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5	A simple, biologically plausible feature detector for language
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16	Running head: A feature detector for language acquisition
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19	
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
42	

# 43 A simple, biologically plausible feature detector for language 44 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., 47 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 49 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. 60 Here, I use sameness/difference relations as a case in point. I will first 61 show that many grammatical rules are based on such relations, especially in 62 morphology and phonology, but that similar relations are critical in many other 63 domains and animals, suggesting that they reflect a linguistic core mechanism 64 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 <i>-nek</i> 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.

191

#### Models of sameness/difference relations

192 A number of models of how sameness-relations might be computed have 193 been proposed in the literature (Arena et al., 2013; Carpenter & Grossberg, 1987; 194 Cope et al., 2018; Engel & Wang, 2011; Hasselmo & Wyble, 1997; J. S. Johnson, 195 Spencer, Luck, & Schöner, 2009; Ludueña & Gros, 2013; Wen, Ulloa, Husain, 196 Horwitz, & Contreras-Vidal, 2008). The underlying principles and assumptions 197 vary substantially across models. Some rely on the fact that repeatedly activated 198 representations suffer some form of neural "fatigue" (Grill-Spector, Henson, & 199 Martin, 2006; Kumaran & Maguire, 2007), others on circuitry where the 200 *combined* input from some form of memory and from sensory representations 201 matching (or mismatching) the memory representations must be sufficiently 202 strong (Carpenter & Grossberg, 1987; Hasselmo & Wyble, 1997; Wen et al., 203 2008) or where the *difference* between input from memory and from sensory 204 representations is the critical variable (Engel & Wang, 2011). Still other models 205 detect reduced levels inhibition for novel compared to previously encountered 206 items (Cope et al., 2018; J. S. Johnson et al., 2009). I discuss these models in 207 more detail in Supplementary Material 1, where I show that they fall short on at 208 least one of two criteria of grammar learning: they either do not generalize to 209 unseen exemplars or they require labeled counter-examples. 210 To better illustrate the computational principles underlying the current

211	dishibition-based circuit, I will first present a version of the model that can detect
212	sameness relations in sequentially presented stimuli. Following this, I will sketch
213	a version of the model that can detect sameness relations in spatially distributed,
214	simultaneously presented stimuli, and finally a model that can detect sameness
215	relations in both simultaneously presented stimuli and sequentially presented
216	stimuli.
217	Results
218	Sameness detection for sequential stimuli
219	Figure 1a shows a possible disinhibition-based architecture of how
220	sameness might be detected for sequentially presented items. (Model equations
221	are given in Appendix A; an R implementation is available online). The model
222	comprises two populations of neurons (hereafter "layers") that encode features of
223	items (e.g., frequency, color and so on; in Figure 1, the features are represented as
224	geometric shapes).
225	The source layer receives input; input can be sensory or non-sensory,
226	depending on where this circuit is located in the brain. Units in the copy layer
227	receive excitatory one-to-one input from units in the source layer that code for the
228	same feature. However, they also receive feature-specific tonic inhibition from an
229	inhibition layer (which might consist of interneurons); tonic inhibition has been
230	observed in a variety of brain regions, and might subserve functions such as
231	maintaining an appropriate level of excitability or the suppression of undesirable
232	motor programs (Benjamin, Staras, & Kemenes, 2010; Farrant & Nusser, 2005;
233	Semyanov, Walker, Kullmann, & Silver, 2004).
234	Due to the inhibition from the inhibition layer to the copy layer, input

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235	from the source layer is not propagated to the copy layer with a single stimulation.
236	The critical aspect of this circuit is that each feature in the source layer also
237	inhibits the corresponding feature in the inhibition layer, which, in turn, reduces
238	inhibitory input to the copy layer for that feature. A similar phenomenon has been
239	observed in auditory fear conditioning, where inhibition of (inhibitory)
240	parvalbumin-positive interneurons allowed for associations between sounds and
241	aversive stimuli to be formed (Letzkus et al., 2011).
242	Accordingly, once the inhibitory input to the copy layer ceases, there will
243	be a time window during which the excitatory input from the source layer can
244	drive the corresponding units in the copy layer. As a result, only repeated items
245	will be propagated to the copy layer. Any readout mechanism for the copy layer
246	(e.g., a population of thresholded neurons) could thus act as a sameness-detector. <sup>1</sup>
247	

<sup>&</sup>lt;sup>1</sup> 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.





250 Figure 1: A disinhibition-based sameness-detector for (a) sequentially (b) simultaneously 251 presented identical items. The geometric shapes (squares and triangles) stand for 252 populations of neurons that encode features of the items (e.g., frequency, shape etc.); filled 253 shapes are currently active while empty shapes are currently inactive. (a) Units in the source 254 layer (bottom gray box) receive (sensory or other) input. Units in the copy layer (top gray 255 box) receive one-to-one excitatory input from the source layer. Critically, units from the 256 inhibition layer (right gray box) exert tonic inhibition on the copy layer. (a, left) Upon initial 257 presentation of a feature (represented here as a square), all units in the inhibition layer are 258 active. As a result, excitatory input from the source layer is not propagated to the copy layer. 259 (a, right, top) Feature-specific inhibition from the source layer to the corresponding units in 260 the inhibition layer shuts down the inhibitory input to the copy layer. If the same item is 261 presented again during the time window of reduced inhibition, input from the source layer is 262 propagated to the copy layer. (a, right, bottom) If a new, non-identical item is presented, the 263 source layer cannot drive the copy layer because the corresponding units in the inhibition 264 layer have not been inhibited. Sameness-detection thus proceeds by reading out the copy 265 layer, as only repeated items are propagated to the copy layer. (b) Sameness-detection in 266 simultaneously presented, spatially arranged items. The source layer consists of populations 267 of neurons coding for features (arranged in the y-direction), but these units encode space as

268	well (arranged in the x-direction). Tonically active inhibitory (inter-)neurons (small gray box
269	on the right) prevent activation in the copy layer (top gray box). Critically, they receive
270	inhibitory input from those units in the source layer that code for the same feature, and
271	excitatory input from units coding for other features. For example, units representing
272	squares in the input layer inhibit all units representing squares in the inhibition layer, and
273	excite all other units. (b, left) If the stimuli consist of two identical items (squares), the
274	combined inhibitory input from the identical items in the source layer shuts down the
275	corresponding units in the inhibition layer, which lets identical items "pass through" to the
276	copy layer (b, right) In contrast, when the stimuli consist of two different items, these
277	singleton features are insufficient to drive the copy population due to inhibition from the
278	inhibition layer.
279	

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 nonrepeated features is low. Repeated items are thus highly discriminable from nonrepeated 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.

287 While the primary goal of this model is to detect when two temporarily 288 adjacent items are identical, whether or not it can detect the sameness of two 289 objects with intervening material depends on the time constants of the 290 disinhibitory effects. If disinhibition is sufficiently long-lasting, the model will 291 also detect the sameness of two non-adjacent items (e.g., of the two A's in the 292 sequence ABA). If so, it would predict that, the further two items are separated (in 293 terms of the amount of intervening time and/or the number of intervening items, 294 which might or might not have separable effects), the harder it should become to 295 detect the sameness of the two items. At least in infants, it might be harder to 296 detect non-adjacent repetitions compared to adjacent repetitions (S. P. Johnson et 297 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,

304	2005). As a result, the representations of initial items are likely stronger than
305	those of medial items and thus create stronger and longer-lasting disinhibition.
306	However, the goal of the current model is just to show that a simple and
307	ubiquitous mechanism such as disinhibition can serve as the basis of a sameness
308	detector, while more detailed predictions require a biophysically more realistic
309	model.



313 Figure 2: Activation of repeated or non-repeated items in the copy layer. The noise level is 314 the standard deviation of normally distributed noise centered at zero. In each curve, the 315 middle line shows the average activation across 50 simulations, representing 50 participants. 316 The shaded areas represent standard errors from the mean. (Top) Activation in the models 317 shown in Figure 1 that detect either sequentially (Figure 1a) or simultaneously presented 318 (Figure 1b) identical items. (Left). In the sequential sameness-detector (Figure 1a), the

- 319 activity of repeated items is highly discriminable from that from non-identical items even for
- 320 high noise levels. (Right). In the *simultaneous* sameness-detector (Figure 1b), the activity of
- 321 repeated items is highly discriminable from that of non-repeated items even for high noise
- 322 levels.
- 323
- 324

#### 325 <u>Sameness detection for simultaneous stimuli</u>

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 343 inhibited, while same-feature input is disinhibited.

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

### 349 for identical features.

350	I simulated this architecture using 50 virtual participants. As shown in
351	Figure 2, identical items are highly discriminable from non-identical items even at
352	high levels of noise. A simple, disinhibition-based circuit can thus detect
353	sameness relations among simultaneously presented identical objects.
354	A combined model of sameness detection for simultaneous and sequential stimuli
355	While the main differences between the sequential and the simultaneous
356	circuit are simply due to how stimuli are presented (i.e., spatial representations
357	and lateral inhibition among features could be added to the sequential model, but
358	are not necessary), the different update orders raise the question of whether a
359	combined model can be developed that detects both sequential and simultaneous
360	sameness relations. Practically speaking, sequential and simultaneous presentation
361	might not be as different as they seem. For example, if observers attend
362	simultaneously presented items one after the other (Liu & Becker, 2013; Vogel,
363	Woodman, & Luck, 2006; but see Mance, Becker, & Liu, 2012), we need a
364	sequential model to account for simultaneous sameness-detection; conversely, if
365	sequential items are placed in some kind of (short-term) memory before being
366	compared, we need a simultaneous model for sameness-detection in sequentially
367	presented items. As such, a combined sequential/simultaneous model might be
368	neither necessary nor desirable.

369

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



371

372 Figure 3: Combined disinhibition-based sameness-detector for both sequential and 373 simultaneous sameness relations. As in the simultaneous circuit from Figure 1b, the source 374 layer (bottom left gray box) consists of populations of neurons coding for features (arranged 375 in the y-direction) and spatial locations (arranged in the x-direction). Tonically active units 376 in the inhibition layer (top right gray box) prevent activation in the copy layer (top left gray 377 box). Units in the inhibition layer receive (i) inhibitory input from the source layer for units 378 coding for the same feature and (ii) excitatory input for units coding for other features, 379 leading to center-surround disinhibition among features and, in the copy layer, to inhibition

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

390	This "combined" sameness-detector is similar to the simultaneous
391	sameness-detector in that it comprises a source layer, a copy layer and an
392	inhibition layer, and that the copy layer receives excitatory input from the source
393	layer. However, (dis-)inhibition is organized differently. The copy layer still
394	receives tonic inhibition from those units in the inhibition layer that code for the
395	same feature and spatial position. Further, each feature of the input layer inhibits
396	the corresponding feature in the inhibition layer across spatial positions (i.e., it
397	disinhibits this feature in the copy layer), and excites all other features.
398	The critical difference is that disinhibition of features at the same location
399	is delayed. To do so, I removed direct connections between the source layer and
400	the inhibition layer that coded for the same feature at the same location (while
401	keeping the center-surround disinhibition at other locations). Instead, I added a
402	self-disinhibition layer where each unit (i) receives excitatory input from the
403	corresponding feature and location in the source layer and (ii) sends inhibitory
404	input to all units coding for the same feature (across locations) in the inhibition
405	layer. (While these modifications might seem to some extent ad-hoc, as
406	mentioned above, it is not clear if a combined sequential/simultaneous model is
407	necessary or desirable in the first place.)
408	As shown in Figure 4, identical items were highly discriminable from non-
409	identical items in the simultaneous situation across noise levels; in contrast, in the

410 sequential situation, discriminability suffered as noise increased.





412 Figure 4: Activation in the copy layer of the combined sequential/simultaneous sameness-

 $413 \qquad {\rm detector} \ ({\rm Figure} \ {\rm 3}). \ ({\rm Left}) \ {\rm In} \ {\rm the \ combined \ sequential/simultaneous \ sameness-detector},$ 

414 repeated features can be repeated either at the same location or at a different location. While

 $415 \qquad \hbox{activation of (same or different location) repeated items is highly discriminable from} \\$ 

- $416 \qquad \text{activation for non-repeated items for moderate noise levels, discriminability becomes much} \\$
- 417 poorer at high noise levels, when the standard deviation of the noise reaches about 15% of
- $418 \qquad \hbox{the activation level of active neurons. (Right) The combined sequential/simultaneous}$

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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#### 799 Appendix A: Model equations

800 <u>A.1 Sequential model</u>

801 The feature *f* is encoded in the source layer, the inhibition layer and the 802 copy layer; the corresponding activations, are  $S_f(t)$  for a unit encoding feature *f* in 803 the source layer,  $I_f(t)$  for such a unit in the inhibition layer and (3)  $C_f(t)$  such for a 804 unit in the copy layer.  $E_f(t)$  is the external input,  $\mathcal{N}(\mu,\sigma)$  is a random value drawn 805 from a normal distribution with mean  $\mu$  and standard deviation  $\sigma$ .

806 Before stimulation, the activation in the source layer and in the copy layer 807 are initialized to zero (plus noise), while the activation in the inhibition layer is 808 initialized to some value  $a_I$  (here arbitrarily set to 1):

809

810 (1)  

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

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

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

811

817

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:

$$w_{f',f}^{C,S} \sim \begin{cases} \mathcal{N}(1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$
818 (2) 
$$w_{f',f}^{C,I} \sim \begin{cases} \mathcal{N}(-1,\sigma_{weight}) & f = f' \\ 0 & f \neq f' \end{cases}$$

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

820 At each time step, the activations in the different layers are then updated 821 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) 
$$C_{f}(t) = w_{f}^{C,S}S_{f}(t) + w_{f}^{C,I}I_{f}(t) + \mathcal{N}(0, \sigma_{activation})$$

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

824

825 At the end of each update cycle, the activations are curtailed to be between 826 zero and one.

827 <u>A.2. Simultaneous model</u>

828 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

830 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

835 initialized to some value  $a_i$  (here arbitrarily set to 1):

836

837 (4)  

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

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

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

838

839 Connection weights now carry indices for both features and spatial 840 locations. For example, a connection between a source layer unit coding for 841 feature *f* at location *l* and a copy layer unit coding for feature *f* at location *l*' is 842 indicated by  $w_{f,l,l,l}^{C,S}$ . The weights are given as follows:

843

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

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

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

845

846 At each time step, the activations in the different layers are then updated 847 as follows; as mentioned in the main text, the update order is critical.

848

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

849 (6) 
$$I_{f,l}(t) = N(a_{l}, \sigma_{activation}) + \sum_{f_{S}, l_{S}} w_{f,l, f_{S}, l_{s}}^{I,S} S_{f_{S}, l_{S}}(t)$$
$$C_{f,l}(t) = \sum_{f_{S}, l_{S}} w_{f,l, f_{S}, l_{s}}^{C,S} S_{f_{S}, l_{S}}(t) + \sum_{f_{I}, l_{I}} w_{f,l, f_{I}, l_{I}}^{C,I} I_{f_{I}, l_{I}}(t) + N(0, \sigma_{activation})$$

851 At the end of each update cycle, the activations are curtailed to be between 852 zero and one.

853

#### A.3. Combined model

854 The combined sequential/simultaneous model is similar to the 855 simultaneous model in that it comprises a source layer, a copy layer and an 856 inhibition layer and that the copy layer receives excitatory input from the source 857 layer as well as tonic inhibition from those units in the inhibition layer that code 858 for the same feature and spatial position. Further, each feature of the input layer 859 inhibits the corresponding feature in the inhibition layer across spatial positions 860 and excites all other features. The critical difference between the simultaneous 861 and the combined model is that there are no connections between the source layer 862 and the inhibition layer that code for the same feature at the same location (while 863 disinhibition occurs for other locations), and that same-location disinhibition of 864 features proceeds through a *self-disinhibition layer* where each unit (1) receives 865 excitatory input from the corresponding feature and location in the source layer 866 (2) sends inhibitory input to all units coding for the same feature (across 867 locations) in the inhibition layer. 868

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

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

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

876

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

879

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

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

$$S80 \quad (8) \qquad C_{f,l}(t) = \sum_{f_{S},l_{S}} W_{f,l,f_{S},l_{S}}^{c,S} S_{f_{S},l_{S}}(t) + \sum_{f_{I},l_{I}} W_{f,l,f_{I},l_{I}}^{c,l} I_{f_{I},l_{I}}(t) + N(0,\sigma_{activation})$$

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

881

882 At the end of each update cycle, the activations are curtailed to be between 883 zero and one.