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**Duplications and domain-generalit**

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Running head: DUPLICATIONS DOMAIN-SPECIFICITY

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## **Abstract**

While specialized, adaptive behavioral traits are ubiquitous in the animal kingdom, at least in humans, there are considerable debates on whether the mind is primarily characterized by various special-purpose, domain-specific mechanisms, or by a few general-purpose, domain-general mechanisms. However, in these debates, domains are generally defined in terms of the types of information that the (domain-specific or domain-general) mechanisms process. Drawing from research on artificial language learning, associative learning, serial learning, executive control and formal linguistics, I argue that neither domain-specificity nor domain-generality provide satisfactory descriptions when considering how cognitive mechanisms are implemented. For example, some cognitive mechanisms might be “domain-bound” – they are available in multiple domains (and thus not domain-specific), but not in other domains (and thus not domain-general). Hence, these computations can be performed in many domains but not in others, can be recruited simultaneously by multiple domains, and, across domains, individual abilities with a given computation are relatively uncorrelated. Domain-bound mechanisms have a straightforward evolutionary interpretation: Analogously to the evolution of molecular and morphological structures, cognitive mechanisms can become duplicated over evolution, with independent copies in different domains. If so, the cognitive mechanisms reviewed here might reflect fairly simple circuits that are plausibly duplicated in different brain areas. These results thus add to growing evidence for the importance of duplications for our cognitive abilities. This, in turn, calls for a revision of the concept domain-generality, suggesting that, in many cases,

46 mechanisms traditionally seen as domain-general might really reflect a collection  
47 of local copies of specialized mechanisms.  
48  
49 Keywords: Domain-Generality; Domain-Specificity; Domain-Boundedness;  
50 Artificial Grammar Learning; Duplication; Serial Learning; Statistical Learning;  
51 Executive Function  
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### **Duplications and domain specificity**

54 Karl Marx and Adam Smith might differ in their political philosophies, but  
55 they agree on one thing: division of labor leads to greater efficiency. Does such a  
56 division of labor also exist in the brain? Are there “domain-specific”  
57 computational mechanisms that are constrained to operate in only one domain  
58 (e.g., face processing) and others in other domains (e.g., language)? Are there  
59 “domain-general” mechanisms that can operate in all domains alike? For  
60 example, are there domain-specific mechanisms involved in language acquisition  
61 (Chomsky, 1980; Fodor, 1983; Lenneberg, 1967), or does language acquisition  
62 rely on computational mechanisms available in essentially any domain (Aslin &  
63 Newport, 2012; McClelland, Rumelhart, & Group, 1986; Seidenberg, 1997)?

64 Here, I propose a new view on such questions, whereby cognitive  
65 mechanisms can become duplicated over the course of evolution (see also Barrett,  
66 2012; Chakraborty & Jarvis, 2015; Endress, Nespors, & Mehler, 2009; Kaas, 1989;  
67 Marcus, 2004; Markram et al., 2004; Perin, Berger, & Markram, 2011; Shukla,  
68 2005; Sperber, 1994, for related proposals). This allows independent copies of a  
69 mechanism to be available in multiple domains, without being fully domain-  
70 general. I will first provide several case studies that seem to require duplication  
71 accounts of some sort. For example, humans and other animals can detect  
72 identity-relations (e.g., noticing that the last syllable is repeated in a sequence  
73 such as *dubaba*). While identity-relations seem to be detected by a specialized  
74 mechanism, this mechanism is available in many domains and species, from  
75 language to vision and olfaction, and from humans to ducklings to bees, and thus  
76 cannot be domain- or human-specific (see below for a more detailed review and



98 helps illustrating some confusion in the literature. From an informational point of  
99 view, a domain is a distinct class of information. This class of information is  
100 recurrent and ecologically relevant in an organism's mental life. As a result, the  
101 organism has evolved mechanisms that process this kind of information (see  
102 Hirschfeld & Gelman, 1994, for a similar definition), though these mechanisms  
103 might come to process different kinds of information than what they evolved to  
104 process (Dehaene & Cohen, 2007; Gould & Vrba, 1982; Sperber, 1994). For  
105 example, given that faces are a critical source of information in social species,  
106 they constitute a recurrent class of information, which might have led to the  
107 evolution of mechanisms that deal with this class of information (e.g., Bonatti,  
108 Frot, Zangl, & Mehler, 2002; Kanwisher, McDermott, & Chun, 1997, but see e.g.,  
109 Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson,  
110 Skudlarski, & Gore, 1999). Under this view, mechanisms that are domain-general  
111 can apply to all domains alike, and mechanisms that are domain-specific process  
112 information only in a single domain.

113         However, there are a number of problems with this definition. First, it  
114 leads to a confusion between the computations a mechanisms implements, and the  
115 implementations itself (Marr & Nishihara, 1992). For example, some  
116 computations we perform on faces might be identical to those we perform on  
117 xylophones (e.g., we might encode the relative spatial positions of object parts for  
118 either class of stimuli). These computations might well be implemented in distinct  
119 brain areas, and might thus be independent. Given the information-based  
120 definition above, these computations would thus count as domain-general  
121 although the instantiations of these computations are domain-specific, and reside

122 as independent instantiations in whatever brain regions process faces and  
123 xylophones. As a result, domains cannot be defined exclusively based on the type  
124 of information that is processed. A viable definition of a domain needs to take  
125 into consideration *how* the information is processed in terms of the underlying  
126 implementations.

127         Second, the definition of a domain above is not fine-grained enough to  
128 account for the hierarchical structure of processing. For example, language is  
129 clearly a domain, but so is phonology, and, within phonology, prosody. Given  
130 that, when we process prosodic information, it comes packaged with phonological  
131 as well as linguistic information, a pure information-based definition of domains  
132 cannot account for this hierarchical domain structure.

133         To avoid such problems, I opt for a definition that integrates the  
134 information-based notion of domain with the mechanism-based notion of module  
135 (i.e., the set of mechanisms that process the information in a domain).  
136 Specifically, in the discussion below, a “domain” refers to a set of  
137 implementations of computational mechanisms that process a certain, ecologically  
138 recurring class of information, and that, together, fulfill an ultimate function in  
139 our interactions with the environment. Examples might include face recognition,  
140 object recognition, music or language. A domain is a set of implementations of  
141 processing mechanisms that *specifically* operate on the kind of information from  
142 which the domain takes its name.

143         For example, if face recognition is a domain, its constituent mechanisms  
144 *specifically* process face-related information. Even if we process relative spatial  
145 positions of object parts for both faces and xylophones, the xylophone-related

146 instantiation of this mechanism would not be part of the face-domain. Further,  
147 some processes operate on different kinds of information; for example, face and  
148 xylophone processing both rely on early visual information processing. These  
149 shared processes are not part of the domain of face recognition, because they are  
150 not *specifically* involved in face processing.

151 This notion is similar to Fodorian modules (Fodor, 1983; see also  
152 Hirschfeld & Gelman, 1994) except that it is defined in terms of functions and  
153 processes rather than in terms of content, and that it is agnostic with respect to the  
154 degree of automaticity of a given process (see Sperber, 1994, for a similar view).

155 Importantly, this definition is hierarchical. Just as every goal can (but need  
156 not) have sub-goals, any (ultimate) function can (but need not) have sub-  
157 functions. Domains thus can have sub-domains as well. For example, patients  
158 with brain damage can have dissociable deficits within the language domain (e.g.,  
159 problems of language perception vs. production, of grammar vs. word-finding  
160 etc.). These functions thus define at least partially independent sub-domains, and  
161 presumably have sub-domains on their own. At least at the genetic level, such a  
162 hierarchical modular organization might be crucial to the evolvability of  
163 organisms (Nothwang, 2016). Further, if the output of modules generally serves  
164 as the input to other modules, such hierarchical processing also increases the  
165 flexibility of cognitive operations (Sperber, 1994).

## 166 **2. Duplication in evolution**

167 The proposal below relies on the duplication of cognitive mechanisms.  
168 Before presenting my (cognitive) case studies, I will thus briefly outline the role  
169 of duplications in evolution. In fact, the importance of the duplication of genes,



170 whole genomes and morphological structures has long been recognized in  
171 evolutionary biology (Allman & Kaas, 1971; Chakraborty & Jarvis, 2015; Hurley,  
172 Hale, & Prince, 2005; Innan & Kondrashov, 2010; Kaas, 1989; Magadum,  
173 Banerjee, Murugan, Gangapur, & Ravikesavan, 2013; Ohno, 1970; Taylor &  
174 Raes, 2004; Zhang, 2003). Innan & Kondrashov (2010) argued that “hardly any  
175 aspect of genome evolution or function is not somehow linked to gene  
176 duplications, which occur in all kinds of life forms and have taken place since  
177 before the last universal common ancestor.” For example, in catarrhines (old-  
178 world monkeys and apes), trichromatic color vision evolved from dichromatic  
179 color vision by duplication of an opsin (Jacobs, 2009; SurrIDGE, Osorio, &  
180 Mundy, 2003), and mammalian sound localization circuits for high frequencies  
181 might be duplicates of earlier circuits (Nothwang, 2016). In fact, just since  
182 humans split from chimpanzees, up to 1,800 gene duplications took place in the  
183 human lineage (Taylor & Raes, 2004; Zhang, 2003).

184         Such results raise the possibility that duplications are important for the  
185 evolution of cognitive abilities as well, and in some form or another, different  
186 authors have made similar proposals (Barrett, 2012; Chakraborty & Jarvis, 2015;  
187 Endress, Nespor, et al., 2009; Kaas, 1989; Marcus, 2004; Perin et al., 2011;  
188 Shukla, 2005; Sperber, 1994). In fact, even entire brain pathways might become  
189 duplicated (Chakraborty & Jarvis, 2015; Kaas, 1989; Nothwang, 2016; Perin et  
190 al., 2011). For example, in vocal-learning bird species, the brain regions involved  
191 in song learning might be duplicates of earlier motor regions, and at least some  
192 parrot species might have yet another duplicate (Chakraborty et al., 2015;  
193 Chakraborty & Jarvis, 2015).

194           Of course, duplicated structures are useful only in so far as they are  
195 functionally embedded in the rest of the organism. However, this is often the case  
196 (see e.g., Chakraborty & Jarvis, 2015; Hurley et al., 2005, for reviews). A well-  
197 understood case is the evolution of trichromacy in old-world and Howler  
198 monkeys (see e.g., Jacobs, 2009; SurrIDGE et al., 2003, for reviews). As mentioned  
199 above, trichromacy evolved from dichromacy through duplication of an opsin.  
200 Both the ancestral copy and the duplicate are functional due to a fairly simple  
201 mechanism. Both copies of the gene are “nearby,” and their expression is  
202 controlled by a common control region. In each cone, this control region thus  
203 stochastically enables expression of only one of the opsins.<sup>2</sup> As a result, some  
204 cones express the ancestral copy, and others the duplicate.

205           Another route that leads to (presumably) functional duplicates is the  
206 duplication of entire brain pathways. In fact, if entire brain circuits are duplicated  
207 by duplicating transcription factors that control both the number and the  
208 placement of these circuits within the brain (Chakraborty et al., 2015;  
209 Chakraborty & Jarvis, 2015), the resulting duplicates would be expected to be  
210 functionally integrated.

211           Functional duplicated structures do not even always require duplicated  
212 genes. Trichromacy provides an example for this possibility as well. In primates,  
213 the gene for one opsin resides on an autosomal (i.e., non-sex) chromosome, while  
214 the gene for the opsin that is duplicated in old-world monkeys resides on the X  
215 chromosome. Critically, this latter opsin is polymorphic. As a result, in females

<sup>2</sup> In Howler monkeys, the control region was duplicated as well.

216 whose X chromosomes differ (i.e., who are heterozygous), cones can express the  
217 opsin from the non-sex chromosome, or either of the two alleles from the X  
218 chromosome. Heterozygous females can thus be trichromates in the absence of a  
219 duplicated opsin. Likewise, in zebra fish, mutations (rather than duplications) of a  
220 regulatory gene can result in extra copies of neurons functionally drive a  
221 behavioral escape response (Liu, Gray, Otto, Fetcho, & Beattie, 2003), and even  
222 injection of mRNA (the type of RNA based on which ribosomes synthesize  
223 proteins) from regulatory genes into embryos is sufficient for the development of  
224 functional extra copies of neurons mediating this escape response (Hale,  
225 Kheirbek, Schriefer, & Prince, 2004). Hence, duplicated structures are often  
226 functional, even when they do not result from duplication at the genetic level.

227         There are also computational reasons for believing that duplicated neural  
228 circuits might be used across domains. In machine learning, it has been shown  
229 that classification performance in an artificial neural network improves by using  
230 connectivity patterns from a network trained on a classification problem in a  
231 *different* domain (Caruana, 1997; Donahue et al., 2014). As neural circuits are  
232 tuned by evolution, duplicated neural circuit might also be computationally  
233 effective in a different domain, though they likely require fine-tuning.

234         It should be noted that the idea of duplication is related to but different  
235 from the concept of exaptation (Gould & Vrba, 1982). An exapted trait is co-  
236 opted for a new function that is different from the one (if any) for which it was  
237 selected. A classic example involves the evolution of bird feathers. Early birds  
238 had probably only limited flight abilities. However, even non-avian dinosaurs  
239 were covered in feathers, suggesting that feathers evolved for other purposes such

240 as thermal insulation or display (Brusatte, O'Connor, & Jarvis, 2015). As a result,  
241 by the time birds evolved from dinosaurs, early birds were likely feathered.  
242 Feathers thus were *not* selected for flight in birds, and are rather an *exaptation* for  
243 flight (Brusatte et al., 2015; Gould & Vrba, 1982).

244 Exaptation has also been proposed for cognitive abilities, such as the  
245 recycling of originally visual brain areas for reading (Dehaene & Cohen, 2007), of  
246 mechanism tracking the number of items for symbolic mathematics (Dehaene &  
247 Cohen, 2007; Halberda, Mazocco, & Feigenson, 2008), or of serial memory  
248 mechanisms for language acquisition and use (Endress, Nespors, et al., 2009;  
249 Fischer-Baum, Charny, & McCloskey, 2011).

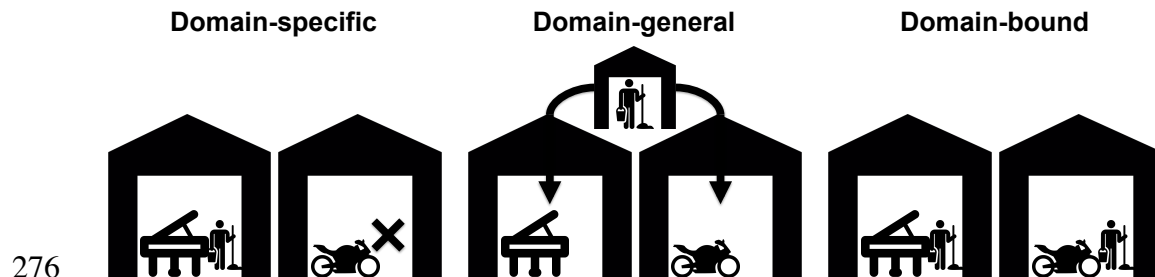
250 In contrast, duplicated traits first become duplicated. Then, they might  
251 retain their original function (or a sub-function thereof), or acquire novel  
252 functions either through adaptation or exaptation (though, in the case of gene  
253 duplications, it is debated to what extent both copies of the duplicated gene retain  
254 a function; M. Lynch & Force, 2000).

255 Figure 1 presents an analogy to illustrate these concepts. In this analogy,  
256 the brain is like a company that manufactures different products in different  
257 factories (e.g., motorcycles in a motorcycle factory, and pianos in a piano factory);  
258 these factories correspond to domains or modules. However, each factory requires  
259 some common functions such as cleaners. If the cleaners are “domain-specific,”  
260 they exist only in one of the factories, with no cleaners in the other factories. If  
261 the cleaners are “domain-general,” they are located *outside* of the factories (e.g.,  
262 at the level of the parent company or with a contractor), and enter the factories  
263 only to perform their services. Lastly, if the cleaners are domain-bound, each

264 factory has its own cleaners. In contrast, an exaptation would be the equivalent of  
265 the factory workers using, say, a shovel to clean the factories; the shovel-wielding  
266 workers might be domain-general, domain-specific or domain-bound.

267 Below, I will provide evidence from behavioral studies that, I argue, are  
268 best explained if cognitive mechanisms can become duplicated as well. I will  
269 mostly focus on descriptions at the psychological level, simply because we don't  
270 know how the relevant mechanisms are implemented at the neuronal level, let  
271 alone how they evolved. However, I will also review some biologically realistic  
272 models that might account for some of the case studies below, and argue that  
273 these duplicated mechanisms might reflect potentially simple circuits that might  
274 well be found in many brain regions.

275



276

277 **Figure 1: Illustration of the concepts domain-specificity, domain-generality**  
278 **and domain-boundedness, using the analogy of a company with factories that**  
279 **manufacture different products (e.g., a motorcycle factory and a piano**  
280 **factory). All factories require cleaners. (Left) “Domain-specific” cleaners**  
281 **exist only in one of the factories, but not in the other one. (Middle) “Domain-**  
282 **general” cleaners are located *outside* of the factories (e.g., at the level of the**  
283 **parent company or with a contractor), and enter the factories only to clean**

284 **them. (Right) If the cleaners are domain-bound, each factory has its own**  
285 **cleaners. Using a shovel to clean the factories would be the equivalent of an**  
286 **exaptation.**

287

### 288 **3. The case of identity-relations**

289 So far, I argued that cognitive mechanisms might (i) be specific to a  
290 domain, (ii) exist as a single instantiation that is common to all domains, or (iii)  
291 have independent instantiations in different domains. Further, I argued that the  
292 latter possibility would be consistent with the duplication of cognitive  
293 mechanisms. I will now review the first cognitive case study for this possibility:  
294 the detection of *identity-relations*. In syllable sequences such as *dubaba*, even  
295 seven-month-olds notice that the last two syllables are identical, and extend this  
296 identity-relation to new items. Specifically, Marcus, Vijayan, Rao, and Vishton  
297 (1999) familiarized seven-months-old infants with syllable sequences such as  
298 *ledidi*, *wijeje* and so on (where the last two syllables were repeated, hereafter  
299 called an ABB pattern). Following such a familiarization, infants were more  
300 familiar with novel sequences with novel syllables that shared the identity-pattern  
301 (e.g., *bapopo*) compared to novel syllable sequences that had a different pattern  
302 (e.g., *babapo*; hereafter called an AAB pattern). They similarly learned AAB  
303 patterns. Infants thus learned an open-ended regularity based on identity-patterns.

#### 304 3.1. How are identity-relations computed?

305 According to Marcus et al. (1999), infants learned abstract relationships  
306 among variables. For example, if the three syllables in a triplet are represented by  
307 three variables *X*, *Y*, and *Z*, the ABB pattern corresponds to the algebraic relation

308  $Y=Z$ . In contrast, based on simulations with artificial neural networks, different  
309 authors proposed that infants do not need to represent open-ended regularities  
310 when learning such patterns, and might just exploit statistical regularities of  
311 various sorts (e.g., Altmann, 2002; Christiansen & Curtin, 1999; McClelland &  
312 Plaut, 1999; Seidenberg & Elman, 1999).

313         However, identity-relations might be detected by a specialized “repetition-  
314 detector.” Specifically, Endress, Dehaene-Lambertz and Mehler (2007) used  
315 triplets of piano tones to ask whether participants could learn the identity-based  
316 rules ABB and ABA and other very simple rules not based on identity-relations  
317 (i.e., low tone-high tone-middle tone vs. middle tone-high tone-low tone). They  
318 showed that learners relying on general algebraic relations between variables  
319 should learn both types of structures equally well, and that the statistical models  
320 of Marcus et al.'s (1999) data (e.g., Altmann, 2002; Christiansen & Curtin, 1999;  
321 McClelland & Plaut, 1999; Seidenberg & Elman, 1999) either predict that both  
322 types of structures should be learned equally easily, or that the non-identity-  
323 patterns should be easier to learn (depending on the specific models).

324         In contrast to both classes of models, participants were much better at  
325 learning identity-patterns than non-identity-patterns, suggesting that identity-  
326 patterns might be detected by a specialized mechanism. Further results showed  
327 that Bayesian general-purpose learners (Frank & Tenenbaum, 2011) do not  
328 explain the learning of identity-relations either (Endress, 2013). Identity-patterns  
329 thus seem to be processed by some sort of specialized repetition-detector.

330         Identity-relations play an important role in many languages. For example,  
331 in Semitic languages such as Arabic and Hebrew, there are constraints on which

332 consonants can occur together in a word; these constraints are based on identity-  
333 relations among these consonants (e.g., Berent & Shimron, 1997; Frisch,  
334 Pierrehumbert, & Broe, 2004; McCarthy, 1979). Other languages use  
335 reduplications for grammatical purposes (McCarthy & Prince, 1999). For  
336 example, in Marshallese, “takin” means sock, while “takinkin” means to wear  
337 socks (Moravcsik, 1978). Such reduplication occur, in some form or another, in  
338 85% of the world’s languages (Rubino, 2013).

339         Despite their importance for language, identity-relations can be perceived  
340 in many non-linguistic domains, and by many non-linguistic animals. Humans can  
341 compute identity matches for speech syllables, tones and visual objects (Dawson  
342 & Gerken, 2009; Endress et al., 2007; Marcus, Fernandes, & Johnson, 2007;  
343 Marcus et al., 1999; Saffran, Pollak, Seibel, & Shkolnik, 2007), and are sensitive  
344 to the identity-relations from birth (Antell, Caron, & Myers, 1985; Gervain,  
345 Berent, & Werker, 2012; Gervain, Macagno, Cogoi, Peña, & Mehler, 2008),  
346 though such patterns might be easier to recognize with speech material (Marcus et  
347 al., 2007). Bees can compute identity-relations for colors, gratings and odors  
348 (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001). Rats and various non-human  
349 primate species can compute such relations for speech and non-speech sounds (de  
350 la Mora & Toro, 2013; Hauser & Glynn, 2009; Murphy, Mondragon, & Murphy,  
351 2008; Neiworth, 2013; but see van Heijningen, Chen, van Laatum, van der Hulst,  
352 & Ten Cate, 2013), and ducklings even imprint to abstract identity-relations  
353 (Martinho & Kacelnik, 2016, but see Hupé, 2017; Langbein & Puppe, 2017).

354         At first sight, these results seem to suggest that identity-relations are  
355 computed by a species- and domain-general mechanism, that is, a mechanism that



356 has access to all domains and modules. However, at least in humans, a closer  
357 examination casts doubt on this hypothesis even for linguistic stimuli. Human  
358 adults and infants appear to readily learn identity-relations with vowels but not  
359 consonants, and seem unable to learn identity-patterns carried by syntactic  
360 categories.

### 361 3.2. Are identity-relations really domain-general? The case from language

#### 362 3.2.1. The case of vowels and consonants

363 Adult speakers are better at detecting identity-patterns on vowels than on  
364 consonants, to the extent that they fail to detect the patterns on consonants (Toro,  
365 Bonatti, Nespors, & Mehler, 2008). In these experiments, participants were  
366 familiarized with a sequence of words in which either the vowels or the  
367 consonants conformed to an identity-pattern (e.g., words like *tapena* and *bodako*,  
368 where the first and the last vowel were identical, or words like *banubE* and *tineto*,  
369 where the first and the last consonant were identical). Participants learned the  
370 identity-pattern over vowels but not over consonants (Toro, Bonatti, et al., 2008),  
371 even when the salience of the vowels was much reduced (Toro, Shukla, Nespors,  
372 & Endress, 2008). Further, rats learn identity-relations equally well on vowels and  
373 on consonants (de la Mora & Toro, 2013), suggesting that consonants do not have  
374 an intrinsic acoustic property that makes learning identity-relations particularly  
375 difficult. Similar results have been observed with human infants (Hochmann,  
376 Benavides-Varela, Nespors, & Mehler, 2011; Pons & Toro, 2010).

377 According to Toro, Bonatti, et al. (2008), the vowel advantage for  
378 generalizations is due to the role of vowels in grammar, because vowels might  
379 play an important role for grammar, while consonants might be more important

380 for lexical processing (Nespor, Peña, & Mehler, 2003). Given that learning  
381 identity-patterns requires rule-like generalizations, they might plausibly be linked  
382 to grammar, and thus show a vowel advantage (but see the next section of  
383 evidence that identity-patterns might not be linked to grammatical processes).  
384 Irrespective of whether this interpretation is correct, these results show that  
385 learning identity-relations is much easier for some classes of linguistic stimuli  
386 than others, a result that is problematic for a fully domain-general identity-  
387 detector.

### 388 3.2.2. The case of syntactic categories

389 While identity-relations can be learned over a variety of stimuli, adult  
390 speakers seem unable to learn them over syntactic categories (Endress & Hauser,  
391 2009). Specifically, participants were familiarized with word triplets conforming  
392 to either an AAB pattern (noun-noun-verb triplets such as *town-leg-choose* and  
393 verb-verb-noun triplets such as *choose-speak-leg*) or an ABB pattern (noun-verb-  
394 verb or verb-verb-noun). Following this, they were presented with AAB or ABB  
395 test triplets made from new words, and had to decide which one was like the  
396 familiarization items. Surprisingly, participants failed to discriminate between  
397 “correct” and “incorrect” patterns.

398 In a desperate attempt to make participants learn these patterns, Endress  
399 and Hauser (2009) primed them on nouns and verbs by having participants first  
400 categorize words into nouns and verbs; results showed that they performed at  
401 ceiling. Then they told them to watch out for a pattern of nouns and verbs, and  
402 finally familiarized them with the triplets. Even under these conditions, most  
403 participants failed to notice the patterns.

404           This failure is surprising because control experiments showed that all the  
405 building blocks for learning the patterns are in place. For example, participants  
406 readily access the categories. They perform at ceiling when categorizing words,  
407 and learn other sequential regularities about the categories (e.g., whether triplets  
408 start or end with nouns). Further, participants learn identity-relations over non-  
409 syntactic categories: When semantic categories were used (e.g., animals and  
410 clothes), or phonological categories, listeners readily learned the identity-  
411 relations. Nor is the failure due to ambiguities between nouns and verbs specific  
412 to English (i.e., that a verb like “run” can be used as a noun as well): Hungarian  
413 speakers (where such ambiguities do not exist) show the same pattern of failure.

414           It turned out that participants could learn the identity-relations over  
415 syntactic categories only when the resulting sentences had a syntactic  
416 interpretation in terms of subjects, objects and so on. For example, when noun-  
417 noun-verb (e.g., baby-water-juggle) and adjective-adjective-noun (e.g., clever-  
418 fragile-water) triplets were used for the AAB pattern, participants readily learned  
419 the corresponding pattern, irrespective of whether or not the word order  
420 corresponded to English or not. The kinds of regularities that can be learned with  
421 syntactic categories is thus highly constrained (Moro, 2008). Most relevant for the  
422 current purposes, there seem to be surprising holes in our ability to learn such  
423 structures, a result that is at odds with views that such relations are computed by  
424 domain-general mechanisms. Still, they can be computed in variety of domains,  
425 including tones, odors, visual stimuli and linguistic items, a result that is  
426 problematic if they were domain-specific.

427 3.2.3. Are there multiple identity-detectors?

428           One explanation for these puzzling results involves independent identity-  
429 detectors for visual, olfactive and tonal stimuli; within the language faculty, there  
430 might be independent identity-detectors for vowels, syllables, semantic categories  
431 and so on, but not for syntactic categories. If so, identity-relations can be detected  
432 in all domains that have an identity-detector, but not in domains that lack such a  
433 mechanism.

434           It turns out that a similar assumption has long been made in linguistic  
435 theory for explaining the admissible patterns of consonant repetitions in Semitic  
436 languages. Specifically, two identical consonants can occur at the end of a word  
437 root, but not at its beginning (Berent & Shimron, 1997; Frisch et al., 2004;  
438 McCarthy, 1979). The traditional explanation involves two independent  
439 computations of identity-relations, one at the phonological level, and one at the  
440 morphological level. At the phonological level, consonant repetitions are illegal in  
441 word roots (McCarthy, 1979). However, some roots have only two consonants  
442 rather than three. This creates a problem at the morphological level, where the  
443 standard word pattern has three consonant slots. As a result, one additional  
444 consonant must be added, and this consonant will be a repetition of the second  
445 consonant, leading to a consonant repetition in the word's final syllable. Such  
446 theories thus assume that there are independent mechanisms sensitive to identity-  
447 relations at the morphological and at the phonological level.

448           Identity-relations might thus be computed by what we called “domain-  
449 bound” mechanisms (Endress, Nespors, et al., 2009), consisting of independent  
450 copies of mechanisms in different domains with similar computational functions;

451 these copies might have arisen through duplication over evolution. In Appendix  
452 A, I will argue that this view is also made plausible by the observation that  
453 identity-relations can be detected using fairly simple neuronal circuits, and  
454 suggest that circuits based on inhibition of inhibition might be a candidates.

### 455 3.3. Are duplicates hierarchically organized?

456 The view that the mechanisms detecting identity-relations exist in  
457 independent copies appears to be problematic in the light of findings that infants  
458 and even bees can generalize identity-relations across modalities (Giurfa et al.,  
459 2001; Marcus et al., 2007), and that presenting multimodal items helps infants  
460 generalize such patterns (Frank, Slemmer, Marcus, & Johnson, 2009). While such  
461 results seem unexpected if an identity-detector were really domain-bound, they  
462 might reflect the hierarchical nature of perception and cognition. For example, a  
463 repeated syllable is presumably also a repeated auditory object, which is also a  
464 repeated object. If each of these hierarchical levels has its own identity-detector,  
465 cross-modal generalizations might be possible (see also Sperber, 1994, for the  
466 proposal that the output of modules might be the input of other modules). In line  
467 with this view, seven-month-olds can learn hierarchical identity-patterns over  
468 identity-patterns (Kovács & Endress, 2014; see also Basirat, Dehaene, &  
469 Dehaene-Lambertz, 2014, for related results). For example, when exposed to  
470 triplets of syllable triplets such as *dubadu lomomo zavuvu*, infants appear to  
471 notice that the last two words have identical identity-patterns.

472 While it is an open question to what extent duplicate cognitive  
473 mechanisms are hierarchically organized, this view would fit well with proposals  
474 that novel cognitive functions can arise from the duplication of entire brain

475 pathways (Chakraborty & Jarvis, 2015; Kaas, 1989). If a brain pathway becomes  
476 duplicated, its underlying computational functions become duplicated as well.  
477 Subsequently, individual computational functions (e.g., the detection of identity-  
478 relations) can be lost independently in different duplicates, either over evolution  
479 or, as I will argue below, over development.

480 This leads to the question of whether there are any truly domain-general  
481 mechanisms, where a single processor has access to a large number of domains.  
482 Three prime candidates come to mind: associative learning, a sensitivity to  
483 sequence-edges and executive control functions. All three candidate mechanisms  
484 can be used by a variety of species in a variety of domains, and might thus be a  
485 species- and domain-general mechanisms. However, I will now argue that even  
486 these candidates might not be truly domain-general.

#### 487 **4. Is associative learning domain-general?**

488 Associative learning exists in many domains, including vision, olfaction,  
489 audition and motor behavior. If we hear, see or feel two objects frequently  
490 occurring together, we form associations between them (e.g., Aslin, Saffran, &  
491 Newport, 1998; C. M. Conway & Christiansen, 2005; Endress, 2010; Fiser &  
492 Aslin, 2002; Saffran, Aslin, & Newport, 1996; Saffran, Johnson, Aslin, &  
493 Newport, 1999; Turk-Browne, Jungé, & Scholl, 2005; Turk-Browne & Scholl,  
494 2009). Similar abilities have been observed in many non-human species,  
495 including rats, cotton-top tamarins and Zebra finches (Chen & Ten Cate, 2015;  
496 Hauser, Newport, & Aslin, 2001; Toro & Trobalón, 2005). It thus seems plausible  
497 to assume that these computations reflect species- and domain-general  
498 mechanisms.



521 appear to be fully domain-general, but rather presents certain specializations.<sup>3</sup> In  
522 fact, at least in *Drosophila*, preferential associations can be evolved in just 40  
523 generations (Dunlap & Stephens, 2014).

524 In line with this view, associative learning works better over consonants  
525 than over vowels (Bonatti, Peña, Nespor, & Mehler, 2005), although the reasons  
526 are debated (Bonatti, Peña, Nespor, & Mehler, 2007; Keidel, Jenison, Kluender,  
527 & Seidenberg, 2007).

528 Further, some apparently closely related forms of associative learning  
529 have different properties. For example, associative learning of locations shows  
530 phenomena such as blocking when learning occurs with respect to landmarks, but

<sup>3</sup> In the 70s and 80s, there have been numerous attempts to find alternative accounts for these results that (1) do not involve adaptive specializations, and (2) fit within general learning theory (see e.g. Domjan, 1983, 2015, for a review of sometimes somewhat complex alternative proposals, and evidence that contradicts at least some of these proposals). One such counterargument relies on earlier experience: maybe rats have learned that tastes are more predictive of sickness than sounds, and vice versa. Critically, however, the preferential associations have been observed in 1 and 5 day-old rats (Gemberling & Domjan, 1982; Gemberling, Domjan, & Amsel, 1980), suggesting a rather limited role of experience. Other developmental studies also reveal the exquisite tuning of preferential associations to the environmental niche that rat pups occupy, and are problematic for most proposals that do not consider preferential associations to be adaptive specializations. For example, before the age of 21-22 days, infant rats are monophagous, and drink only their mothers' milk. They can certainly acquire taste aversions at this age, but if the taste is presented in a suckling context, no taste aversion develops; in contrast, older infants (who also eat non-milk foods) develop taste aversion in a suckling context as well (Martin & Alberts, 1979). Critically, associations between tactile stimuli (e.g., air puffs) and electric shocks are *not* blocked in a suckling context (Alberts & Gubernick, 1984). The most striking aspect of these data comes from pups for whom weaning is delayed by preventing them from exposure to non-milk foods. Specifically, in 26-day-old pups, suckling usually does *not* block taste aversion, but, when weaning is delayed, a suckling context prevents taste aversion in these older pups as well. In contrast, just four hours of experience with (non-toxic) solid food is sufficient to prevent blocking of taste aversion – irrespective of whether this experience is given two days prior to taste aversion training, or two days *afterwards* (Gubernick & Alberts, 1984). To my knowledge, no theory has been developed that explains these dissociations between classical conditioning and taste aversion learning that does not appeal to adaptive specializations.



531 not with respect to boundaries (Doeller & Burgess, 2008), and these types of  
532 learning rely on different neural substrates (Doeller, King, & Burgess, 2008). It  
533 thus appears that associative learning is not a unitary, domain-general mechanism.  
534 Rather, independent associative learning abilities might exist in a variety of  
535 domains, perhaps with slightly different properties, which would suggest that they  
536 might have been duplicated.

#### 537 4.2. The case of cross-domain correlations

538 Further evidence that associative learning might not be a unitary ability  
539 comes from Siegelman and Frost's (2015) experiments. They administered a  
540 battery of statistical learning tasks, and concluded that they did not reflect a  
541 unitary ability (see Frost, Armstrong, Siegelman, & Christiansen, 2015, for a  
542 different take on these results from that advocated here). Specifically, they  
543 administered five statistical learning tasks to the same (human adult) participants  
544 that differed in whether participants had to compute statistical relations among  
545 adjacent syllables, among adjacent non-linguistic sounds, among non-adjacent  
546 consonants, or among adjacent visual shapes; they also performed a serial reaction  
547 time task. Surprisingly, performance in these different tasks was virtually  
548 uncorrelated. It thus appears that there is no single, overall mechanism that  
549 computes associations; rather, associations seem to be computed by more  
550 localized mechanisms.

551 Such a pattern of results has an intuitive explanation. For the sake of the  
552 argument, let us assume that associations are computed according to the principle  
553 of “what fires together fires together”, and that this type of correlational learning  
554 reflects long-term potentiation (LTP) at the neuronal level (see M. A. Lynch,

555 2004, for a discussion of this possibility, but see Gallistel, 2017, for arguments  
556 that associative learning might not rely on LTM, and might rather rely on  
557 intracellular processes; for the current purposes, I just assume that associative  
558 learning relies on *some* widely available mechanism, and use LTM as a label for  
559 it). Given that LTP has been observed in different cell types within different brain  
560 regions, albeit with slightly different properties (Malenka & Bear, 2004),  
561 statistical learning should occur in different brain regions as well, again with  
562 globally similar, but slightly different properties, and, crucially, in the absence of  
563 a unitary statistical processor. Rather, all brain regions would have their own  
564 associative machinery because they have the machinery required for LTP. Hence,  
565 there is no a priori expectation either that all associations are equally easy to  
566 compute.<sup>4</sup>

567         The situation might be similar with respect to identity-relations: different  
568 brain regions might have their own “identity-detectors”, with slightly different  
569 properties each. As a result, such mechanisms are neither domain-general nor  
570 domain-specific, but rather consist of a collection of localized and domain-  
571 specific copies of the same mechanism. We have called this situation “domain-  
572 bound” (Endress, Nespors, et al., 2009). Such a situation might arise if key  
573 mechanisms are duplicated over evolution, and potentially acquire domain- and

<sup>4</sup> This view also suggests that correlated task performance across different domains would *not* provide evidence for domain-general mechanisms even if such correlations could be found. It is possible that individuals differ in some respect that makes all circuits underlying these abilities more or less effective, even though there might be distinct and independent instantiations of these circuits in different brain areas. In contrast, an absence of cross-domain correlations probably provides evidence against a purely domain-general ability.

574 species-specific properties; in Appendix A, I will argue that this possibility is  
575 made plausible by the observation that, as in the case of associative learning,  
576 identity-detection might be implemented by fairly simple circuits; further, I will  
577 suggest that identity relations might be detected based on inhibition of inhibition.

### 578 **5. Is a sensitivity to sequence-edges domain-general?**

579 Humans, and other animals, are sensitive to the items that occur at  
580 sequence edges (i.e., in the first and last position). This sensitivity is probably due  
581 to a mechanism of serial memory that encodes the positions of items in sequences  
582 relative to the first and last item. For example, in sequences like ABCD, this  
583 mechanism retains that A came first, that D came last, and that B and C had some  
584 position *relative* to the first and last one (for reviews, see e.g. Fischer-Baum et al.,  
585 2011; Henson, 1998).

586 Such regularities are extensively used in language. For example, affixes  
587 (e.g., the English *-ed* past-tense) tend to occur at word edges, while infixes (e.g.,  
588 fun-fucking-tastic; McCarthy, 1982) are relatively rare. Further, there are many  
589 other linguistic processes that rely on edges, from stress assignment to the  
590 coordination of different linguistic hierarchies (see Endress, Nespors, et al., 2009,  
591 for a review).

592 In humans, learning of such affixation-like regularities has been  
593 demonstrated for syllable sequences, visual action sequences and chimpanzee  
594 vocalizations (Endress, Carden, Versace, & Hauser, 2010; Endress & Hauser,  
595 2011; Endress & Mehler, 2009; Endress & Wood, 2011; Marchetto & Bonatti,  
596 2013), though a sensitivity to edges is also important for other aspects of  
597 language, notably word segmentation (Monaghan & Christiansen, 2010; Seidl &

598 Johnson, 2006, 2008; Shukla, Nespov, & Mehler, 2007; Shukla, White, & Aslin,  
599 2011), and the representation of written words (Fischer-Baum et al., 2011;  
600 Fischer-Baum, McCloskey, & Rapp, 2010; Fischer-Baum & McCloskey, 2015).

601 As with identity-relations, a sensitivity to sequence-edges is found in  
602 many non-human animals, including chimpanzees, cotton-top tamarins, and Zebra  
603 finches (Chen, Jansen, & Ten Cate, 2016; Endress, Cahill, Block, Watumull, &  
604 Hauser, 2009; Endress et al., 2010). Both cotton-top tamarins and Zebra finches  
605 can even learn language-like affixation patterns (Chen et al., 2016; Endress,  
606 Cahill, et al., 2009). As a result, a sensitivity to edges is clearly not domain- or  
607 species-specific.

608 However, the patterns found in the world's languages suggest that the  
609 sensitivity to edges is not domain-general either. Various theories from formal  
610 linguistics assume independent copies of edge-based codes for different linguistic  
611 constituents (see Endress, Nespov, et al., 2009, for a review), and these codes  
612 account for numerous linguistic regularities (McCarthy & Prince, 1993).  
613 Phonotactic constraints are a case in point. Such constraints determine the  
614 permissible phoneme sequences in a language. For example, English words  
615 cannot start with the sound at the end of "sing," and cannot end with the sound at  
616 the onset of "hat," while other languages have different constraints. Many  
617 constraints appeal to edges of constituents, and some phonotactic appeal to edges  
618 at different levels of the prosodic hierarchy. For example, in some languages such  
619 as German, syllable-final obstruents become devoiced in all syllables (e.g., sounds  
620 such as /d/ are pronounced as /t/); in other languages such as Polish and Walloon,  
621 syllable-final obstruents are devoiced only at the end of (prosodic) words, and

622 thus at the edge of constituents at a different level of the prosodic hierarchy  
623 (Wetzels & Mascaró, 2001). Further, the constraints that can be learned at the  
624 edges of words are different from those that can be learned at syllable edges that  
625 are not word-edges (Endress & Mehler, 2010).

626 Another example for the importance for multiple, independent edge  
627 representations comes from alignment theories (McCarthy & Prince, 1993;  
628 Nespor & Vogel, 1986). For example, the English plural [s] is a morpheme (in the  
629 morphosyntactic hierarchy), but not a syllable (in the prosodic hierarchy).  
630 However, even though the two hierarchies are not isomorphic, the right edge of  
631 the [s] morpheme is aligned with the syllable comprising the plural [s].

632 Alignment of edges of different linguistic constituents can explain a  
633 variety of linguistic regularities, from syllabification to morphology and the  
634 coordination of different hierarchies (McCarthy & Prince, 1993; Nespor & Vogel,  
635 1986). Critically, however, different edges can only be aligned if each linguistic  
636 constituent has its own edges to begin with. In the terminology used here, this  
637 would mean that each linguistic constituent has its own, domain-bound sensitivity  
638 to edges.

639 There is some indirect evidence for this possibility from brain imaging  
640 experiments. Specifically, different English grammatical affixes (i.e., the plural  
641 and the third person *-s*) activate different brain regions (Longe, Randall,  
642 Stamatakis, & Tyler, 2007), suggesting that there are at least partially independent  
643 representations of an [s] in an edge position. However, it is unclear whether such  
644 activation differences reflect the affixes per se, or their different grammatical  
645 roles. For example, different brain activations for the inflection of nouns and

646 verbs might not reflect the affixation-pattern per se, but rather the interpretative  
647 processes associated with their respective grammatical functions.

648         Be that as it might, the data reviewed above make it at least plausible that  
649 independent sensitivities to edges might exist in different domains. Further, as in  
650 the case of the ubiquitous machinery for associative learning, this view is also  
651 supported by the observation that circuits that are sensitive to onsets and offsets  
652 have been observed in various brain areas.

653         In the visual modality, ganglion cells responding to onsets and offsets of  
654 signals have been reported since Hartline (1938; see also Nelson & Kolb, 2003).  
655 In the auditory modality, neurons that respond to sound onsets and offsets are  
656 found throughout the auditory hierarchy (see He, 2001, and references therein).  
657 Onset and offset responses seem to rely on different inputs, as they are tuned to  
658 different frequencies and have a different balance of excitation and inhibition,  
659 though the latter might be a consequence of the former (Scholl, Gao, & Wehr,  
660 2010). However, the kinds of edges that are relevant for linguistic alignment  
661 theories are often abstract, with few perceptual cues. To be sensitive to such  
662 edges, the edges must be computed at more abstract levels as well. As a result, it  
663 is an important question for further research whether the neural mechanisms that  
664 are used to compute perceptual sequence edges can also be used to compute more  
665 abstract edges. However, it is at least plausible that these mechanisms might  
666 reflect simple circuits that are duplicated profusely.

## 667         **6. Are cognitive control mechanisms domain-general?**

668         Another set of mechanisms that might be domain-general comprises  
669 attentional and control mechanisms. However, even these mechanisms might not

670 be fully domain general. For example, indirect evidence from working memory  
671 (WM) studies suggests that control mechanisms might not be entirely unitary, and  
672 some animals might have a domain-specific inhibitory system, a view that is in  
673 line with recent theories of inhibition as well.

#### 674 6.1. The case of Working Memory (WM)

675 According to the most prominent theories of working memory (WM),  
676 items in WM are actively maintained by attentional or executive mechanisms; the  
677 limitations of WM are thus really the limitations of these processes (see, among  
678 many others, A. R. Conway, Kane, & Engle, 2003; Cowan, 1995; Engle, 2002).  
679 For example, we might retain three items in WM by (mentally) attending to them.

680 There is substantial evidence that WM is at least in part domain-specific  
681 (Baddeley, 1996; Cowan, Saults, & Blume, 2014; Fournie, Zughni, Godwin, &  
682 Marois, 2015; Wong, Peterson, & Thompson, 2008; Wood, 2008, 2009). For  
683 example, verbal WM is famously independent of WM in other domains  
684 (Baddeley, 1996, 2003). If so, the underlying mechanisms should be partially  
685 domain-specific as well. If these mechanisms are attentional and control  
686 mechanisms (e.g., A. R. Conway et al., 2003; Cowan, 1995; Engle, 2002, but see  
687 Banta Lavenex, Boujon, Ndarugendamwo, & Lavenex, 2015; Carroll et al., 2010;  
688 Endress & Potter, 2014; Endress & Szabó, in press; Shipstead & Engle, 2013),  
689 then these processes would be domain-specific as well, and WM would provide  
690 evidence for domain-specific attentional or executive functions. However, given  
691 the variety of existing models of WM, it is still an open question how domain-  
692 specific attentional and executive control mechanisms are in humans in the  
693 context of WM.

694

## 6.2. The case of inhibition

695           The evidence for domain-bound copies of control mechanisms is stronger  
696 in the case of inhibition than in the case of WM. Of course, inhibition can have  
697 wide-ranging consequences in different domains. For example, resistance to  
698 temptation in preschoolers (e.g., in the marshmallow test) famously predicts  
699 outcomes in variety of domains, from social functioning to academic performance  
700 (Mischel, Shoda, & Rodriguez, 1989).

701           However, in other cases, inhibitory abilities seem much more linked to  
702 specific domains. For example, in the wild, cleaner wrasse face a marshmallow  
703 test of sorts in feeding contexts. They feed on ectoparasites carried by “client”  
704 fish. However, they prefer to eat the client fish’s mucus (Grutter & Bshary, 2003).  
705 As client fish punish cleaners who feed on their mucus (Bshary & Grutter, 2002;  
706 Bshary & Schäffer, 2002), cleaner wrasse have to inhibit their tendency to feed on  
707 client mucus to avoid punishment. Danisman, Bshary, and Bergmüller (2010)  
708 asked whether this led to better domain-general inhibition in a reverse reward  
709 contingency task. In this task, subjects have to choose the smaller of two rewards  
710 to obtain the larger one; this has been used as a test of inhibitory function in many  
711 species. If the requirement for inhibition during foraging led to an improvement in  
712 domain-general inhibition, cleaner wrasse should perform well on the reverse-  
713 contingency task. In contrast, most cleaner fish simply failed on this task. While  
714 there are probably many differences between inhibition in a feeding context and  
715 the task demands of a reverse contingency task, these results are at least  
716 compatible with the interpretation that cleaner fish did not develop better domain-  
717 general inhibitory abilities, and that some animals might have domain-specific



718 copies of inhibitory control mechanisms due to its feeding ecology.

719           Domain-specific inhibitory abilities have been proposed in humans as  
720 well. For example, Bjorklund and Kipp (1996) reviewed results suggesting that  
721 inhibitory abilities are at least partially (and at least in children) domain-specific,  
722 and that certain inhibitory abilities are specifically enhanced in human females  
723 due to their much higher parental investment (Trivers, 1972). Specifically,  
724 Bjorklund and Kipp (1996) proposed that females had better inhibitory control in  
725 social contexts, notably for controlling how they displayed emotions, and for  
726 inhibiting behaviors, notably for resisting temptation and self-regulation.  
727 Critically, this inhibitory female advantage did not translate to an overall  
728 inhibitory advantage; for example, there was no female advantage in Stroop tasks.  
729 However, Bjorklund and Kipp's (1996) review was based on experiments with  
730 children whose focus were not necessarily gender-differences. In young adults,  
731 evidence for such a female advantage is mixed (e.g., Cross, Copping, &  
732 Campbell, 2011; Silverman, 2003a, 2003b), and might depend on the stage of the  
733 menstrual cycle (Hosseini-Kamkar & Morton, 2014). As a result, the evidence for  
734 such gender-differences appears strongest in populations that do not yet reproduce  
735 sexually, and might also be due to maturational differences between boys and  
736 girls. Irrespective of whether such differences reflect differential parental  
737 investment or not, they suggest that inhibitory abilities sometimes seem to be  
738 dissociable.

739           Other evidence also suggests that inhibitory abilities are at least partially  
740 independent. For example, Shilling, Chetwynd and Rabbitt (2002) used four

741 Stroop-like tasks, and measured correlations in performance.<sup>5</sup> While performance  
742 in each task was consistent across blocks in a given participants, performance  
743 across tasks was uncorrelated (see also Bjorklund & Kipp, 1996, for a review of  
744 studies suggesting that inhibitory abilities are at least partially independent,  
745 though cross-task correlations might be observed when the tasks are extremely  
746 similar; Shilling, Chetwynd and Rabbitt, 2002). Likewise, Cipolotti et al. (2016)  
747 tested frontal patients on a Stroop task, and on the Hayling Sentence Completion  
748 test, where participants have to complete a sentence fragment with an *unrelated*  
749 word; for example, completing the fragment “London is a very busy...” with an  
750 unrelated word such as “...banana” would be a correct response, while a related  
751 continuation such as “... city” would be an incorrect response. Cipolotti et al.  
752 (2016) found that, after controlling for fluid intelligence, performance on the two  
753 tasks was uncorrelated. Further, patients with left-lateralized lesions were  
754 impaired on the Stroop task, but much less impaired on the sentence completion  
755 task, while patients with right-lateralized lesions showed the opposite pattern.  
756 Together, results such as Shilling et al.'s (2002) and Cipolotti et al.'s (2016) thus  
757 echo the statistical learning results by Siegelman and Frost (2015), who also

<sup>5</sup> During the first task, participants saw a digit made of other digits (e.g., a big 2 made of individual 2 characters). If participants have to report the small digit, they show Stroop-like interference when the global digit mismatches the local one (Navon, 1977). During the second task, participants saw one to four identical digits on a screen, and had to report their number. Stroop-like interference ensues if the identity of the digits does not match their number (e.g., reporting that there are four digits in 3 3 3 3; Windes, 1968). In the third task, participants saw a large arrow pointing in one of the four cardinal directions, and with a word corresponding to a direction printed inside the arrow; a mismatch between the printed direction and the arrow direction (e.g., the word LEFT printed inside an arrow pointing to the right) leads to interference (Shor, 1970). The fourth task was the classic Stroop task, producing interference between color labels and their font color (Stroop, 1935).

758 showed that statistical learning abilities are largely uncorrelated across domains  
759 even though they appear to be domain-general. The same conclusions might be  
760 drawn for inhibitory abilities: there appear to be at least partially independent  
761 inhibitory abilities.

762         That being said, these results do not imply that different inhibitory tasks  
763 have nothing in common. For example, Friedman and Miyake (2004; see also  
764 Miyake et al., 2000) separated inhibitory mechanisms into three distinct  
765 complexes – prepotent response inhibition, resistance to distractor interference,  
766 and resistance to proactive interference. Participants then completed three tasks  
767 tapping into each of these complexes, as well as a number of other tasks.<sup>6</sup> As  
768 Shilling et al. (2002), Friedman and Miyake (2004) found that correlations across  
769 tasks were fairly low. However, using structural equation modeling, they found  
770 that the tasks testing prepotent response inhibition and resistance to distractor  
771 interferences correlated with a common latent variable. Further, the tasks testing  
772 resistance to proactive interference correlated with a different latent variable.  
773 Friedman and Miyake (2017) suggested that the common prepotent response and  
774 distractor inhibition variable might reflect goal maintenance, though both of  
775 Cicolotti et al.'s (2016) inhibition tasks might well map onto this variable, and yet  
776 involve dissociable brain mechanisms.

<sup>6</sup> Prepotent response inhibition was measured through an antisaccade task, a stop signal, where participants had to withhold a trained response on a subset of the trials, and by a Stroop task. Resistance to distractor interference was measured using the Eriksen flanker task, a word naming task in the presence of distractor words, as well as a shape matching task in the presence of distractor shapes. Resistance to proactive interference was measured in a Brown-Peterson task, a paired associates task and a cued recall task, where participants learned both a target and a distractor list.

777           Be that as it might, the results reviewed so far suggest that inhibitory  
778 abilities are partially independent and dissociable. I thus suggest that they are  
779 domain-bound, might reflect duplicates of an inhibitory circuit. This possibility is  
780 also consistent with some recent neurobiological models of inhibition. It has long  
781 been observed that frontal regions are activated by a variety of tasks, and might  
782 thus implement domain-general mechanisms (e.g., Duncan & Owen, 2000;  
783 Fedorenko, Duncan, & Kanwisher, 2013), leading some investigators to call these  
784 regions the “multi-demand cortex” (MDC; e.g., Duncan, 2010). However, this  
785 common activation in the MDC might reflect the requirement to dynamically  
786 track task- and goal-relevant aspects of the task (e.g., Duncan, 2010). Critically,  
787 recent models suggest that this might occur through a distributed set of duplicated  
788 (or at least similar) circuit mechanisms. Specifically, if the MDC tracks task- and  
789 goal-relevant representations, it might provide top-down amplification of these  
790 representations. In contrast, (inhibitory) control might occur in local circuits  
791 through local competition among representations. Due to their top-down  
792 amplification, task-relevant representations are then more likely to win this  
793 competition against irrelevant representations that do not receive such  
794 amplification (e.g., Egnor & Hirsch, 2005; Erika-Florence, Leech, & Hampshire,  
795 2014; Hampshire & Sharp, 2015; see also Banich & Depue, 2015; Munakata et  
796 al., 2011, for related proposals). If so, even cognitive control might be  
797 implemented through potentially duplicated mechanisms that might be as simple  
798 as lateral inhibition.

799           This view also provides a rather straightforward account of apparently  
800 domain-specific control abilities. Species and domains with domain-specific



825 perform the same computation in multiple domains simultaneously. Third,  
826 performance on tasks that appear to reflect very similar computations is  
827 uncorrelated across domains. Fourth, there are biologically plausible candidate  
828 implementations that are fairly simple, and might exist widely in the brain. I will  
829 now discuss two alternative solutions to the first two observations (though they do  
830 not address the remaining observations). Specifically, the putatively duplicated  
831 mechanisms might really reflect single central mechanisms. However, these  
832 central mechanisms might not be “connected” to some domains, and might  
833 support multiplexing so that they can deal with multiple regularities  
834 simultaneously.

#### 835 7.1. Are domain-general mechanisms selectively connected to different domains?

836 A possible alternative to duplicated mechanisms are central mechanisms that are  
837 selectively connected to some domains, but not others. For example, a single,  
838 central identity-detector might be connected to a variety of domains, but not to  
839 those domains dealing with consonants, syntactic categories and so on.

840         Developmental considerations make this view particularly plausible. In  
841 particular, 4-month-olds might learn certain identity-patterns over musical  
842 material that 7-month-olds cannot learn (Dawson & Gerken, 2009). This  
843 observation raises the possibility that apparently domain-bound mechanisms are  
844 initially present in *all* domains, but then get pruned. This view would be  
845 analogous to how certain perceptual abilities are lost within the first year of life  
846 (Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002; Weikum et al., 2007;  
847 Werker & Tees, 1984). For example, while infants can initially discriminate all  
848 phonemes from all human languages, they lose those discrimination abilities that

849 are not used in their native language within their first year of life (Werker & Tees,  
850 1984). Similar results have been found in face perception (Kelly et al., 2007;  
851 Pascalis et al., 2002).

852         This pruning might take at least two routes. First, there might be central  
853 mechanisms (e.g., an identity-detector), and the connections of these mechanisms  
854 to different domains get cut. However, existing data are problematic for this and  
855 other accounts. For example, and as mentioned above, infants older than seven  
856 months have difficulty learning identity-relations with musical stimuli. However,  
857 they perform better when exposed to identity-relations with speech stimuli before  
858 (Dawson & Gerken, 2009; Marcus et al., 2007). Under a domain-general view  
859 with a single, central identity-detector, it is not clear why training with one set of  
860 stimuli should improve detection with a different set of stimuli; after all, the  
861 musical stimuli should either be connected to the identity-detector, or they should  
862 not. A possible explanation is that both speech items and musical stimuli are  
863 connected to this central identity-detector. However, the connections between the  
864 musical stimuli and the repetition-pattern might be weak; as a result, the identity-  
865 detector needs to be primed with speech items so that musical stimuli can drive it.  
866 While this view would obviate the need for duplicated mechanisms, more  
867 research is needed to establish it.

868         Crucially, pruning might also occur through a second route that is  
869 compatible with the duplication view. Specifically, each domain might initially  
870 have its own copies of the duplicate mechanisms, and these copies are lost over  
871 development. Further, if entire brain pathways can become duplicated  
872 (Chakraborty & Jarvis, 2015), their constituent computational mechanisms can be

873 lost individually in each duplicate, either over evolution, or over development  
874 through pruning.

875         Be that as it might, a central, domain-general mechanism (whose  
876 connections to certain domains get pruned) does not explain why performance on  
877 tasks such as the Stroop task or statistical learning is uncorrelated across domains  
878 (e.g., Cipolotti et al., 2016; Shilling et al., 2002; Siegelman & Frost, 2015), nor  
879 how the same mechanism can be used simultaneously on multiple stimuli if there  
880 is only a single copy of the mechanism. I will discuss the latter issue in the next  
881 section.

#### 882                 7.2. Can domain-general mechanisms be multiplexed?

883         As mentioned above, there is theoretical and empirical evidence  
884 suggesting that the same computation can be performed independently and  
885 simultaneously on multiple stimuli. Examples include the restrictions on  
886 consonant repetitions in Semitic languages (Berent & Shimron, 1997; Frisch et  
887 al., 2004; McCarthy, 1979), infants' ability to learn multi-level repetition-patterns  
888 (Kovács & Endress, 2014), and the requirement for multiple independent edges in  
889 alignment theories.

890         One possible solution to make such results consistent with single copies of  
891 central, domain-general mechanisms is to postulate that these central mechanisms  
892 are capable of “multiplexing:” They might be able to process stimuli from  
893 different domains by switching back and forth between the stimuli, or possibly by  
894 keeping the stimuli separate using some other mechanism, similar to how a radio  
895 receiver can separate the signals of different radio stations although they are all  
896 carried by different frequencies in the electromagnetic spectrum. However, such



897 multiplexing capabilities come at the cost of a rather complex, and possibly  
898 implausible, architecture, compared to the fairly simple circuits that might support  
899 local computations. I will now outline these requirements in more detail.

900         In the case of edges, alignment theories require the detection of  
901 simultaneously occurring edges from different constituents, which likely rules out  
902 time-sharing-based multiplexing, and likely requires multiple edge detectors  
903 within the central edge detector. Moreover, it requires the central mechanism to  
904 keep track of the sources of the different edges. For example, when, during a  
905 conversation, a phone starts ringing, the ringtone certainly provides auditory  
906 edges, but these edges are unlikely to have any effect whatsoever on grammatical  
907 processing of edges during the conversation, among many other reasons because  
908 the ringtone is perceived in a different “stream” from speech (Bregman, 1990).  
909 As a result, it is not sufficient to simply detect edges, but the central mechanism  
910 would also need to keep track of the *kinds of edges* it detects, and process them  
911 accordingly. A central, domain-general edge-detector would thus likely postulate  
912 *central* copies of the edge-detector *within* the central edge-detector instead of  
913 local distributed copies, and would additionally require considerable processing  
914 capabilities to keep track of the kinds of edges it is processing.

915         Such a view is also in direct contradiction to the hierarchical organization  
916 of perception and cognition. After all, to detect edges in a variety of domains, and  
917 for different linguistic constituents, such a mechanism would need access to fairly  
918 low-level information from a variety of domains, and process it.

919         For these reasons, I believe that a central, domain-general edge-detector is  
920 implausible at best. In contrast, local (copies of) edge-detectors can rely on fairly

921 simple and possibly widespread circuits, and detecting edge-alignment would  
922 require little more than coincidence detection of the output of these local circuits,  
923 even though it is an open question whether these simple circuits would support  
924 more abstract edges as well.

925         A central, domain-general mechanism for repetition-detection is  
926 implausible for related reasons, but would additionally require a working-memory  
927 component. Specifically, a central repetition-detector might process hierarchical  
928 repetition-patterns of repetition-patterns (Kovács & Endress, 2014) either through  
929 some form of time-sharing-based multiplexing, or through some other route. If it  
930 uses time-sharing, it needs to retain the results of the lower-level repetition-  
931 detection in some kind of memory; these memories then need to be compared in  
932 order to detect the higher-level repetition-pattern. If multiplexing occurs through  
933 some other route, the central repetition-pattern would likely need multiple internal  
934 copies of a repetition-detector that also keep track of the source of the repetition.  
935 Again, local copies of the mechanisms would simply be replaced with central  
936 copies.

937         In contrast to this complex model, repetition-patterns of repetition-patterns  
938 can be detected in a straightforward way by local, but hierarchically organized  
939 copies of repetition-detectors: repetitions might be detected at the lower level, and  
940 the output of these detectors might be compared at the next level.

## 941                   **8. Elemental computations vs. domains**

942         The discussion so far focused on elemental computations such as identity-  
943 detectors and statistical learning. However, discussions of domain-specificity and  
944 domain-generality typically focus on larger and complex entities, such as a

945 “language module” or a “face processing module,” whether they exist at all, and  
946 whether they are specific to humans. However, as these “modules” are defined as  
947 the sets of mechanisms that deal with a certain type of information (e.g.,  
948 language), they are likely complex and diverse, and likely use many different  
949 elemental computational mechanisms. For example, the language “module”  
950 includes identity-relations (for reduplication), pitch perception (for prosody), the  
951 syntactic computations involved in c-command (whatever they are), and many  
952 others. Some of these elemental computations are likely available in other  
953 domains and species as well; others might be specific to one domain. Discussions  
954 of domain- and species-specificity thus become more falsifiable if they are  
955 situated at the level of computations as well as their implementations that might  
956 or might not be domain- and species-specific.

## 957 **9. Conclusions**

958 The case studies reviewed above suggest that some cognitive mechanisms  
959 might have become duplicated for the course of evolution. There are three types  
960 of evidence for this view. First, some computations can be performed in many  
961 domains, but not in others. Second, some tasks that tap into apparently similar  
962 computations are largely uncorrelated across domains; further, tasks such as  
963 statistical learning seem to have different properties depending on which can of  
964 stimuli it operates over. Third, some computations can be performed  
965 simultaneously in multiple domains or at different hierarchical levels. All of these  
966 observations are explained naturally if each domain has its own instantiations of  
967 the underlying mechanisms.

968 There is a fourth but more speculative argument for the existence of

969 duplicated cognitive mechanisms. At least the case studies reviewed here might  
970 reflect fairly simple circuit motifs, some of which (e.g., lateral inhibition) are  
971 known to be ubiquitous in the brain. However, it is entirely unknown whether  
972 such circuits would support more computations on abstract representations as  
973 well.

974         Considering the computations as well as the instantiations of the  
975 mechanisms performing these computations will thus reveal a much more fine-  
976 grained picture of domain-general. Some mechanisms might be truly domain-  
977 specific, others truly domain-general, and yet others domain-bound. As a result,  
978 what might make a domain special relative to other domains, however, is the set  
979 of the available elemental computational operations, and how they can be  
980 combined (Barrett, 2012; Endress, Nespors, et al., 2009). Individual elemental  
981 computational mechanism can be specific to a single domain as well, but need  
982 not.

983

984                   **Appendix A: Biological models of identity detection**

985                   Identity matches are crucial for many if not most aspects of cognition,  
986 including motor learning (Brooks, 1986), any aspect of cognition where a  
987 prediction or internal state needs to be compared to sensory input, novelty  
988 detection (e.g., in the hippocampus; e.g. Kumaran & Maguire, 2007), and tasks  
989 such as delayed-match to sample tasks. (In such tasks, a sample is shown, and,  
990 after a delay, the (human or non-human) participant has to decide whether or not a  
991 probe matches the sample.)

992                   Two broad classes of mechanisms have been proposed for the detection of  
993 stimulus repetition (see e.g. Grill-Spector, Henson, & Martin, 2006; Kumaran &  
994 Maguire, 2007, for reviews). On the one hand, repeated stimuli elicit less  
995 activation, due to neuronal “fatigue” or sharpening of the representations. As a  
996 result, novel, non-repeated representations have relatively higher levels of  
997 activation. However, such models cannot explain why repetition-patterns can be  
998 generalized: after detecting the repetition in *babagu*, an item with new syllables  
999 and the same repetition-pattern (e.g., *wowofe*) will be just as unfamiliar as an item  
1000 with new syllables and another repetition-pattern (e.g., *wofefe*). As a result, an  
1001 explicit representation of identity vs. difference (or match vs. non-match) is  
1002 required.

1003                   The second class of mechanisms involves some kind of comparator  
1004 between memory representations and sensory input, though there are few explicit  
1005 and biologically realistic models of identity matches. For example, it has been  
1006 proposed that the hippocampal CA1 region (and maybe the CA3 region,  
1007 depending on the studies) are crucial for detecting matches between memory

1008 representations and sensory input (while the CA3 regions might have an  
1009 additional role in retrieving associations; e.g., Hasselmo, 2005; Lisman, 1999;  
1010 Lisman & Otmakhova, 2001).

1011 A.1. Hasselmo and Wyble's (1997) model

1012 Hasselmo and Wyble (1997) provided an explicit model of this possibility  
1013 in their simulation of memory retrieval in the hippocampus, based on the anatomy  
1014 of the trisynaptic circuit. Specifically, the hippocampus receives sensory input  
1015 from the entorhinal cortex, which in turn projects to region CA3 (via the dentate  
1016 gyrus). In contrast, CA1 receives input both from CA3 (via the Schaffer  
1017 collaterals) as well as directly from the entorhinal cortex. If memories are  
1018 encoded in CA3, the simultaneous input from the entorhinal cortex and CA3  
1019 might allow CA1 to detect matches between sensory input (from the entorhinal  
1020 cortex) and memory representations (from CA3).

1021 Specifically, during encoding of novel items, combined sensory and  
1022 memory (from CA1) input leads to novel self-organized representations in CA1.  
1023 To activate these representations during recognition (i.e., to enter the  
1024 corresponding attractor state), input from both the entorhinal cortex and CA3 is  
1025 required; sensory input alone does not activate the attractor state. In other words,  
1026 CA1 enters an attractor state only when the current sensory input matches  
1027 currently active memory representations in CA3 (see also Ludueña & Gros, 2013,  
1028 for a model that uses anti-Hebbian learning to configure a *mismatch* detector).  
1029 Relatedly, some working memory models detect matches between the contents of  
1030 working memory and current sensory input by *adding* input from sensory input  
1031 and WM (e.g., Carpenter & Grossberg, 1987; Wen, Ulloa, Husain, Horwitz, &

1032 Contreras-Vidal, 2008). If an item is in WM, it will provide an additional input.  
1033 As a result, matches between sensory input and WM can be detected using some  
1034 threshold (though such a mechanism might not be robust as it depends on the  
1035 *absolute* fire firing rates; Engel & Wang, 2011).

#### 1036 A.2. Engel and Wang's (2011) model

1037 While these models detect matches because the combined output of  
1038 memory representations and matching sensory input trigger the retrieval of other  
1039 representations, it is also possible to detect matches by *subtracting* sensory input  
1040 and memory representation. Such a model has been proposed in the context of  
1041 delayed-match-to-sample tasks. Specifically, Engel and Wang (2011) proposed a  
1042 biologically realistic model that detects matches through (i) a working memory  
1043 (WM) sub-network, (ii) comparator sub-network, and (iii) a decision network  
1044 receiving input from the comparator network. Neurons in the WM network  
1045 receive sensory input (but only when attention is directed to the input), can  
1046 maintain memory traces through self-excitation. Critically, the comparator  
1047 network is composed of two distinct populations. One receives both sensory input  
1048 and input from the WM network (hereafter called sensory+WM neurons). The  
1049 other receives *only* sensory input but no WM input (hereafter called sensory-only  
1050 neurons). Engel and Wang (2011) make two other critical assumptions. First, they  
1051 assume that the total level of excitation should be similar for matches in the  
1052 sensory+WM population, and for mismatches in the sensory-only population; as  
1053 the sensory+WM population has an extra excitatory input, they achieved this by  
1054 scaling down the synaptic excitation targeting the sensory+WM population.  
1055 Second, the comparator units show center-surround inhibition: there is a (limited

1056 level of) excitation from similar stimuli, and much stronger inhibition from  
1057 dissimilar stimuli.

1058         These assumptions conspire to yield stronger activation in the  
1059 sensory+WM population for matches, and stronger activation in the sensory-only  
1060 population for mismatches. As a result, to decide whether a probe matches the  
1061 target, the decision network just needs to compare the activation of the  
1062 sensory+WM population and the sensory-only populations. More specifically, in  
1063 the matching case, the sensory+WM neurons receive input both from the probe  
1064 and from the matching content of WM; in contrast, the sensory-only neurons  
1065 receive input only from the sensory representations of the probe. As a result, there  
1066 is stronger activation in the sensory+WM population. In contrast, in the case of a  
1067 mismatch, both populations receive input from the sensory representations of the  
1068 probe. As Engel and Wang (2011) assume that excitatory input is stronger for the  
1069 sensory-only population, this population is expected to receive somewhat stronger  
1070 input than the sensory+WM population. Further, the sensory+WM population also  
1071 receives input from the (mismatching) WM representation; due to the center-  
1072 surround inhibition in the network, the probe and the (mismatching) target inhibit  
1073 each other, further reducing the activation in the sensory+WM population. The  
1074 decision network just has to decide whether similar orientations have stronger  
1075 presentation in the sensory+WM population or the sensory-only population.<sup>7,8</sup>

<sup>7</sup> This model assumes that WM is mediated by self-sustained activity in a population of neurons. However, it has been questioned whether such self-sustained activation really plays a crucial role in WM (e.g., Rose et al., 2016; Stokes, 2015).

<sup>8</sup> Another WM model that explicitly incorporates a same/different distinction has been



1076 A.3. Difficulties of these models with generalizable repetition patterns

1077 In their current instantiations such models are unlikely to account for the  
1078 generalization of repetition-patterns (nor were these models intended to do so).  
1079 For example, after exposure to *pupu*, they are unlikely to recognize *baba* over,  
1080 say, *bapu* when the syllables are novel. In Hasselmo and Wyble's (1997) model,  
1081 items like *baba* have no memory representation, and thus cannot trigger CA1-like  
1082 activation any more than *bapu* sequences. That said, a version of Hasselmo and  
1083 Wyble's (1997) model might act as a repetition-detector if each item undergoes  
1084 element-by-element encoding-retrieval cycles. For example, when processing the  
1085 item *pupu*, the network might first encode the first instance of the syllable *pu*;  
1086 upon presentation of the second instance of *pu*, a CA1-like structure might enter  
1087 an attractor state as the current sensory input matches an existing memory  
1088 representation. In contrast, for items like *bapu*, the second element has no  
1089 corresponding existing memory representation, and thus does not activate an  
1090 attractor in a CA1-like structure. Hence, a readout mechanism to a CA1-like  
1091 structure could, in principle, act as a repetition-detector. However, there are a

proposed by Johnson, Spencer, Luck, and Schöner (2009). In their model, sensory input excites (self-sustained) WM representations, which, in turn, inhibits the corresponding sensory activation (with center-surround inhibition in all areas). As a result, upon presentation of the sample stimulus, there is a self-sustained representation of the memory items in WM, but little activation in sensory areas due to the inhibitory input from WM. Hence, if a later sensory input matches the items in memory, the sensory areas will remain largely silent. In contrast, if the sensory input differs from the memory items, sensory input will be uninhibited. Hence, in this model, “decision” neurons that receive excitation from WM will respond to matches, while decision neurons receiving excitation from sensory input will respond to mismatches, at least with mutual inhibition between these decision populations. However, there are a number of problems with this model. First, and as mentioned above, it has been questioned whether WM really relies on self-sustained activity (e.g., Rose et al., 2016; Stokes, 2015). Second, and crucially, items in (working) memory seem to *attract* attention (e.g., Awh & Jonides, 2001; Downing, 2000; Fan & Turk-Browne, 2016) which seems inconsistent with the proposal that memory items suppress perceptual input.

1092 number of problems with such an architecture as well. For example, after  
1093 exposure to both *pupu* and *bapu*, the model might classify *bapu* as a repetition,  
1094 because the syllable *pu* has an existing memory representation from a previous  
1095 item. In other words, the model would show proactive interference in repetition-  
1096 detection, and there is no evidence that this might be the case.

1097         Likewise, such a model will face difficulties discriminating *ABB* patterns  
1098 as in *pulili* from *ABA* patterns as in *pulipu*. It is also unclear whether a memory-  
1099 based repetition-detector can detect the identity of simultaneously (rather than  
1100 sequentially) presented items, and whether such models would “recognize” an  
1101 item in the presence of distractors; after all, a CA1-like region would receive  
1102 input from the distractors as well, which will bring up the total level of activity.  
1103 As a result, considerable computational and neuroscientific research is needed to  
1104 decide whether such an architecture might act as a repetition-detector.

1105         Similar problems arise Engel and Wang's (2011) model. First, the model  
1106 would show proactive interference, and should falsely detect repetitions in non-  
1107 repetition sequences if the second item has been placed in working memory on a  
1108 considerable number of earlier occasions. While this is an empirical prediction, it  
1109 seems, at first sight, implausible.<sup>9</sup> Second, it is unclear whether a memory-based

<sup>9</sup> Engel and Wang's (2011) model can detect matches between the *A* items in *ABBA* trials. However, they achieve this by assuming that the WM subnetwork receives sensory input only when the input is attentionally encoded. As a result, only the first *A* from the *ABBA* items ever reaches WM. However, this would predict that participants do not notice the repetition of the *B* items. It thus seems that the WM component in Engel and Wang's (2011) has a similar function as (pre-) frontal regions in the recent models of inhibition discussed above (e.g., Egnér & Hirsch, 2005; Erika-Florence, Leech, & Hampshire, 2014; Hampshire & Sharp, 2015): it serves to highlight task-relevant representations.

1110 repetition-detector would be able to detect the identity of simultaneously  
1111 presented items. Third, Engel and Wang (2011) use supervised training to teach  
1112 units to subtract the activation of sensory+WM neurons and sensory-only  
1113 neurons, respectively. However, in all experiments on repetition learning in  
1114 infancy, learning is unsupervised; further, the reliance on supervised training  
1115 prevents the model from generalizing to items that are dissimilar from those it has  
1116 been trained on (see Marcus, 1998a, 1998b, for discussion).

1117         There is another reason for which such memory-based repetition-detectors  
1118 are unlikely to support the kinds of generalizations reviewed here. Given how  
1119 widespread the ability to compute repetition-patterns is, one would expect it to  
1120 rely on fairly simple circuits. However, these memory-based models rely on the  
1121 interaction of different brain areas (the entorhinal cortex as well as CA1 and CA3  
1122 in the case of Hasselmo and Wyble's (1997) model, and a sensory as well as a  
1123 working memory system in the case of Engel and Wang's (2011) model).  
1124 However, the underlying circuitry might well be simpler.

#### 1125                     A.4. A disinhibition model of identity-detection

1126         One possibility is that repetition-detection might possibly rely on  
1127 inhibition of inhibition (also referred to as reciprocal inhibition or disinhibition in  
1128 the literature). Disinhibition has been observed in a variety of brain areas (e.g.,  
1129 Chevalier & Deniau, 1990), and some interneuron populations specifically inhibit  
1130 other inhibitory interneurons (e.g., Hangya, Pi, Kvitsiani, Ranade, & Kepecs,  
1131 2014; Xu, Jeong, Tremblay, & Rudy, 2013). Critically, some interneuron types  
1132 receiving both local and long-range input have been found to inhibit other  
1133 inhibitory interneurons in auditory (Pi et al., 2013), visual (Pfeffer, Xue, He,

1134 Huang, & Scanziani, 2013), somatosensory (Lee, Kruglikov, Huang, Fishell, &  
1135 Rudy, 2013) and prefrontal cortex (Pi et al., 2013); accordingly, Hangya et al.  
1136 (2014) argued that this disinhibitory circuit might be a cortical circuit motif (see  
1137 also Goddard, Mysore, Bryant, Huguenard, & Knudsen, 2014; Mysore &  
1138 Knudsen, 2012, for the proposal that there might be disinhibitory circuit motifs).  
1139 Disinhibitory circuits have been proposed to be the basis of a variety of cognitive  
1140 phenomena, including attentional selection (van Der Velde & de Kamps, 2001)  
1141 and categorization of stimuli (into the categories of strongest vs. other, e.g.  
1142 Goddard et al., 2014; Mysore & Knudsen, 2012, or into the categories of target  
1143 vs. non-target, Kusunoki, Sigala, Nili, Gaffan, & Duncan, 2010). Critically, such  
1144 circuits have also been proposed for sequential discriminations between the  
1145 strength of stimuli (e.g., Machens, Romo, & Brody, 2005; Miller & Wang, 2006;  
1146 but see Barak, Sussillo, Romo, Tsodyks, & Abbott, 2013, for arguments that such  
1147 models might not fit the observed neural dynamics).

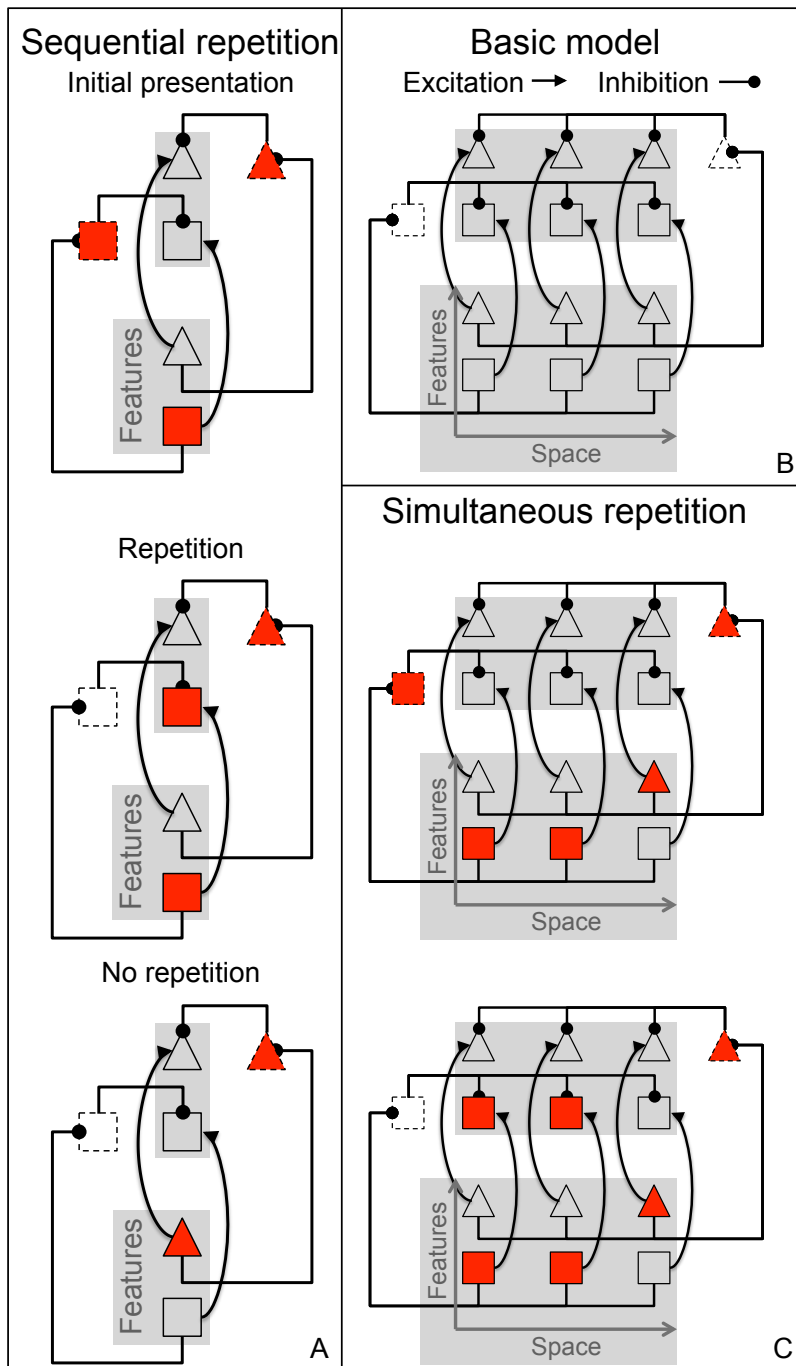
1148         Figure 2 shows a possible (and entirely speculative) disinhibition-based  
1149 architecture of how repetitions *might* be detected. In this model, there are two  
1150 populations of neurons that encode features of items (e.g., frequency, color and so  
1151 on). The “source” population receives sensory input. The “copy” population  
1152 receives excitatory input from the source population (whence its name). However,  
1153 it also receives tonic inhibition (e.g., from a population of interneurons). Due to  
1154 this inhibition, the source cannot drive the copy with a single stimulation. The  
1155 critical aspect of this mechanism is that the source also *inhibits the tonic*  
1156 *inhibition* of the copy. Once the inhibitory input to the copy ceases, there will be a  
1157 time window during which the excitatory input from the source can drive the

1158 copy. As a result, the presence of activity in the copy population would indicate  
1159 the presence of a repeated item. A readout mechanism for the copy could thus act  
1160 as a repetition-detector. Figure 2 shows a sketch of such a model for both  
1161 sequential presentation of the stimuli and for simultaneous presentation.

1162         However, there is a major problem with this model: it cannot discriminate  
1163 between items that are presented multiple times and items that are presented for  
1164 longer durations (a problem that Engel and Wang's (2011) model presumably  
1165 shares). However, this problem does not arise if activity in the source population  
1166 decreases even in the presence of external input; if so, repeated rather than  
1167 prolonged stimulation is required to drive the copy population. This could be  
1168 implemented either if the source population responds only to the onset of the  
1169 stimulation, or by adding self-inhibition (through an additional interneuron  
1170 population) to the source population. However, given the speculative nature of  
1171 this proposal, my main conclusion is that it is currently unknown how repetition-  
1172 patterns are detected, and that we need biologically models of repetition-  
1173 detection. Critically, however, the underlying circuits are plausibly fairly simple,  
1174 and present in a variety of brain areas.

1175

1176



1177

1178 **Figure 2: Sketch of a disinhibition-based model of repetition-detection. (A)**

1179 **Model for the detection of sequentially repeated items. The geometric shapes**

1180 (squares and triangles) stand for populations of neurons that encode features  
1181 of the items (e.g., frequency, shape etc); filled shapes are currently active  
1182 while empty shapes are currently inactive. Populations in the “source” layer  
1183 (bottom gray box) receive sensory input. Populations in the “copy” layer (top  
1184 gray box) receive excitatory input from the source layer. Critically, another  
1185 population of (inter-)neurons (indicated by dashed lines) exerts tonic  
1186 inhibition on the copy layer. (A, top) Upon initial presentation of a feature  
1187 (here a square), the inhibitory interneurons are still active. As a result,  
1188 excitatory input from the source layer is insufficient to drive the copy layer.  
1189 (A, middle) Inhibition from the source population to the corresponding  
1190 interneurons population shuts down the inhibitory input on the copy layer. If  
1191 the same item is presented again during the time window of reduced  
1192 inhibition, the source layer can drive the copy layer. (A, bottom) In contrast,  
1193 if a non-repeated item is presented, the source layer cannot drive the copy  
1194 layer because the corresponding interneurons have not been inhibited. (B)  
1195 Basic model for the detection of spatially arranged identical items. Again, the  
1196 source layer consists of populations of neurons coding for features (arranged  
1197 in the y-direction), but these population are topologically arranged (here in  
1198 the x-direction). Tonicly active inhibitory (inter-)neurons prevent  
1199 activation in the copy layer (top gray box), but are inhibited by neurons in  
1200 the source population in turn. (B) The stimuli consist of two identical items  
1201 (squares) and one different item (triangle). The combined inhibitory input  
1202 from the “repeated” items shuts down inhibitory input from the  
1203 interneurons, and lets repeated items “pass through.” In contrast, the

1204 **singleton feature is insufficient due drive the copy population due to**

1205 **inhibition from the interneuron population.**

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