1$ of the other chain (**Figure 2**, black arrows). Additionally, each neuron in the network receives an independent Poisson spike train that yields a mean membrane potential of 15 mV (Campbell’s theorem, see Papoulis, 1991). To activate a lower level chain, a stimulus of a Gaussian distributed spike volley with the same parameters as a natural pulse propagating through the chain is applied to the initial group. The spike volley is characterized by the number of spikes contained a and their temporal precision σ (Diesmann et al., 1999). The model is summarized in **Table 1**. Unless otherwise stated, the model parameters are as given in **Table 2**.

The activity in each upper level chain is mapped to a uniform velocity in one of the four directions “up,” “down,” “left,” and “right,” as described in Sec. 2.2. Note that this differs from the approach taken in Abeles et al. (2004), in which the lower level chains are considered as primitives and the upper level chains as composite objects. In this study the binding of lower level chains with an upper level chain constitutes a primitive, whereas concurrent activity in upper level chains represents a composite object. **Figure 4B** demonstrates the binding of lower level chains to activate specific upper level chains. At 100 ms, lower level chains 1 and 2 are stimulated near-synchronously (chain 1 at 100 ms, chain 2 at 106 ms). This causes them to bind and activate the upper level chain representing the direction “up.” At around 300 ms, chains 1, 2, and 3 are stimulated near-synchronously (chain 1 at 300, chain 2 at 306, chain 3 at 302 ms). All three chains bind, thus activating the upper level chains representing the directions “up” and “right.” As the number of bound chains increases, so does the level of inhibition, making it progressively harder for further

chains to join the binding state. This can be seen at around 500 ms, where although all lower level chains are stimulated (chain 1 at 500, chain 2 at 506, chain 3 at 502, chain 4 at 503 ms), only chains 1, 3, and 4 enter a binding state, so only the upper level chains “left” and “down” are activated. Although the relative stimulation times for the first three chains are the same as before, the earlier stimulation of the fourth generates sufficient mutual inhibition such that chain 2 cannot join the binding state. The eight different drawing strokes that can be generated by the network through near-synchronous stimulation of two or three lower level chains (cf. **Figure 4B** at 100 and 300 ms) are illustrated in **Figure 4C**.

3.2 SEQUENTIAL COMPOSITION OF PRIMITIVES

In the previous section we showed that by means of binding and competition, a hierarchic architecture of synfire chains can realize compositionality of behavior in terms of superimposing primitives. Here, we show that such an architecture is also capable of realizing sequential compositionality. In our example, this consists of generating a sequence of primitive and composed drawing strokes. We modify the model architecture illustrated in **Figure 4A** and summarized in **Table 1** by connecting the lower level chains in a loop. In the modified architecture, the final group of each lower level chain projects to 40 neurons in the first groups of all the lower level chains. This can be visualized as a cylinder of interconnected synfire “rings” as shown in **Figure 5A**. All other aspects of the architecture, including the interconnections with the upper level chains, remain the same. Due to the cyclical structure, the activity in the network is self-sustained after a single initial stimulus (here, to chains 1 and 2 to activate the direction “up”). Each “round” of activity results in a different binding among the lower level chains and thus to a random sequence of primitives and combinations of primitives. **Figure 5B** shows a resulting motion trajectory from five seconds of network activity. The individual primitive

Table 1 | Tabular description of network model after Nordlie et al. (2009).

A: MODEL SUMMARY			
Populations	Two levels of synfire chains, four chains in each level		
Connectivity	Feed-forward connections within one chain, cross connections between chains, random inhibition within one level		
Neuron model	Leaky integrate-and-fire, fixed voltage threshold, fixed absolute refractory time (voltage clamp), α -current synapses		
Input	Independent fixed-rate Poisson spike trains to all neurons, pulse stimuli to first groups of lower level chains.		
Measurements	Spike activity		
B: POPULATIONS			
Name	Elements	Size	
Network	Synfire chain Ch_j	8	
Ch_j	Synfire groups G_{ij}	50	
G_{ij}	Neuron populations E_{ij}, I_{ij}	One excitatory population E , per group G_i One inhibitory population I , per group G_i	
E_{ij}	laf neuron	100	
I_{ij}	laf neuron	25	
C: CONNECTIVITY			
Name	Source	Target	Pattern
FF	E_{ij}	$E_{i+1,j} + I_{i+1,j}$	Random divergent, $1 \rightarrow C_{Ex}$, weight J_{Ei} , delay d
INH_j	I_{ij} for $j \in \{1 \dots 4\}$	Ch_j for $j \in \{1 \dots 4\}$	Random divergent, $1 \rightarrow C_{Inj}$, weight J_{Ij} , delay d
INH_u	I_{ij} for $j \in \{5 \dots 8\}$	Ch_j for $j \in \{5 \dots 8\}$	Random divergent, $1 \rightarrow C_{Inu}$, weight J_{Ij} , delay d
X_{ll}	E_{ij} for $j \in \{1 \dots 4\}$	$E_{i+1,k}$ for $k \in \{1 \dots 4\}, j \neq k$	Random divergent, $1 \rightarrow C_{ll}$, weight J_{Ei} , delay d
X_{ul}	E_{ij} for $j \in \{1 \dots 4\}$	$E_{i+1,k}$ for $k \in \{5 \dots 8\}$	Random divergent, $1 \rightarrow C_{ul}$, weight J_{Ei} , delay d . According to Figure 4 .
X_{lu}	E_{ij} for $j \in \{5 \dots 8\}$	$E_{i+1,k}$ for $k \in \{1 \dots 4\}$	Random divergent, $1 \rightarrow C_{lu}$, weight J_{Ei} , delay d . According to Figure 4 .
FF_{loop}	E_{50j} for $j \in \{1 \dots 4\}$	E_{1j} for $j \in \{1 \dots 4\}$	If present, random divergent, $1 \rightarrow C_{Ex}$, weight J_{Ei} , delay d
D: NEURON MODELS			
Name	laf neuron		
Type	Leaky integrate-and fire, α -current input		
Subthreshold dynamics	$\text{if } (t > t^* + \tau_{ref}): dV/dt = -V/\tau_m + I_{syn}(t)/C_m$ $\text{else: } V(t) = V_{reset}$ $I_{syn} = \sum_i \sum_{s \in S_i} J_{i\alpha} (t - s - d) \quad I_{\alpha}(t) = \frac{\theta}{\tau_{\alpha}} t e^{-t/\tau_{\alpha}}$		
Spiking	If $V(t) < \Theta$ AND $V(t+) \geq \Theta$ 1. set $t^* = t$ 2. emit spike with time stamp t^*		
E: INPUT			
Type	Target	Description	
Poisson generator	All E_x, I_x	Independent for each neuron, rate v_x , weight J_x	
Pulse packet	$E_{1j} + I_{1j}$ for $j \in \{1 \dots 4\}$	Spike volleys with Gaussian distribution containing a spikes with temporal precision σ , weight J_{pp}	
F: MEASUREMENTS			
Spikes from all upper and lower level chains			

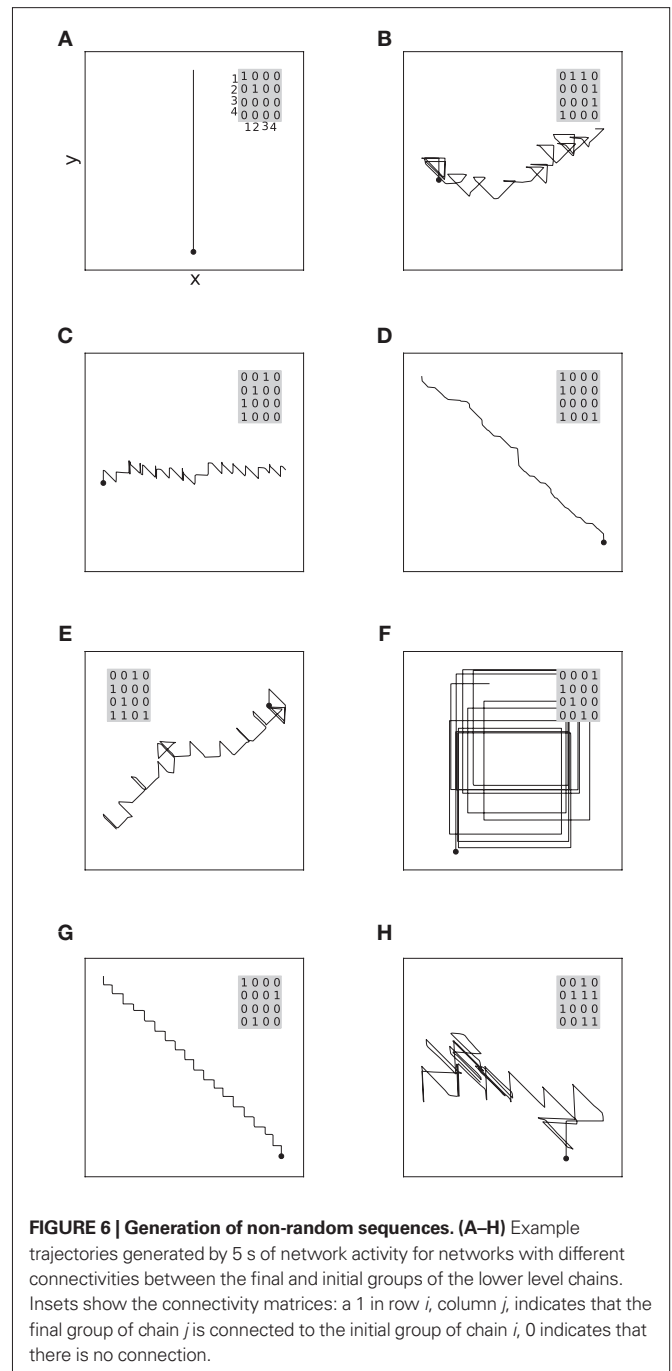
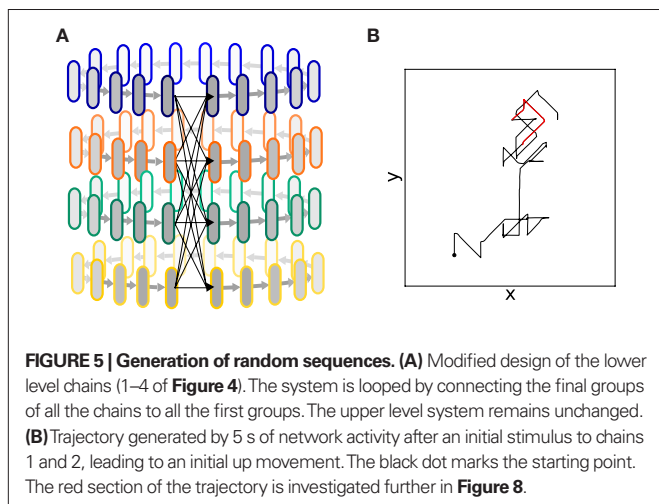
and composed drawing strokes can be clearly seen, as can occasional sections where temporarily no meaningful binding state exists, resulting in somewhat more “dithery” drawing behavior.

The sequence of primitive and composed drawing strokes shown in **Figure 5** is generated by a network with connections that close the lower level chains at the seam of the loop: the final group of each chain makes feed-forward connections to the initial groups of every chain. Due to this symmetry, any binding state is equally likely and a random sequence is produced. However, under

the assumption that asymmetric connections between specific final and initial groups could develop, **Figure 6** demonstrates that stereotypical or deterministic sequences can also be generated. For example, if chain 1 projects onto itself and chains 2 and 4 project onto each other, a sequence consisting of alternating “up” and “left” strokes is produced (**Figure 6G**). These results show that a hierarchic architecture of synfire chains is in principle capable of realizing at least a rudimentary syntax, as previously suggested (Bienenstock, 1991b).

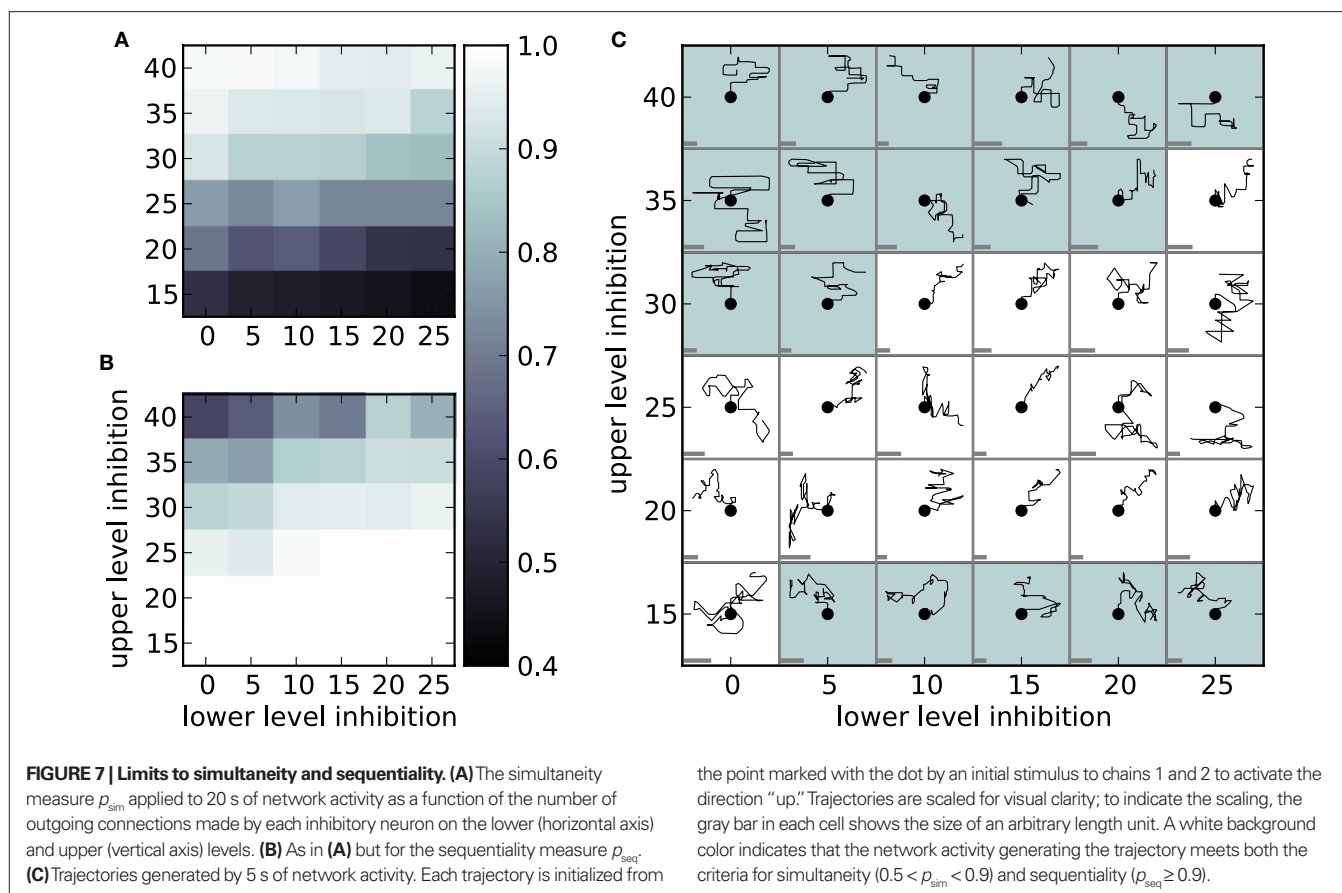
Table 2 | Simulation parameters.

Name	Value	Description
A: CONNECTIVITY		
C_{Ex}	40	Number of outgoing feed-forward connections from each excitatory neuron
C_{Inl}	5	Number of outgoing connections from each lower level inhibitory neuron
C_{Inu}	25	Number of outgoing connections from each upper level inhibitory neuron
C_{ll}	3	Number of outgoing lower level cross-connections from each lower level excitatory neuron
C_{ul}	8	Number of outgoing upper level cross-connections from each lower level excitatory neuron
C_{lu}	8	Number of outgoing lower level cross-connections from each upper level excitatory neuron
J_E	17.92 pA	Amplitude of excitatory connection, $\Rightarrow 0.2$ mV EPSP amplitude
J_I	-71.70 pA	Amplitude of inhibitory connection, $\Rightarrow -0.8$ mV EPSP amplitude
d	1 ms	Synaptic transmission delay
B: NEURON MODEL		
τ_m	20 ms	Membrane time constant
C_m	200 pF	Membrane capacitance
Θ	20 mV	Fixed firing threshold
V_0	0 mV	Resting potential
V_{reset}	V_0	Reset potential
τ_{ref}	2 ms	Absolute refractory period
τ_α	1 ms	Rise time of post-synaptic current
C: INPUT		
v_x	6157 Hz	External Poisson rate
J_x	8.96 pA	Amplitude of external excitatory connection $\Rightarrow 0.1$ mV EPSP amplitude
J_{pp}	17.92 pA	Amplitude of pulse packet connection $\Rightarrow 0.2$ mV EPSP amplitude
a	100	Number of spikes in a volley
σ	1 ms	Standard deviation of a Gaussian spike volley



3.3 LIMITS TO SIMULTANEITY AND SEQUENTIALITY

Having demonstrated in the previous sections that an architecture of synfire chains can realize both simultaneous and sequential compositionality, we now investigate the robustness of this finding using the measures p_{sim} and p_{seq} defined in Sec. 2.3. The simultaneity measure p_{sim} is the inverse of the average number of chains active in the upper level. Figure 7A shows p_{sim} as a function the number of outgoing connections made by each upper and lower level inhibitory neuron. For strong upper level inhibition and weak lower level inhibition, $p_{sim} = 1$, indicating that only one chain is active at a time and thus that the criterion of simultaneity is not fulfilled. This is due to the stiff competition in the upper level preventing multiple



upper level chains from entering a binding state. For weak upper level inhibition and strong lower level inhibition, p_{sim} is reduced to 0.4, indicating that on average more than two upper level chains are active. Such low values of p_{sim} also violate simultaneity, as they can only occur in our simple model if incompatible primitives are being executed at the same time. We therefore define $0.5 < p_{sim} < 0.9$ as the range in which simultaneity is fulfilled.

The sequentiality measure p_{seq} is the proportion of rounds of activity in the lower level for which at least one upper level chain was significantly active. For weak upper level inhibition, $p_{seq} = 1$, indicating that there is always at least one upper level chain active and thus that the sequence of primitives is unbroken. For stronger upper level inhibition p_{seq} drops to 0.67. This means that the activity in the lower level chains fails to ignite activity in the upper level for one third of the rounds of activity. We define a successful sequential execution of primitives to have taken place when at least one upper level chain is active in at least 90% of all rounds, i.e., $p_{seq} \geq 0.9$.

We apply our criteria for simultaneity, $0.5 < p_{sim} < 0.9$, and sequentiality, $p_{seq} \geq 0.9$, in **Figure 7C**, which shows example sequences of drawing strokes generated by the model for different configurations of upper level and lower level inhibition. The white background demarcates the range of parameters for which our criteria for simultaneity and sequentiality are both met. In the top left section p_{seq} is too low and p_{sim} is too high, resulting in short sequences consisting only of individual primitives. In the bottom right section p_{sim} is too low. The selection of incompatible primitives generates dithery trajectories. In the middle section both simultaneity and

sequentiality are fulfilled. The sequences are long and contain both individual primitives and compatible combinations. Since previous investigation have revealed fairly general conditions for the robust propagation of activity in synfire chains (Herrmann et al., 1995; Diesmann et al., 1999, 2001), we conclude that the competition between primitives is determined by the balance of inhibition in the upper and lower levels, and that the criteria of simultaneity and sequentiality can be met for a wide range of parameters.

3.4 ACTIVITY SIGNATURES OF SYNFIRE CHAIN COMPUTATION

So far we have studied the complex behavior that can be generated out of superpositions and sequences of simple primitives, focusing on the behavioral output of our model. In this section, we will examine what features of the dynamics could be detectable by an experimenter investigating the nature of neural activity generating complex behavior. A researcher may measure mass signals of neural activity, such as the local field potential (LFP), the electroencephalogram (EEG), or the electrocorticogram (EcoG). Alternatively, the single unit activity of a limited number of neurons can be recorded. In the latter case, current techniques do not allow massively parallel recordings; through multiple electrodes or optical imaging methods, measurements would be unlikely to record the spike trains of more than 200 neurons. Of those neurons, it cannot be expected that all of them are involved with the generation of the behavior under investigation. Moreover, it cannot be assumed that the ordering of the spike trains in the recording reflects the ordering of connectivity in any underlying feed-forward structure.

Spike activity recorded from our model therefore constitutes by far the best case in terms of analysis, as all neurons are only involved with the generation of the trajectory and the underlying structure is known.

Figure 8 shows the spike activity recorded for a short section of the drawing displayed in **Figure 5**. When the activity is displayed taking the architecture of the underlying synfire chains into consideration (**Figure 5B**), the relationship of the spiking activity to the generated behavior is clear. Due to the connectivity of all the final groups to all the initial groups of the lower level chains, the synfire activity in all the lower level groups is approximately synchronous. As the activities of the individual lower level chains are plotted over one another (cf. **Figure 4**), the collective activity appears similar to the activity in just one chain. Each time the activity volley reaches the end of the lower level chains, a new binding state is possible. The result is a different selection of upper level chains and thus a different drawing stroke or combination of drawing strokes (**Figure 5A**).

If the underlying structure of the network is not taken into consideration, an attribution of the generated behavior to the spiking activity becomes much harder. **Figures 5C,D** show the shuffled activity of 200 neurons from the upper and lower levels, respectively. The highly ordered spike activity of **Figure 5A** that is the typical

hallmark of synfire activity is no longer visible. However, some signatures of synfire activity are still visible. The spike trains from the lower level chains (**Figure 5C**) exhibit a high degree of repetition, as the synfire activity repeats in every chain every 125 ms. Repeating spike patterns have previously been identified as possible indications of synfire activity (e.g., Abeles et al., 1993). The spike trains from the upper level (**Figure 5D**) do not show such strong repetition, but a decrease in rate is clearly visible at the beginning of each trajectory segment. Even though the model dynamics consists solely of near-synchronous activity volleys, vertical stripes in the spike activity plots indicating strong synchrony only become evident when considering a much larger amount of neurons than could reasonably be recorded using currently available techniques (**Figures 8B,D**). We therefore conclude that signatures of synfire activity are unlikely to be found by searching for synchrony in spike trains.

As an alternative to massive parallel recordings of single unit activity, mass signals can be recorded to examine global effects. We have modeled such a signal as a histogram of the shuffled spiking data in **Figures 8C–F**. A particularly good impression of the global dynamics is gained when a large number of neurons contribute to the mass signal (**Figures 5E,F**). The large variance of the signal indicates a strong global synchronization, exhibiting fast ripples

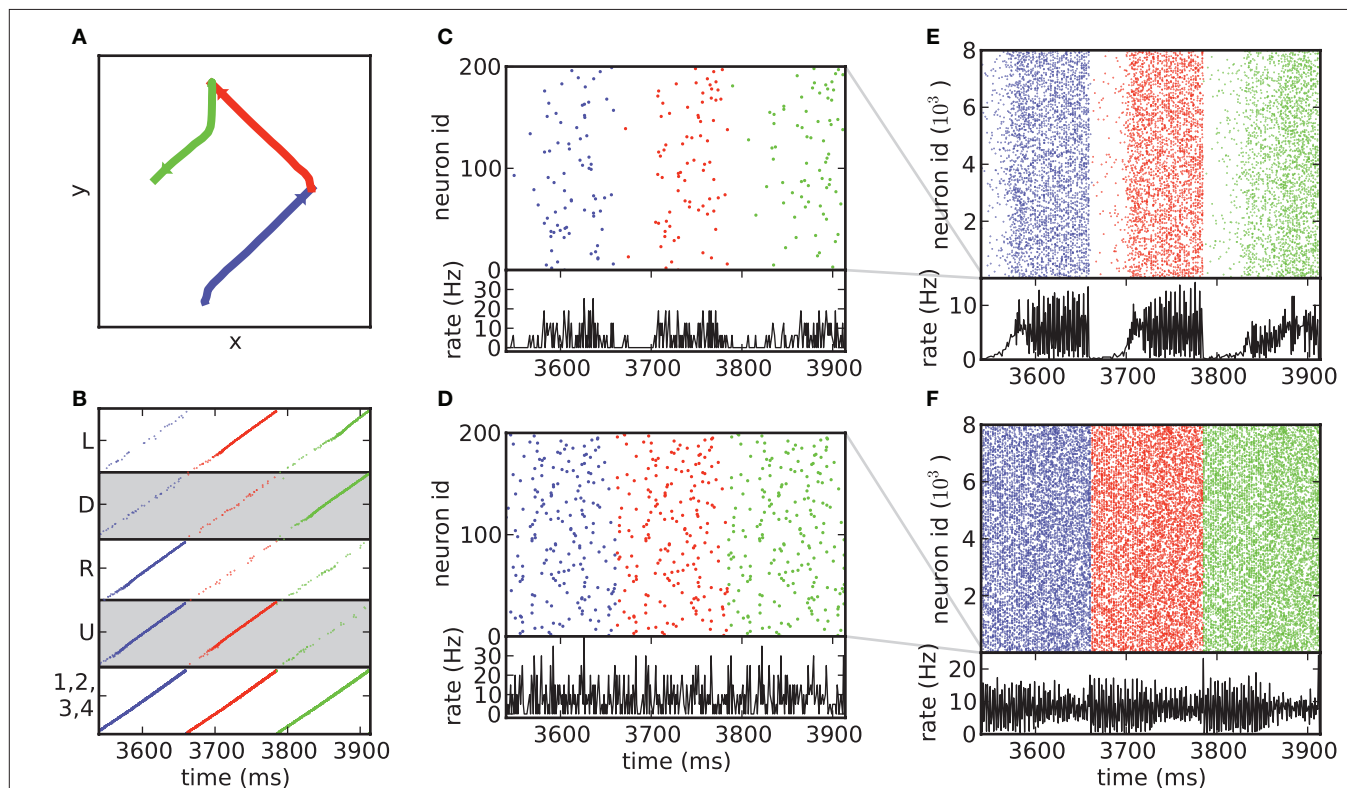


FIGURE 8 | Activity signatures during action execution. (A) Enlargement of the section of the trajectory marked in red in **Figure 5B**. The section contains three combinations of primitives. First, an “up/right” stroke (blue), then “up/left” (red), followed by a stroke which is initially “down” but turns into “left/down” midway through execution (green). Arrowheads mark the direction of stroke execution. **(B)** The underlying synfire chain activity. Each spike time marker is

colored according to the drawing stroke in **(A)** that is being generated at that time. **(C)** Upper panel: shuffled spiking activity of 200 neurons from the upper level chains, spike time markers colored as in **(B)**. Lower panel: histogram of spiking activity with a bin size of 1 ms and normalized by the number of neurons. **(D)** As in **(C)**, but for the lower level chains. **(E,F)** As in **(C,D)**, but for 8000 neurons. Gray lines indicate the range of neurons shown in **(C)** and **(D)**.

at around 400 Hz. The highly synchronous activity periods are interspersed with periods of silence (**Figure 8E**) or less synchronous activity (**Figure 8F**). These results enable us to make specific predictions about the relationship of an experimental protocol to the activity patterns observed in collective signals. First, execution of a primitive or a set of primitives is accompanied by high-frequency fluctuations in collective signals. Second, this high-frequency component is suppressed at decision points in the experimental protocol where a set of primitives is about to be activated.

4 DISCUSSION

In this study we demonstrate that a simple hierarchic architecture of synfire chains is able to generate composed behavior. To visualize the computational features of such a network, we associated primitive activity with drawing strokes in different directions. The network can combine orthogonal primitive drawing strokes into a composed diagonal stroke. In our model, the lower level chains have all-to-all cross-connections, so all specific combinations of chains can bind together. However, not all combinations of lower level chains activate upper level chains. This implements a semantics in the sense of assigning meaning to the binding states of lower level chains.

When the lower level chains are connected in a loop, the self-sustained activity in the network produces sequences of primitive and composed strokes. The characteristics of the sequences depend on the structure of the feed-forward connections between the final and initial groups of the lower level synfire chains. If these connections are symmetric, any sequence of primitives can occur, thus generating an random trajectory. By breaking the symmetry (see also Wennekers et al., 2006; Wennekers, 2007), it is possible to prescribe the transition probabilities between one primitive and the next, i.e., a basic syntax can also be implemented.

We have demonstrated that a single network model can generate actions that exhibit both simultaneity and sequentiality, resulting in much richer behavior than previous synfire chain based models which studied these aspects in isolation. Models accounting for sequentiality in the production of birdsong syntax (Okanoya, 2004; Jin, 2009) have not considered the superposition of primitives, as this does not occur in the target system. Similarly, studies demonstrating superposition (Abeles et al., 2004) did not provide an explanation for series of actions.

The two aspects of compositionality are realized by two different dynamical properties of synfire chains. Simultaneity is brought about by the synchronization of synfire chains, whereas sequentiality relies on feed-forward connections between the final group of one chain and the initial groups of potential successor chains. Hence we can derive the key architectural principles of a network model capable of combining both aspects of compositionality. Sequences of actions can be carried out if the final group of the synfire chain of one primitives makes feed-forward connections to the initial groups of all possible successor primitives, such that the activity volley can propagate from one chain to the next. The strength of the feed-forward connections determines the transition probabilities. Primitives that can be carried out simultaneously must be capable of mutual excitation to synchronize, whereas primitives that cannot be carried out simultaneously need mutual inhibition. The strength of the inhibition regulates the stiffness of the competition.

Using quantitative measures of sequentiality and simultaneity during synfire chain activity, we conclude that sequential and simultaneous compositionality is achievable over a wide range of balanced inhibition in the upper and lower levels. For simple models like the one investigated here, including inhibitory neurons in the synfire chains that make random connections to other neurons in the same level is sufficient; for more complicated models structured inhibition between specific groups of primitives might be necessary. Recently, first steps have been made toward the construction of large-scale compositional systems (Trengove, 2007).

The compatibility of the two types of synfire chain computation and the diversity of the behavior produced lend support to the hypothesis that synfire chains provide the substrate for some cortical functions. Specifically, our results support the theory that synfire chains are a possible substrate for the recognition and production of sequences, for example in processing language (Bienenstock, 1991a,b; Pulvermüller, 1999, 2002) or planning and executing motor programs (Jin, 2009; Hanuschkin et al., 2010b).

However, the two-dimensional drawing strokes we selected as primitives are merely an easy visualization of complex behavior, rather than attempting to account for the generation of movement. Although there is evidence for motor primitives and compositionality (Soechting and Terzuolo, 1987; Thoroughman and Shadmehr, 2000; Polyakov et al., 2009a,b), there are many features of motor behavior which cannot be captured by such a simple model as studied here. For example, a movement can be performed quickly or slowly, whereas a synfire chain is active for a fixed duration, in our model in the order of 100 ms. This duration is in line with the generation of birdsong syllable sequences (Woolley and Rubel, 1997; Hahnloser et al., 2002; Sakata and Brainard, 2008), but appears too short to model elongated movements such as reaching, which are executed within about 500 ms. Generally, longer or shorter activity durations can be generated by adjusting the chain length chains or the propagation speed through appropriately chosen synaptic delays or PSP rise-times (Wennekers and Palm, 1996). On the other hand, a single primitive does not necessarily need to represent a complete action. In the terminology of Rohrer et al. (2002), primitives represent the “atoms” of behavior. Any desired duration can be reached by appropriate concatenation.

Moreover, motor behavior is typically more complex than the straight lines at constant velocity used in this study for the purposes of illustration. To extend this model to movement compositionality would therefore require the identification of more realistic primitives. Candidates include dynamic motion primitives as force fields (Mussa-Ivaldi and Bizzi, 2000) and kinematic primitives such as parabolas (Flash and Handzel, 2007; Polyakov et al., 2009b). However, the use of more complex primitives immediately raises the question of how an appropriate coordinate system can be defined. The activity of prefrontal neurons in reaching tasks has been shown to represent coordinate systems centered around the hand, target, eye fixation point, and even the shoulder (Pesaran et al., 2006). When a complex movement is performed, like handwriting or grasping an object, basic motion features can be observed which repeat elsewhere in an altered fashion. For example, we can almost immediately write using our foot in the sand, without having to practice it. This suggests

that the writing trajectories of letters have not been trained to be restricted to our hand but as a sequence of accelerations in general. The representation of trajectories may even be independent of a particular task (such as writing or catching a ball), but rather an abstract instance to be used in a variety of contexts. This leads to the conclusion that complex movements may be assembled from simpler, context-free building blocks. Hierarchical organizations of synfire chains might therefore realize a movement syntax within one coordinate system or across multiple systems. This could enable a form of binding-based coordinate transformation (Salinas and Abbott, 1995).

The existence of synfire chains and the capacity of the brain to develop them are aspects which have been presupposed in this work. Synfire chains have been postulated to underlie experimentally observed precise spike timing, for example in mammalian cortex (Eckhorn et al., 1988; Abeles et al., 1993; Prut et al., 1998; Ikegaya et al., 2004; Pulvermüller and Shtyrov, 2009) or avian area HVC (Hahnloser et al., 2002; Jin et al., 2007; Kozhevnikov and Fee, 2007) and methods are being developed to detect them in parallel spike train recordings (Schrader et al., 2008). Though it might be possible that such feed-forward structures are hardwired in the cortical or basal ganglia structure, it appears more plausible that they are imprinted by some Hebbian-like mechanism. For this, neuron groups must be repeatedly activated, possibly by means of sensory input or from other areas such as the hippocampus (Ji and Wilson, 2007), leading to stronger synapses between groups. Studies on this issue report conflicting results. While feed-forward structure has been shown to develop in some network models (Izhikevich et al., 2004; Buonomano, 2005; Doursat and Bienenstock, 2006; Jun and Jin, 2007; Fiete et al., 2010), these results do not scale up to large-scale networks with biologically realistic numbers of synapses per neuron (Morrison et al., 2007; Kunkel et al., 2010). Further studies are needed to determine the conditions under which the divergent–convergent connectivity of synfire chains can develop in cortical networks.

Despite these issues, the indirect evidence for synfire chains is great enough that one can legitimately be interested in investigating their capabilities. Indeed, although our model consists exclusively of synfire chains, standard measurement techniques applied to the spiking data can also only produce indirect evidence for synfire activity. Only the activity of the lower level neurons exhibited strong patterns; upper level activity indicated the transition from one primitive or group of primitives to the next with a decrease in spiking activity. By construction, our model predicts a synchronized activity between neurons that code for a particular primitive, as well as synchronization between the upper and lower levels. In principle, those levels may be located in different brain areas. Experimental studies have reported coherent oscillations between different motor areas during action execution, such as M1 and premotor areas (Brovelli et al., 2004).

The exact frequency of the oscillations visible in the mass signal during execution of a complex action is largely determined by the choice of synaptic delay; however, any selection within a reasonable range for this delay would result in oscillatory activity in the order of 100 Hz. Induced gamma activity (as opposed to evoked gamma) lies well in this order (Ball et al., 2008) and may reflect such activity. In addition, our model predicts the presence

of desynchronized activity at the transition between primitives, thus potentially accounting for event-related desynchronization (Pfurtscheller and Lopes da Silva, 1999; Miller et al., 2010).

Our model thus provides us with a theoretical basis to investigate the correlation between composed behavior and neuronal activity. For example, the activity of the network is interpreted in terms of a rate code of directionally tuned neuronal populations. However, as each neuron is only briefly active during the propagation of activity through a synfire chain, it only contributes to a particular phase of a drawing stroke, rather than to the entire duration. Additionally, as the lower level chains are constantly active in the looped network, they can be active during a drawing stroke in any direction. Hence, although the entire system produces reliable output, many of the neurons exhibit weak or negligible direction tuning. This insight may well be relevant for experimental studies of the neural correlates of motor control, which classically assume that neurons involved with movement exhibit directional tuning.

To execute specific non-ongoing sequences, a correct sequence of synchronous pulse stimuli would need to be delivered to the first groups of the relevant lower level chains whilst other activity is inhibited. Up to now, no attempt has been made to explain where the precise instruction pulse sequences arriving at the lower level system should originate. Due to the relatively small binding window (<20 ms), stimuli must be generated very precisely and reliably. Though sensory systems might be too slow to reach such a precision (Thorpe et al., 1996), higher areas such as the cerebellum or the basal ganglia are able to produce this kind of time locking (Dreher and Grafman, 2002). In this work, our focus lies on the generation of the sequences; learning the correct sequence of stimuli to produce a useful sequence of primitives is outside the current scope. However, other studies have already made significant progress in developing learning agents that would be able to learn such sequences (e.g., Baras and Meir, 2007; Farries and Fairhall, 2007; Izhikevich, 2007; Potjans et al., 2009a,b; Vasilaki et al., 2009). Therefore, an interesting future extension of our work is to investigate to what extent our model can fulfill the role of an action selector in network models of learning agents.

Due to the mutual inhibition between chains (unbound chains are less likely to join a synchronized state), our system implements a winner-take-all functionality of action selection. Competing synfire chains provide a neural solution to the selection problem, and exhibit many features of an ideal selection mechanism (for a review see Redgrave et al., 1999). An effective action selector has to choose from a large pool of behaviors depending on their importance or feasibility. Selection must be carried out quickly and also under close-run conditions (*clean switching*), a criterion which is met in our model. During execution, competing “votes” may not interfere with the current behavior (*distortion*), a property also inherent in the running of synfire chains. Once a primitive has been activated, it is executed completely, i.e., actions have *persistence*. Conversely, in any trajectory involving a sequence of primitives, there is an opportunity to choose a more important action at the switch-over point between primitives, i.e., the system exhibits *interruptibility*. In future work we will investigate the relationship between the structure and dynamics of the hierarchic model and its expression of these features.

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