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5	A simple, biologically plausible feature detector for language
6	acquisition
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9	Ansgar D. Endress
10	City, University of London
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16	Running head: A feature detector for language acquisition
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20	Abstract
21	Language has a complex grammatical system we still have to understand
22	computationally and biologically (Hauser et al., 2002; Yang, 2013). However,
23	some evolutionarily ancient mechanisms have been repurposed for grammar
24	(Dehaene & Cohen, 2007; Endress, Cahill, et al., 2009; Endress, Nespor, et al.,
25	2009; Fitch, 2017) so that we can use insight from other taxa into possible circuit-
26	level mechanisms of grammar. Drawing upon recent evidence for the importance
27	of disinhibitory circuits across taxa and brain regions (Chevalier & Deniau, 1990;
28	Letzkus et al., 2015; Hangya et al., 2014; Xu et al., 2013; Goddard et al., 2014;
29	Mysore & Knudsen, 2012; Koyama et al., 2016; Koyama & Pujala, 2018), I
30	suggest a simple circuit that explains the acquisition of core grammatical rules
31	used in 85% of the world's languages (Rubino, 2013): grammatical rules based on
32	sameness/difference relations. This circuit acts as a sameness-detector. Different
33	items are suppressed through inhibition, but presenting two identical items leads
34	to inhibition of inhibition. The items are thus propagated for further processing.
35	This sameness-detector thus acts as a feature detector for a grammatical rule. I
36	suggest that having a set of feature detectors for elementary grammatical rules
37	might make language acquisition feasible based on relatively simple
38	computational mechanisms.
39	
40	Keywords: Language Acquisition; Rule Learning; Perceptual or Memory
41	Primitives; Disinhibition; Circuit Motifs; Reduplication
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43	A simple, biologically plausible feature detector for language
14	acquisition
45	Language acquisition is fast, largely based on positive evidence (or
46	sometimes no evidence at all; Goldin-Meadow & Mylander, 1998; Senghas et al.,
1 7	2004), goes far beyond what learners hear or see in their environment (Chomsky,
48	1959; Pinker, 1984) and results in a uniquely complex grammatical system that
19	stands out in the animal kingdom (Hauser et al., 2002; Yang, 2013). Even
50	seemingly straightforward "memory" problems such as learning the meanings of
51	words hide complexities that call for human-specific grammatical adaptations
52	(Medina, Snedeker, Trueswell, & Gleitman, 2011; Pinker & Jackendoff, 2005).
53	Unsurprisingly, we know very little about the underlying computational
54	mechanisms at the circuit level.
55	However, some linguistic mechanisms are evolutionarily ancient and have
56	been repurposed for linguistic use (Dehaene & Cohen, 2007; Endress, Cahill, et
57	al., 2009; Endress, Nespor, et al., 2009; Fitch, 2017). In such cases, it might be
58	possible to identify core linguistic mechanism whose systems-level
59	implementation might be tractable due to its evolutionary history.
50	Here, I use sameness/difference relations as a case in point. I will first
51	show that many grammatical rules are based on such relations, especially in
52	morphology and phonology, but that similar relations are critical in many other
53	domains and animals, suggesting that they reflect a linguistic core mechanism
54	with evolutionarily ancient roots. I will then suggest that such relations can be
65	computed using an ubiquitous processing motif: disinhibition among neurons or
66	neural populations.

67	Sameness/difference relations in language and other domains and animals
68	Sameness/difference relations are critical for many aspects of linguistic
69	structure, especially in phonology and morphology. For example, some 85% of
70	the world's languages use some form of reduplication (Rubino, 2013). Among
71	many other uses, reduplications can signal changes in word class (e.g., from noun
72	to verb, as in the Marshallese contrast between "takin – sock" and "takinkin – to
73	wear socks"; Moravcsik, 1978), attenuation (as in the Alabama contrast between
74	"kasatka – cold" and "kássatka – cool"; Hardy & Montler, 1988) or
75	intensification; they can mark differences in number (e.g., singular vs. plural),
76	tense (e.g., past vs. present), aspect (e.g., continued vs. repeated occurrence or
77	temporary vs. permanent), size or case (see Rubino, 2013, and references therein).
78	Phonological processes also often appeal to sameness/difference relations,
79	with some processes requiring some features to be identical within a relevant
80	constituent, and others requiring them to be different. Processes that require
81	identical features include vowel harmony and assimilation. Specifically, in
82	languages with vowel harmony, vowels within words (or smaller domains) need
83	to have one or more features in common (Rose & Walker, 2011). For example,
84	Hungarian words generally have either only back vowels or only front vowels;
85	grammatical suffixes thus come in two varieties, one with back vowels and one
86	with front vowels. Accordingly, the dative suffix is -nak for words like "ablak -
87	window" (resulting in forms like "ablaknak") and -nek for words like "bíró -
88	judge" (resulting in forms like "bírónek"; Hayes & Londe, 2006). Likewise, in
89	languages with consonant assimilation, consonants must share a feature with other
90	surrounding consonants. For example, in English, "football" might be pronounced

91 as "foopball" because the place of articulation of the [t] at the end of [foot] gets 92 assimilated to the place of articulation of the [b] at the start of "ball"; in contrast, 93 in French, "football" might be pronounced as "foodball" because the voicing 94 feature of the [t] (but not the place feature) gets assimilated to the following [b] 95 (Darcy, Ramus, Christophe, Kinzler, & Dupoux, 2009). Both vowel harmony and 96 assimilation thus introduce sameness relations among phonemes. Listeners use 97 these sameness relations not only in word recognition (Darcy et al., 2009; Mitterer 98 & Blomert, 2003; Suomi, McQueen, & Cutler, 1997), but also as cues to learn 99 new words (Vroomen, Tuomainen, & de Gelder, 1998). Further, sameness 100 relations in the form of vowel harmony often interact with other area of grammar, 101 such as stress assignment or morphology (Rose & Walker, 2011). 102 While vowel harmony and assimilation require sameness relations among 103 phonemic features, other phonological processes impose difference relations. 104 Such processes include the Obligatory Contour Principle (Frisch, Pierrehumbert, 105 & Broe, 2004; McCarthy, 1986). Initially, the Obligatory Contour Principle was 106 proposed to account for the observation that, in certain tone languages, tones 107 cannot be repeated within words, but it also applies to other phonological 108 phenomena. For example, in Semitic languages like Arabic and Hebrew, the basic 109 meaning of verbs is given by their consonantal root; roots like /k t b/ are then 110 transformed into surface forms such as "kataba – he wrote" and "kutiba – it was 111 written" (Frisch et al., 2004). The OCP prevents consonantal roots from having 112 repeated consonants, while other morphological processes can create (rather than 113 prevent) sameness relations among consonants (Frisch et al., 2004; McCarthy, 114 1986). Such rules might also interact with other areas of grammar (Yip, 1988) and

115	speakers apply them even when presented with novel non-sense words (e.g.,
116	Berent & Shimron, 1997; Frisch & Zawaydeh, 2001).
117	Sameness relations are also important during language acquisition.
118	Reduplications are prominent in child-directed speech across languages
119	(Ferguson, 1964) and children themselves "invent" forms with reduplicated
120	syllables; these reduplicated forms might be important for acquiring multisyllabic
121	words (Schwartz, Leonard, Wilcox, & Folger, 1980) and syllable-final consonants
122	that would otherwise be lost (Fee & Ingram, 1982).
123	More generally, sameness relations have been critical for defining the
124	computational complexity of phonological rules (Culy, 1985; Manaster-Ramer,
125	1986), and, in developmental psychology, rules based on sameness relations have
126	been the most prominent assay for studying rule-learning in human infants
127	(Marcus et al., 1999), to the extent that in a recent meta-analysis of "rule-
128	learning" in infancy, rule-learning was treated as synonymous with the learning of
129	sameness relations (Rabagliati, Ferguson, & Lew-Williams, 2019).
130	Sameness relations are also important for other forms of language use. Not
131	only are rhymes and alliterations important in poetry (Fabb, 2015), but many
132	language games that spontaneously arise in children also make extensive use of
133	sameness relations in the form of reduplications (Bagemihl, 1995). For example,
134	in the Chinese May-ka language game, syllables are duplicated and then the
135	vowel of the first duplicate is replaced by "ay" and the consonant of the second
136	duplicate by "k"; ma (mother) thus becomes may-ka (Bao, 1990; Yip, 1982).
137	Despite their simplicity, sameness relations thus appear to be a core part of
138	the language faculty.

139	However, sameness/difference rules are clearly not specific to language.
140	They are crucial for many other aspects of cognition, including motor learning
141	(Brooks, 1986), any comparison of sensory input to predictions or internal state
142	(e.g., novelty detection in the hippocampus; Kumaran & Maguire, 2007) and
143	short-term memory tasks such as delayed-match to sample tasks (Cope et al.,
144	2018; Engel & Wang, 2011). Accordingly, grammar-like rules based on
145	sameness/difference relations can be learned in many non-linguistic domains in
146	humans (Dawson & Gerken, 2009; Endress, Dehaene-Lambertz, & Mehler, 2007;
147	Marcus, Fernandes, & Johnson, 2007; Saffran, Pollak, Seibel, & Shkolnik, 2007)
148	and by many non-human animals (de la Mora & Toro, 2013; Hauser & Glynn,
149	2009; Martinho & Kacelnik, 2016; Murphy, Mondragon, & Murphy, 2008;
150	Neiworth, 2013; Pepperberg, 1987; Smirnova, Zorina, Obozova, & Wasserman,
151	2015; Versace, Spierings, Caffini, Ten Cate, & Vallortigara, 2017; but see
152	Heijningen, Visser, Zuidema, & Cate, 2009; Hupé, 2017; Langbein & Puppe,
153	2017), possibly through a specialized sameness-detector (Endress, 2013; Endress
154	et al., 2007) that might exist from birth (Antell, Caron, & Myers, 1985; Gervain,
155	Berent, & Werker, 2012; Gervain, Macagno, Cogoi, Peña, & Mehler, 2008). The
156	computations underlying sameness/difference relations thus reflect a core
157	linguistic mechanism whose systems-level implementation might be tractable due
158	to its evolutionary history.
159	Disinhibition-based computations
160	Here, drawing upon recent evidence stressing the importance of
161	disinhibitory circuits (neurons that inhibit other inhibitory neurons) across a
162	variety of taxa and brain regions (Chevalier & Deniau, 1990; Goddard et al.,

163 2014; Hangya et al., 2014; Koyama et al., 2016; Mysore & Knudsen, 2012; Xu et 164 al., 2013), I suggest a simple circuit that acts as a sameness-detector. Disinhibition 165 has been observed in a variety of brain areas (Chevalier & Deniau, 1990; Letzkus 166 et al., 2015), and some interneuron populations specifically inhibit other 167 inhibitory interneurons (Hangya et al., 2014; Xu et al., 2013). Critically, some 168 interneuron types receive both local and long-range input; such interneurons have 169 been found to inhibit other inhibitory interneurons in auditory (Pi et al., 2013), 170 visual (Pfeffer, Xue, He, Huang, & Scanziani, 2013), somatosensory (Lee, 171 Kruglikov, Huang, Fishell, & Rudy, 2013) and prefrontal cortex (Pi et al., 2013), 172 from where they can exert spatially remarkably specific disinhibition on other 173 populations (Zhang et al., 2014). Accordingly, Hangya et al. (2014) argued that 174 this disinhibitory circuit might be a cortical circuit motif. Other authors suggested 175 a more local disinhibitory circuit motif with mutual inhibition among inhibitory 176 neurons (Goddard et al., 2014; Koyama et al., 2016; Koyama & Pujala, 2018; 177 Mysore & Knudsen, 2012). 178 Disinhibitory circuits have been proposed to account for a variety of 179 cognitive phenomena, including attentional selection (van Der Velde & de 180 Kamps, 2001; Zhang et al., 2014), gain control (Fu et al., 2014), sequential 181 discriminations of stimulus strength of stimuli (Machens, Romo, & Brody, 2005; 182 Miller & Wang, 2006; but see Barak, Sussillo, Romo, Tsodyks, & Abbott, 2013) 183 categorization of stimuli (Goddard et al., 2014; Kusunoki, Sigala, Nili, Gaffan, & 184 Duncan, 2010; Mysore & Knudsen, 2012), behavioral response selection (Jovanic 185 et al., 2016; Zhao et al., 2019), associative learning (Letzkus et al., 2011), 186 plasticity (Fu, Kaneko, Tang, Alvarez-Buylla, & Stryker, 2015) and social

behavior (Marlin, Mitre, D'amour, Chao, & Froemke, 2015; Owen et al., 2013). Here, I suggest that the same biological mechanisms might provide a circuit-level mechanism for a core grammatical computation based on sameness vs. difference computations.

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Models of sameness/difference relations

A number of models of how sameness-relations might be computed have been proposed in the literature (Arena et al., 2013; Carpenter & Grossberg, 1987; Cope et al., 2018; Engel & Wang, 2011; Hasselmo & Wyble, 1997; J. S. Johnson, Spencer, Luck, & Schöner, 2009; Ludueña & Gros, 2013; Wen, Ulloa, Husain, Horwitz, & Contreras-Vidal, 2008). The underlying principles and assumptions vary substantially across models. Some rely on the fact that repeatedly activated representations suffer some form of neural "fatigue" (Grill-Spector, Henson, & Martin, 2006; Kumaran & Maguire, 2007), others on circuitry where the combined input from some form of memory and from sensory representations matching (or mismatching) the memory representations must be sufficiently strong (Carpenter & Grossberg, 1987; Hasselmo & Wyble, 1997; Wen et al., 2008) or where the *difference* between input from memory and from sensory representations is the critical variable (Engel & Wang, 2011). Still other models detect reduced levels inhibition for novel compared to previously encountered items (Cope et al., 2018; J. S. Johnson et al., 2009). I discuss these models in more detail in Supplementary Material 1, where I show that they fall short on at least one of two criteria of grammar learning: they either do not generalize to unseen exemplars or they require labeled counter-examples.

To better illustrate the computational principles underlying the current

dishibition-based circuit, I will first present a version of the model that can detect sameness relations in sequentially presented stimuli. Following this, I will sketch a version of the model that can detect sameness relations in spatially distributed, simultaneously presented stimuli, and finally a model that can detect sameness relations in both simultaneously presented stimuli and sequentially presented stimuli.

217 Results

Sameness detection for sequential stimuli

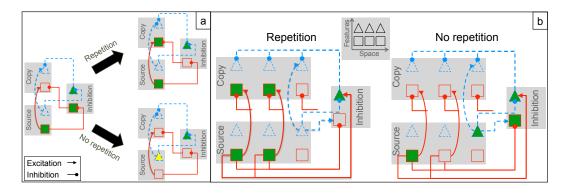
Figure 1a shows a possible disinhibition-based architecture of how sameness might be detected for sequentially presented items. (Model equations are given in Appendix A; an R implementation is available online). The model comprises two populations of neurons (hereafter "layers") that encode features of items (e.g., frequency, color and so on; in Figure 1, the features are represented as geometric shapes).

The *source layer* receives input; input can be sensory or non-sensory, depending on where this circuit is located in the brain. Units in the *copy layer* receive excitatory one-to-one input from units in the source layer that code for the same feature. However, they also receive feature-specific tonic inhibition from an *inhibition layer* (which might consist of interneurons); tonic inhibition has been observed in a variety of brain regions, and might subserve functions such as maintaining an appropriate level of excitability or the suppression of undesirable motor programs (Benjamin, Staras, & Kemenes, 2010; Farrant & Nusser, 2005; Semyanov, Walker, Kullmann, & Silver, 2004).

Due to the inhibition from the inhibition layer to the copy layer, input

from the source layer is not propagated to the copy layer with a single stimulation.		
The critical aspect of this circuit is that each feature in the source layer also		
inhibits the corresponding feature in the inhibition layer, which, in turn, reduces		
inhibitory input to the copy layer for that feature. A similar phenomenon has been		
observed in auditory fear conditioning, where inhibition of (inhibitory)		
parvalbumin-positive interneurons allowed for associations between sounds and		
aversive stimuli to be formed (Letzkus et al., 2011).		
Accordingly, once the inhibitory input to the copy layer ceases, there will		
be a time window during which the excitatory input from the source layer can		
drive the corresponding units in the copy layer. As a result, only repeated items		
will be propagated to the copy layer. Any readout mechanism for the copy layer		
(e.g., a population of thresholded neurons) could thus act as a sameness-detector.		

While I model disinhibition across different neural populations, the same computational principles could be implemented using reciprocal inhibition among inhibitory neurons as in earlier models of stimulus selection and categorization (Goddard, Mysore, Bryant, Huguenard, & Knudsen, 2014; Koyama et al., 2016; Koyama & Pujala, 2018; Mysore & Knudsen, 2012). To do so, one would simply replace the inhibitory connections from the source layer to the inhibition layer with inhibition in the source layer that is itself subject to lateral inhibition.



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Figure 1: A disinhibition-based sameness-detector for (a) sequentially (b) simultaneously presented identical items. The geometric shapes (squares and triangles) stand for populations of neurons that encode features of the items (e.g., frequency, shape etc.); filled shapes are currently active while empty shapes are currently inactive. (a) Units in the source layer (bottom gray box) receive (sensory or other) input. Units in the copy layer (top gray box) receive one-to-one excitatory input from the source layer. Critically, units from the inhibition layer (right gray box) exert tonic inhibition on the copy layer. (a, left) Upon initial presentation of a feature (represented here as a square), all units in the inhibition layer are active. As a result, excitatory input from the source layer is not propagated to the copy layer. (a, right, top) Feature-specific inhibition from the source layer to the corresponding units in the inhibition layer shuts down the inhibitory input to the copy layer. If the same item is presented again during the time window of reduced inhibition, input from the source layer is propagated to the copy layer. (a, right, bottom) If a new, non-identical item is presented, the source layer cannot drive the copy layer because the corresponding units in the inhibition layer have not been inhibited. Sameness-detection thus proceeds by reading out the copy layer, as only repeated items are propagated to the copy layer. (b) Sameness-detection in simultaneously presented, spatially arranged items. The source layer consists of populations of neurons coding for features (arranged in the y-direction), but these units encode space as

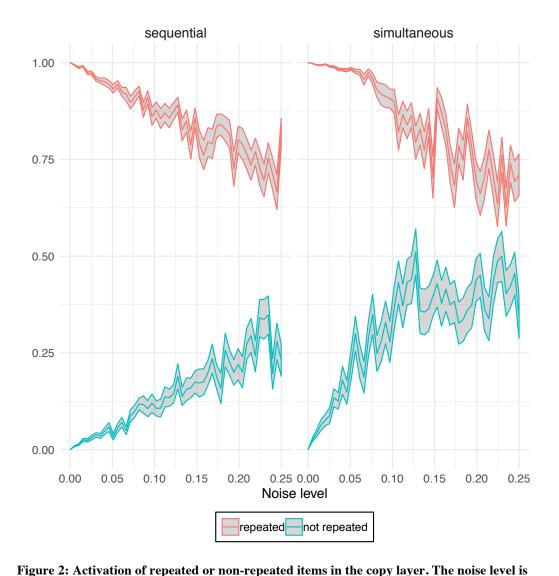
well (arranged in the x-direction). Tonically active inhibitory (inter-)neurons (small gray box on the right) prevent activation in the copy layer (top gray box). Critically, they receive inhibitory input from those units in the source layer that code for the same feature, and excitatory input from units coding for other features. For example, units representing squares in the input layer inhibit all units representing squares in the inhibition layer, and excite all other units. (b, left) If the stimuli consist of two identical items (squares), the combined inhibitory input from the identical items in the source layer shuts down the corresponding units in the inhibition layer, which lets identical items "pass through" to the copy layer (b, right) In contrast, when the stimuli consist of two different items, these singleton features are insufficient to drive the copy population due to inhibition from the inhibition layer.

I simulated this model at various levels of noise; at each noise level, I ran 50 simulations, representing 50 virtual participants. Figure 2 (left) shows that, in the copy layer, activation for repeated features is high, while activation for non-repeated features is low. Repeated items are thus highly discriminable from non-repeated items. This result is robust to the simulated noise level. A simple disinhibition-based circuit can thus act as a sameness-detector that discriminates repeated features from not repeated features.

While the primary goal of this model is to detect when two temporarily adjacent items are identical, whether or not it can detect the sameness of two objects with intervening material depends on the time constants of the disinhibitory effects. If disinhibition is sufficiently long-lasting, the model will also detect the sameness of two non-adjacent items (e.g., of the two *A*'s in the sequence *ABA*). If so, it would predict that, the further two items are separated (in terms of the amount of intervening time and/or the number of intervening items, which might or might not have separable effects), the harder it should become to detect the sameness of the two items. At least in infants, it might be harder to detect non-adjacent repetitions compared to adjacent repetitions (S. P. Johnson et al., 2009; Kovács & Mehler, 2008, 2009).

That being said, the separation of two items is unlikely to be the only determinant of how it easy it is to detect whether they are the same. For example, in a longer sequence like *ABCDEDFGA*, the two *A*'s are further apart than the two *D*'s. Still, it might easier to detect the sameness of the two *A*'s than of the two *D*'s despite their greater distance because initial and final items are more salient than medial items (Benavides-Varela & Mehler, 2015; Endress, Scholl, & Mehler,

2005). As a result, the representations of initial items are likely stronger than
those of medial items and thus create stronger and longer-lasting disinhibition.
However, the goal of the current model is just to show that a simple and
ubiquitous mechanism such as disinhibition can serve as the basis of a sameness
detector, while more detailed predictions require a biophysically more realistic
model.



the standard deviation of normally distributed noise centered at zero. In each curve, the middle line shows the average activation across 50 simulations, representing 50 participants. The shaded areas represent standard errors from the mean. (Top) Activation in the models shown in Figure 1 that detect either sequentially (Figure 1a) or simultaneously presented

(Figure 1b) identical items. (Left). In the sequential sameness-detector (Figure 1a), the

activity of repeated items is highly discriminable from that from non-identical items even for high noise levels. (Right). In the *simultaneous* sameness-detector (Figure 1b), the activity of repeated items is highly discriminable from that of non-repeated items even for high noise levels.

325 Sameness detection for simultaneous stimuli 326 In its current stage, the model can detect the sameness of sequentially presented 327 stimuli, but not of spatially distributed, simultaneously presented stimuli, simply 328 because space is not represented. Figure 1b shows a version of the model where 329 items are presented simultaneously rather than sequentially. Again, there is a 330 source layer, a copy layer, and an inhibition layer. The model differs from the 331 sequential model in three critical aspects. First, all layers now represent space. In 332 Figure 1b, the vertical axis represents the features as before, while the horizontal 333 axis represents the spatial locations of the items (though space is presumably 334 represented in some topological order in real neuronal populations). This change 335 is necessary so that two simultaneously presented identical objects can be 336 represented. 337 Second, the connectivity between the source layer and the inhibition layer 338 has been changed. Units in the source layer send (i) inhibitory input to all units in 339 the inhibition layer that code for the same feature across all locations and (ii) 340 excitatory input to all units in the inhibition layer that code for different features; 341 in other words, there is center-surround disinhibition among features. This ensures 342 that, in the copy layer, different-feature input from the source layer stays

Third, the sequential model needs to update the activation of the copy layer before that of the inhibition layer; if the inhibition layer were updated first, a single presentation of a feature would be sufficient to produce disinhibition. In contrast, the simultaneous model needs to update the inhibition layer before the copy layer; if the copy layer were updated first, there would be no disinhibition

inhibited, while same-feature input is disinhibited.

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for identical features.

I simulated this architecture using 50 virtual participants. As shown in Figure 2, identical items are highly discriminable from non-identical items even at high levels of noise. A simple, disinhibition-based circuit can thus detect sameness relations among simultaneously presented identical objects.

A combined model of sameness detection for simultaneous and sequential stimuli While the main differences between the sequential and the simultaneous

While the main differences between the sequential and the simultaneous circuit are simply due to how stimuli are presented (i.e., spatial representations and lateral inhibition among features could be added to the sequential model, but are not necessary), the different update orders raise the question of whether a combined model can be developed that detects both sequential and simultaneous sameness relations. Practically speaking, sequential and simultaneous presentation might not be as different as they seem. For example, if observers attend simultaneously presented items one after the other (Liu & Becker, 2013; Vogel, Woodman, & Luck, 2006; but see Mance, Becker, & Liu, 2012), we need a sequential model to account for *simultaneous* sameness-detection; conversely, if sequential items are placed in some kind of (short-term) memory before being compared, we need a simultaneous model for sameness-detection in sequentially presented items. As such, a combined sequential/simultaneous model might be neither necessary nor desirable.

Be that as it might, such a combined model is shown in Figure 3.

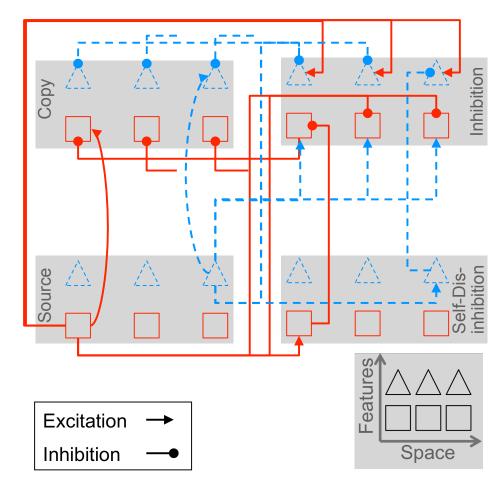


Figure 3: Combined disinhibition-based sameness-detector for both sequential and simultaneous sameness relations. As in the simultaneous circuit from Figure 1b, the source layer (bottom left gray box) consists of populations of neurons coding for features (arranged in the y-direction) and spatial locations (arranged in the x-direction). Tonically active units in the inhibition layer (top right gray box) prevent activation in the copy layer (top left gray box). Units in the inhibition layer receive (i) inhibitory input from the source layer for units coding for the same feature and (ii) excitatory input for units coding for other features, leading to center-surround disinhibition among features and, in the copy layer, to inhibition

for different-feature input and disinhibition for same-feature input. Critically, and in contrast to the simultaneous model from Figure 1b, units in the source layer do not inhibit units in the inhibition layer that code for features at their own spatial location; they disinhibit features only at other locations. To obtain disinhibition at the spatial location of a given unit, a self-inhibition layer (bottom right gray box) was added that receives one-to-one input from the source layer, and that specifically inhibits units in the inhibition layer that code for the same feature at the same spatial location. This delays same-feature/same-location disinhibition to prevent a single sequential presentation of a feature from disinhibiting that feature.

This "combined" sameness-detector is similar to the simultaneous sameness-detector in that it comprises a source layer, a copy layer and an inhibition layer, and that the copy layer receives excitatory input from the source layer. However, (dis-)inhibition is organized differently. The copy layer still receives tonic inhibition from those units in the inhibition layer that code for the same feature and spatial position. Further, each feature of the input layer inhibits the corresponding feature in the inhibition layer across spatial positions (i.e., it disinhibits this feature in the copy layer), and excites all other features.

The critical difference is that disinhibition of features at the same location is delayed. To do so, I removed direct connections between the source layer and the inhibition layer that coded for the same feature at the same location (while keeping the center-surround disinhibition at other locations). Instead, I added a *self-disinhibition layer* where each unit (i) receives excitatory input from the corresponding feature and location in the source layer and (ii) sends inhibitory input to all units coding for the same feature (across locations) in the inhibition layer. (While these modifications might seem to some extent *ad-hoc*, as mentioned above, it is not clear if a combined sequential/simultaneous model is necessary or desirable in the first place.)

As shown in Figure 4, identical items were highly discriminable from non-identical items in the simultaneous situation across noise levels; in contrast, in the sequential situation, discriminability suffered as noise increased.

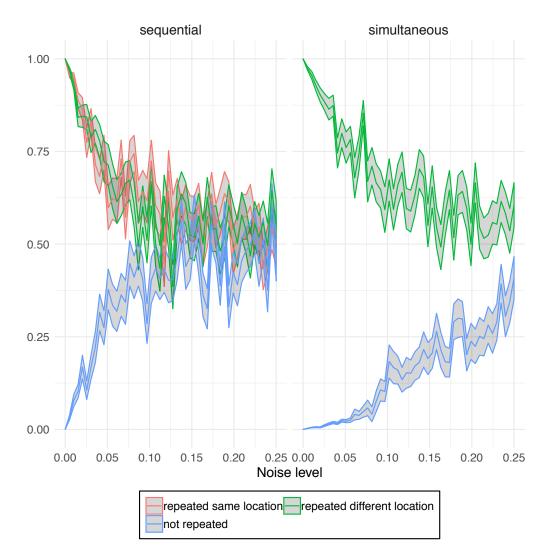


Figure 4: Activation in the copy layer of the combined sequential/simultaneous sameness-detector (Figure 3). (Left) In the combined sequential/simultaneous sameness-detector, repeated features can be repeated either at the same location or at a different location. While activation of (same or different location) repeated items is highly discriminable from activation for non-repeated items for moderate noise levels, discriminability becomes much poorer at high noise levels, when the standard deviation of the noise reaches about 15% of the activation level of active neurons. (Right) The combined sequential/simultaneous

419 sameness-detector (Figure 3) shows that the activation in the copy layer is highly 420 discriminable between simultaneously repeated items and non-repeated items, even for high 421 noise levels. 422 **Discussion** 423 The current results thus show that a simple and biologically realistic 424 circuit can support a core grammatical computation that is used in more than 80% 425 of the world's languages: grammatical rules based on sameness/difference 426 relationships. In this circuit, non-identical items are filtered out through tonic 427 inhibition as well as center-surround inhibition. In contrast, when identical items 428 are presented sequentially or simultaneously, inhibition is inhibited; this 429 disinhibition of identical items then allows them to be propagated for further 430 processing. 431 Unlike previous models of sameness-detection (Arena et al., 2013; 432 Carpenter & Grossberg, 1987; Cope et al., 2018; Engel & Wang, 2011; Hasselmo 433 & Wyble, 1997; Johnson, Spencer, Luck, & Schöner, 2009; Ludueña & Gros, 434 2013; Wen, Ulloa, Husain, Horwitz, & Contreras-Vidal, 2008; see Supplementary 435 Material 1), the model satisfies critical criteria of grammar acquisition: (1) It 436 generalizes to unseen stimuli and (2) does not require any labeled 437 counterexamples for learning, simply because this circuit architecture does not 438 require any learning at all. 439 Once such a sameness-detector is available, it can be used for building 440 more complex grammatical rules. For example, after exposure to syllable 441 sequences such as dubaba, seven-month-olds notice that the last two syllables are 442 identical, and generalize this sameness-relation to new items (Marcus et al.,

443	1999). Critically, they do not only have to detect the sameness relation between
444	the last two syllables, but also have to associate it with the correct serial position
445	(Endress et al., 2007; Gervain et al., 2012). Once a sameness-detector is available
446	it can form associations with representations of sequential positions or other
447	stimuli (Kabdebon & Dehaene-Lambertz, 2019), allowing learners to acquire
448	more complex, composite rules, which is one of the hallmarks of complex
449	cognition (Corballis, 2014; Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015
450	Fitch & Martins, 2014; Hauser & Watumull, 2017).
451	This, in turn, suggests a fundamentally new view on language acquisition.
452	Learners might be equipped with a potentially large number of potentially
453	complex detectors for a variety of rules that act as feature detectors for
454	grammatical rules (Endress, Nespor, et al., 2009). Learning then involves
455	combining these features, potentially through the use of associative mechanisms.
456	This would be consistent with results from formal language theory, where suitable
457	pre-processing (e.g., through feature detectors) can reduce the complexity of the
458	required computational mechanism. For example, a finite state automaton
459	operating on trees can recognize context-free languages (Morgan, 1986) and even
460	humble rules based on sameness relations can be shown to be beyond the reach of
461	even context-free grammars (Culy, 1985; Manaster-Ramer, 1986).
462	Feature detectors for elementary grammatical rules might thus expand the
463	range of grammars that even simple learning mechanisms (such as associative
464	mechanisms) can learn, which, in turn might make language acquisition feasible
465	using relatively simple computational machinery.

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Appendix A: Model equations

A.1 Sequential model

The feature f is encoded in the source layer, the inhibition layer and the copy layer; the corresponding activations, are $S_f(t)$ for a unit encoding feature f in the source layer, $I_f(t)$ for such a unit in the inhibition layer and (3) $C_f(t)$ such for a unit in the copy layer. $E_f(t)$ is the external input, $\mathcal{N}(\mu,\sigma)$ is a random value drawn from a normal distribution with mean μ and standard deviation σ .

Before stimulation, the activation in the source layer and in the copy layer are initialized to zero (plus noise), while the activation in the inhibition layer is initialized to some value a_l (here arbitrarily set to 1):

$$S_f(t=0) \sim \mathcal{N}(0, \sigma_{activation})$$
 810 (1)
$$C_f(t=0) \sim \mathcal{N}(0, \sigma_{activation})$$

$$I_f(t=0) \sim \mathcal{N}(a_I, \sigma_{activation})$$

The connection weights between units in the different layers are indicated by w: $w^{I,S}$ from the source layer to the inhibition layer, $w^{C,S}$ from the source layer to the copy layer and $w^{C,I}$ from the inhibition layer to the copy layer. A connection between a source layer unit coding for feature f and a copy layer unit coding for feature f is indicated by $w^{C,S}_{f,f}$. The weights are given as follows:

$$w_{f',f}^{C,S} \sim \begin{cases} \mathcal{N}(1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

$$w_{f',f}^{C,I} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

$$w_{f',f}^{I,S} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

$$w_{f',f}^{I,S} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

At each time step, the activations in the different layers are then updated as follows; as mentioned in the main text, the update order is critical.

822

$$S_{f}(t) = E_{f}(t) + \mathcal{N}(0, \sigma_{activation})$$
823 (3)
$$C_{f}(t) = w_{f}^{C,S}S_{f}(t) + w_{f}^{C,I}I_{f}(t) + \mathcal{N}(0, \sigma_{activation})$$

$$I_{f}(t) = \mathcal{N}(a_{I}, \sigma_{activation}) + w_{f}^{I,S}S_{f}(t)$$

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At the end of each update cycle, the activations are curtailed to be between zero and one.

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A.2. Simultaneous model

In the simultaneous model, units represent both features and spatial locations. $S_{f,l}(t)$ is thus the activation of a unit in the source layer that encodes feature f at location l, $I_{f,l}(t)$ is the corresponding activation in the inhibition layer and (3) $C_{f,l}(t)$ is the corresponding activation in the copy layer. $E_{f,l}(t)$ is the external input.

Before stimulation, the activation in the source layer and in the copy layer are initialized to zero (plus noise), while the activation in the inhibition layer is

initialized to some value a_l (here arbitrarily set to 1):

836

837 (4)
$$S_{f,l}(t=0) \sim \mathcal{N}(0, \sigma_{activation})$$

$$C_{f,l}(t=0) \sim \mathcal{N}(0, \sigma_{activation})$$

$$I_{f,l}(t=0) \sim \mathcal{N}(a_{l}, \sigma_{activation})$$

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Connection weights now carry indices for both features and spatial locations. For example, a connection between a source layer unit coding for feature f at location l and a copy layer unit coding for feature f at location l is indicated by $w^{C,S}_{f,f,l',l}$. The weights are given as follows:

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$$w_{f',f,l',l}^{C,S} \sim \begin{cases} \mathcal{N}(1,\sigma_{weight}) & f = f', l = l' \\ 0 & \text{otherwise} \end{cases}$$

$$844 \qquad (5) \qquad w_{f',f,l',l}^{C,I} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

$$w_{f',f,l',l}^{I,S} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ \mathcal{N}(1,\sigma_{weight}) & f \neq f' \end{cases}$$

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At each time step, the activations in the different layers are then updated as follows; as mentioned in the main text, the update order is critical.

$$S_{f,l}(t) = E_{f,l}(t) + N(0, \sigma_{activation})$$

$$I_{f,l}(t) = N(a_{I}, \sigma_{activation}) + \sum_{f_{S},l_{S}} w_{f,l,f_{S},l_{S}}^{I,S} S_{f_{S},l_{S}}(t)$$

$$C_{f,l}(t) = \sum_{f_{S},l_{S}} w_{f,l,f_{S},l_{S}}^{C,S} S_{f_{S},l_{S}}(t) + \sum_{f_{I},l_{I}} w_{f,l,f_{I},l_{I}}^{C,I} I_{f_{I},l_{I}}(t) + N(0, \sigma_{activation})$$

At the end of each update cycle, the activations are curtailed to be between zero and one.

A.3. Combined model

The combined sequential/simultaneous model is similar to the simultaneous model in that it comprises a source layer, a copy layer and an inhibition layer and that the copy layer receives excitatory input from the source layer as well as tonic inhibition from those units in the inhibition layer that code for the same feature and spatial position. Further, each feature of the input layer inhibits the corresponding feature in the inhibition layer across spatial positions and excites all other features. The critical difference between the simultaneous and the combined model is that there are no connections between the source layer and the inhibition layer that code for the same feature *at the same location* (while disinhibition occurs for other locations), and that same-location disinhibition of features proceeds through a *self-disinhibition layer* where each unit (1) receives excitatory input from the corresponding feature and location in the source layer (2) sends inhibitory input to all units coding for the same feature (across locations) in the inhibition layer.

The symbols for the activation in the source, inhibition and copy layers are the same as in the simultaneous model; activation in the self-disinhibition layer for a unit coding for feature f at location l is designated as $D_{f,l}(t)$ and is initialized using random values around zero.

The symbols for the connection weights are similar to those in the simultaneous model, but the weights reflect the changes above:

$$w_{f',f,l',l}^{C,S} \sim \begin{cases} \mathcal{N}(1,\sigma_{weight}) & f = f', l = l' \\ 0 & \text{otherwise} \end{cases}$$

$$w_{f',f,l',l}^{D,S} \sim \begin{cases} \mathcal{N}(1,\sigma_{weight}) & f = f', l = l' \\ 0 & \text{otherwise} \end{cases}$$

$$875 \qquad (7) \qquad w_{f',f,l',l}^{C,I} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

$$w_{f',f,l',l}^{I,S} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f', l \neq l' \\ 0 & f = f', l = l' \\ \mathcal{N}(1,\sigma_{weight}) & f \neq f' \end{cases}$$

$$w_{f',f,l',l}^{D,D} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

At each time step, the activations in the different layers are then updated as follows; again, the update order is critical.

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$$S_{f,l}(t) = E_{f,l}(t) + N(0, \sigma_{activation})$$

$$I_{f,l}(t) = N(a_{I}, \sigma_{activation}) + \sum_{f_{S}, l_{S}} W_{f,l,f_{S},l_{s}}^{I,S} S_{f_{S},l_{S}}(t) + \sum_{f_{D}, l_{D}} W_{f,l,f_{D},l_{D}}^{I,D} D_{f_{D},l_{D}}(t)$$

$$C_{f,l}(t) = \sum_{f_{S}, l_{S}} W_{f,l,f_{S},l_{s}}^{C,S} S_{f_{S},l_{S}}(t) + \sum_{f_{I}, l_{I}} W_{f,l,f_{I},l_{I}}^{C,I} I_{f_{I},l_{I}}(t) + N(0, \sigma_{activation})$$

$$D_{f,l}(t) = \sum_{f_{S}, l_{S}} W_{f,l,f_{S},l_{s}}^{D,S} S_{f_{S},l_{S}}(t) + N(0, \sigma_{activation})$$

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At the end of each update cycle, the activations are curtailed to be between zero and one.