

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

Domain generality vs. modality specificity:

The paradox of statistical learning

Ram Frost^{1,2,3}, Blair C. Armstrong³, Noam Siegelman¹,

and

Morten H. Christiansen^{2,4,5}

1. The Hebrew University of Jerusalem
2. Haskins Laboratories, New Haven, CT
3. Basque Center for Cognition, Brain, and Language
4. Cornell University, Ithaca, NY
5. University of Southern Denmark

Corresponding author: Frost, R. (ram.frost@mail.huji.ac.il)

Mailing addresses:

Ram Frost,
Department of Psychology, The Hebrew University
Jerusalem, Israel

Noam Siegelman,
Department of Psychology, The Hebrew University
Jerusalem, Israel

Blair C. Armstrong,
The Basque Center on Cognition, Brain and Language (BCBL),
San Sebastian, Spain

Morten H. Christiansen,
Department of Psychology, Cornell University
Ithaca, NY

36
37

Abstract

38

39 Statistical learning is typically considered to be a domain-general mechanism by
40 which cognitive systems discover the underlying distributional properties of the input.
41 Recent studies examining whether there are commonalities in the learning of
42 distributional information across different domains or modalities consistently reveal,
43 however, modality and stimulus specificity. An important question is, therefore, how and
44 why a hypothesized domain-general learning mechanism systematically produces such
45 effects. We offer a theoretical framework according to which statistical learning is not a
46 unitary mechanism, but a set of domain-general computational principles, that operate
47 in different modalities and therefore are subject to the specific constraints characteristic
48 of their respective brain regions. This framework offers testable predictions and we
49 discuss its computational and neurobiological plausibility.

50

51

52 **Keywords: Statistical learning, domain-general mechanisms, modality specificity,**
53 **stimulus specificity, neurobiologically plausible models.**

54

55 The promise of statistical learning

56 Humans and other animals are constantly bombarded by streams of sensory
57 information. Statistical learning (SL)—the extraction of distributional properties from
58 sensory input across time and space—provides a mechanism by which cognitive
59 systems discover the underlying structure of such stimulation. SL therefore plays a key
60 role in the detection of regularities and quasi-regularities in the environment, results in
61 discrimination, categorization and segmentation of continuous information, allows
62 prediction of upcoming events, and thereby shapes the basic representations underlying
63 a wide range of sensory, motor, and cognitive abilities.

64 In cognitive science, theories of SL have emerged as potential domain-general
65 alternatives to the influential domain-specific Chomskyan account of language
66 acquisition ([1], see also [2] for related claims). Rather than assuming an innate,
67 modular, and neurobiologically hardwired human capacity for processing linguistic
68 information, SL, as a theoretical construct, was offered as a general mechanism for
69 learning and processing any type of sensory input that unfolds across time and space.
70 To date, evidence for SL have been found across an array of cognitive functions, such
71 as segmenting continuous auditory input [3], visual search [4], contextual cuing [5],
72 visuomotor learning [6], conditioning (e.g., [7]), and in general, any predictive behavior
73 (e.g., [8,9]).

74 In this paper, we propose a broad theoretical account of SL, starting with a
75 discussion of how a domain-general ability may be subject to modality- (see glossary)
76 and stimulus-specific constraints. We define ‘learning’ as the process responsible for
77 updating internal representations given specific input and encoding potential

78 relationships between them, thereby improving the processing of that input. Similarly,
79 ‘processing’ is construed as determining how an input to a neural system interacts with
80 the current knowledge stored in that system to generate internal representations.
81 Knowledge in the system is thus continuously updated via learning. Specifically, we take
82 SL to reflect updates based on the discovery of systematic regularities embedded in the
83 input, and provide a mechanistic account of how distributional properties are picked up
84 across domains, eventually shaping behavior. We further outline how this account is
85 constrained by neuroanatomy and systems neuroscience, offering independent insights
86 into the specific constraints on SL. Finally, we highlight individual differences in abilities
87 for SL as a major, largely untapped source of evidence for which our account makes
88 clear predictions.

89

90 **Domain generality versus domain specificity**

91 Originally, domain generality was invoked to argue against language modularity;
92 its definition therefore implicitly implied “something that is not language specific”.
93 Consequently, within this context, “domain” implies a range of stimuli that share physical
94 and structural properties (e.g., spoken words, musical tones, tactile input), whereas
95 “generality” is taken to be “something that does not operate along principles restricted to
96 language learning”. Note, however, that this approach says what domain generality is
97 not, rather than saying what it is (e.g., [10]). More recent accounts of SL ascribe domain
98 generality to a unitary learning system (e.g., [11]), that executes similar computations
99 across stimuli (e.g., [12]), and that can be observed across domains (e.g., [13]), and
100 across species (e.g., [14,15]).

101 As a theoretical construct, SL promised to bring together a wide range of
102 cognitive functions within a single mechanism. Extensive research over the last decade
103 has therefore focused on mapping the commonalities involved in the learning of
104 distributional information across different domains. From an operational perspective,
105 these studies investigated whether overall performance in SL tasks is indeed similar
106 across different types of stimuli [16], whether there is transfer of learning across
107 domains (see Box 1), whether there is interference between simultaneously learning of
108 multiple artificial grammars (e.g., [17]) or from multiple input streams within and across
109 domains [18], or whether individual capacities in detecting distributional probabilities in a
110 variety of SL tasks are correlated ([19]).

111 The pattern of results across these different studies is intriguingly consistent:
112 contrary to the most intuitive predictions of domain-generality, the evidence persistently
113 shows patterns of modality specificity and sometimes even stimulus specificity. For
114 example, studies of artificial grammar learning (AGL, see Glossary) systematically
115 demonstrate very limited transfer of learning across modalities, if at all (e.g., [20,21]).
116 Similarly, the simultaneous learning of two artificial grammars can proceed without
117 interference once they are implemented in separate modalities [17]. Modality specificity
118 is also revealed by qualitative differences in patterns of SL in the auditory, visual, and
119 tactile modalities [16], sometimes with opposite effects of presentation parameters
120 across modalities [22]. To complicate matters even further, SL within modality reveals
121 striking stimulus specificity, so that no transfer (and conversely, no interference) occurs
122 within modality provided the stimuli have separable perceptual features (e.g., [17,23]).
123 Finally, although performance in SL tasks displays substantial test-retest reliability

124 within modality, there is no evidence of any correlation within individuals in their
125 capacities to detect conditional probabilities across modalities and across stimuli
126 (Siegelman & Frost, unpublished). This contrasts with what might be expected if SL was
127 subserved by a unitary learning system: that individual variation in its basic function
128 would manifest itself in at least some degree of correlation across different SL tasks. If
129 not, its unitary aspect remains theoretically empty because it does not have an empirical
130 reality in terms of specific testable predictions. Taken together, these studies suggest
131 that there are independent modality constraints in learning distributional information
132 [16], pointing to modality specificity, and further to stimulus specificity akin to perceptual
133 learning [24].

134 Whereas this set of findings is not easy to reconcile with the notion of a unitary,
135 domain-general system for SL, it does not necessarily invalidate the promise of SL to
136 provide an overarching framework underlying learning across domains. Instead, what is
137 needed is an account of SL that can explicate the manifestations of domain-generality in
138 distributional learning with the evidence of its modality- and stimulus-specificity,
139 restricted generalization, little transfer, and very low correlations of performance
140 between tasks within individuals. More broadly, any general theory of learning that aims
141 to describe a wide range of phenomena through a specific set of computational
142 principles has to offer a theoretical account of how and why transfer, discrimination, and
143 generalization take place, or not.

144

145 **Towards a mechanistic model of SL**

146 Our approach construes SL as involving a set of domain-general neurobiological

147 mechanisms for learning, representation, and processing that detect and encode a wide
148 range of distributional properties within different modalities or types of input (see [13],
149 for a related approach). Crucially, though, in our account, these principles are not
150 instantiated by a unitary learning system but, rather, by separate neural networks in
151 different cortical areas (e.g., visual, auditory, and somatosensory cortex). Thus, the
152 process of encoding an internal representation follows constraints that are determined
153 by the specific properties of the input processed in the respective cortices. As a result,
154 the outcomes of computations in these networks are necessarily modality specific,
155 despite multiple cortical and subcortical regions invoking similar sets of computational
156 principles and some shared brain regions (e.g., Hebbian learning, reinforcement
157 learning; for discussion, see [25,26]).

158 For example, the auditory cortex displays lower sensitivity to spatial information but
159 enhanced sensitivity to temporal information, whereas the visual cortex displays
160 enhanced sensitivity to spatial information, but lower sensitivity to temporal information
161 (e.g., [27,28]). Iconic memory is short-lived (scale of ms), whereas echoic memory lasts
162 significantly longer (scale of seconds; e.g., [29]). Because auditory information unfolds
163 in time, the auditory cortex must be sensitive to the temporal accumulation of
164 information in order to make sense of the input. In contrast, visual information is
165 instantaneous, and although temporal integration is necessary in some cases such as in
166 deciphering motion, the visual cortex is relatively less sensitive to temporal
167 accumulation of information over extended periods of time. These inherent differences
168 are reflected in the way the sensory input eventually is encoded into internal
169 representations for further computation. Moreover, within modality, encoding of events

170 displays graded stimulus specificity given their complexity, similarity, saliency, and other
171 factors related to the quality and nature of the input (see [30,31], for evidence in visual
172 SL). For example, participants are able to learn two separate artificial grammars
173 simultaneously in the visual domain when the stimuli are from separate perceptual
174 dimensions—such as color and shape—but not when they are from within the same
175 perceptual dimension [16]. Figure 1 represents a schematic account of our approach
176 and shows how the same learning and representation principles result in modality and
177 stimulus specificity because they are instantiated in different brain regions, each with
178 their characteristic constraints.

179 Note that modality-specific constraints do not preclude the neurobiological ability to
180 process multimodal events. Indeed, this has recently been shown within SL using the
181 McGurk effect (see Glossary) in a cross-modal segmentation study [32]. More generally,
182 perception of the world routinely involves multisensory integration (e.g., [33]), occurring
183 at both low levels (i.e., the thalamus, [34]; the dorsal cochlear nucleus, [35]) and higher
184 levels of cortical processing (e.g., anterior temporal poles; [36]). Critically, however,
185 each of these multimodal areas would be subject to its own distinct set of constraints,
186 which would not necessarily be the same as those from the unimodal regions that feed
187 into it or to the constraints in other multimodal areas. For example, coherence in the
188 timing at which an auditory and a visual stimulus unfold is important for specific types of
189 integration [18] in audio-visual brain areas [37], but not as important for detecting
190 regularities in the case of integrating two different visual representations in the visual
191 system. Note that this view is distinct from alternative accounts suggesting that a unitary
192 learning mechanism operates on “abstract” amodal representations (e.g., [38]; see

193 Glossary). Instead, we suggest that multimodal regions are shaped by their own distinct
194 sets of constraints.

195 This brings us to an operational definition of ‘domain generality’. Within our
196 framework, domain generality primarily emerges because neural networks across
197 modalities instantiate similar computational principles. Moreover, domain generality may
198 also arise either through the possible engagement of partially-shared neural networks
199 that modulate the encoding of the to-be-learned statistical structure [39], or if stimulus
200 input representations encoded in a given modality (e.g., visual or auditory) are fed into a
201 multi-modal region for further computation and learning. As we shall see next, the
202 current neurobiological evidence is consistent with both of these latter possibilities.

203

204 **The neurobiological bases of SL**

205 Recent neuroimaging studies have shown that statistical regularities of visual shapes
206 results in activation in higher-level visual networks (e.g., lateral occipital cortex, inferior
207 temporal gyrus; [40,41]), whereas statistical regularities in auditory stimuli result in
208 activation in analogous auditory networks (e.g., left temporal and inferior parietal
209 cortices; frontotemporal networks including portions of the inferior frontal gyrus, motor
210 areas involved in speech production, [42]; and the pars opercularis and pars triangularis
211 regions of the left inferior frontal gyrus; [43]). Since these studies contrasted activation
212 for structured vs. random blocks of stimuli, the stronger activation for structured stimuli
213 in the above ROIs is consistent with the notion that some SL occurs already in brain
214 regions that are largely dedicated to processing unimodal stimuli, thus allowing for
215 modality-specific constraints to shape the outcome of computations.

216 In addition to identifying modality-specific learning mechanisms, studies that employ
217 neuroimaging or analyze event-related potentials point to some brain regions that are
218 active regardless of the modality in which the stimulus is presented. Often, this work has
219 associated SL effects with the hippocampus, and more generally with the medial
220 temporal lobe (MTL) memory system (see, e.g., [44]). This is consistent with
221 considerable systems neuroscience work that has established the hippocampus as a
222 locus for encoding and binding temporal and spatial contingencies presented in multiple
223 different modalities [40,44–48], as well as for consolidation of representations.

224 Hippocampal involvement in SL could consist of indirect modulation of the
225 representations in sensory areas or direct computations on hippocampal
226 representations that are driven by sensorimotor representations (see [48] for a
227 discussion). Note, however, that even in the case of direct hippocampal computations,
228 the computed representations are not necessarily amodal, as traces of their original
229 specificity nevertheless remain (e.g., [49]). Sub-regions of the hippocampus have been
230 shown to send and receive different types of information from different brain regions,
231 while developing specialization for representing those different types of information [50].
232 In addition, representations within the hippocampus itself are typically sparse, and are
233 wired to be maximally dissimilar even when stimuli evoke similar activation in a given
234 sensorimotor region [51–54]. Thus, even with a direct hippocampal involvement in SL,
235 such computations would likely result in a high degree of stimulus specificity, as
236 observed across many SL studies.

237 Additional imaging work has identified regions of the basal ganglia [55] and
238 thalamus [42,56] as important collaborating brain regions that work with the MTL

239 memory system to complete relevant sub-tasks involved in statistical learning. For
240 instance, the thalamus may provide synchronizing oscillatory activity in the alpha-
241 gamma and theta-gamma ranges that enables the rapid and accurate encoding of
242 sequences of events [56]. Thus, as summarized in Figure 2, the current neurobiological
243 evidence indeed suggests that detection of statistical regularities emerges from local
244 computations carried out within a given modality, and through a multi-domain
245 neurocognitive system that either modulates or operates on inputs from modality-
246 specific representations. Whether unimodal computations are necessary or sufficient for
247 SL, remains an open question. Whereas some studies report no learning following
248 hippocampal damage [44], other report significant SL in spite of such damage (e.g.,
249 [57]). In this context we should note, that lack of SL cannot be unequivocally attributed
250 to neurobiological impairment. Many normal participants do not show SL even with an
251 intact MTL system (see, for example, performance of a subset of the control participants
252 observed by [44], who do not fare better than the specific reported patient). This leads
253 us to our next section on individual differences.

254

255 **Individual and group differences in SL**

256 The proposed framework leads us to argue that individual differences provide key
257 evidence for understanding the mechanism of SL. In past work, it has often been
258 assumed that individual variance in implicit learning tasks is significantly smaller than
259 that of explicit learning (e.g., [58]). Consequently, the source of variability in
260 performance in SL has been largely overlooked, and had led researchers to focus on
261 average success rate (but see [19,59–61]).

262 In the context of SL, however, measures of central tendency can be particularly
263 misleading, as often about one third of the sample or more is not performing the task
264 above chance level (e.g., [12,60,61]). Moreover, tracking individual learning trajectories
265 throughout the phases of a given SL task has recently suggested that there is a
266 commensurate high level of variability in the learning curves of different individuals (e.g.,
267 [43,61]). In several areas of cognitive science, it is now well established that
268 understanding the source of individual differences holds the promise of revealing critical
269 insight regarding the cognitive operations underlying performance, leading to more
270 refined theories of behaviour. Furthermore, a theory that addresses individual
271 differences should aim to explain how learning mechanisms operate online to gradually
272 extract statistical structure, as opposed to focusing strictly on the outcome of a learning
273 phase in a subsequent test (e.g., [62]).

274 As a first approximation, our theoretical model splits the variance across
275 individuals into two main sources. First, as indicated by Figure 1, there is the variance
276 related to efficiency in encoding representations within modality in the visual, auditory,
277 and somatosensory cortex. This variance could derive from individual differences in the
278 efficacy of encoding fast sequential inputs or complex spatial stimuli, and thus
279 potentially could be traced to the neuronal mechanisms that determine the effective
280 resolution of one's sensory system. The second variance relates to the relative
281 computational efficiency of processing multiple temporally and spatially encoded
282 representations and detecting their distributional properties. This variance potentially
283 could be traced to cellular- and systems-level differences in factors that include (but are
284 not limited to) white matter density, which have been shown to affect AGL performance

285 [63], and variation in the speed of changes in synaptic efficacy [64]. In modeling terms,
286 these factors would relate to parameters such as connectivity, learning rates, and the
287 quality and type of information to be encoded and transmitted by a given brain region
288 (see Box 2).

289 The advantage of this approach is that it offers precise and testable predictions
290 that can be empirically evaluated. Thus, individuals can display relatively increased
291 sensitivity in encoding auditory information, but a relative disadvantage in encoding
292 sequential visual information. Conversely, two individuals that have similar efficiency in
293 terms of representational encoding in a given modality could differ in their relative
294 efficiency in computing the distributional properties of visual or auditory events. In either
295 case, low correlation in performance within individuals in two SL tasks, would be the
296 outcome, as has been reported in recent studies (e.g., [19]). However, as exemplified in
297 Box 3, accurate individual trajectories of SL can in principle be obtained by employing
298 parametric designs that independently target the two sources of variance.

299 Individual differences are particularly intriguing given recent claims regarding
300 developmental invariance in some types of SL (e.g., [65]). If SL capacities per se do not
301 change, and brain maturation and experience are primarily driving improvements in
302 processes “peripheral” to SL such as attention, then the bulk of variability in individual
303 developmental trajectories in SL abilities should be explained by these peripheral
304 factors only. We believe that the current empirical support for this claim is limited (see
305 [66] for a discussion). Further progress, however, requires a better fundamental
306 understanding of individual differences in SL, as elaborated in Box 3.

307

308 Concluding remarks

309 The present paper offers a novel theoretical perspective on SL that considers
310 computational and neurobiological constraints. Previous work on SL offered a possible
311 cognitive mechanistic account of how distributional properties are computed, with
312 explicit demonstrations being provided only within the domain of language [65,67]. The
313 perspective we offer has the advantage of providing a unifying neurobiological account
314 of SL across domains, modalities, neural and cognitive investigations, and cross-
315 species studies, thus connecting with and explaining an extensive set of data. The core
316 claim of our framework is that SL reflects contributions from domain-general learning
317 principles that are constrained to operate in specific modalities, with potential
318 contributions from partially shared brain regions common to learning in different
319 modalities. Both of these notions are well grounded in neuroscience. Moreover, they
320 provide our account with the flexibility needed to explain the apparently contradictory SL
321 phenomena observed both within and between individuals, such as stimulus and
322 modality specificity, while still being constrained by the capacities of the brain regions
323 that subserve the processing of different types of stimuli. In addition to descriptive
324 adequacy, our approach also provides targeted guidance for future investigations of SL
325 via explicit neurobiological modeling and studies of the mechanics underlying individual
326 differences. We therefore offer our framework as a novel platform for understanding and
327 advancing the study of SL and related phenomena.

328

329

330

331

References

- 332 1 Chomsky, N. (1959) A Review of B.F. Skinner's Verbal Behavior. *Language*
333 (*Baltim.*) 35, 26–58
- 334 2 Eimas, P.D. *et al.* (1971) Speech perception in infants. *Science* (80-.). 171, 303–
335 306
- 336 3 Saffran, J.R. *et al.* (1996) Statistical Learning by 8-Month-Old Infants. *Science*
337 (80-.). 274, 1926–1928
- 338 4 Baker, C.I. *et al.* (2004) Role of attention and perceptual grouping in visual
339 statistical learning. *Psychol. Sci.* 15, 460–466
- 340 5 Goujon, A. and Fagot, J. (2013) Learning of spatial statistics in nonhuman
341 primates: Contextual cueing in baboons (*Papio papio*). *Behav. Brain Res.* 247,
342 101–109
- 343 6 Hunt, R.H. and Aslin, R.N. (2001) Statistical learning in a serial reaction time task:
344 access to separable statistical cues by individual learners. *J. Exp. Psychol. Gen.*
345 130, 658–680
- 346 7 Courville, A.C. *et al.* (2006) Bayesian theories of conditioning in a changing world.
347 *Trends Cogn. Sci.* 10, 294–300
- 348 8 Friston, K. (2010) The free-energy principle: a unified brain theory? *Nat. Rev.*
349 *Neurosci.* 11, 127–138
- 350 9 Tishby, N. and Polani, D. (2011) Information theory of decisions and actions. In
351 *Perception-Action Cycle* pp. 601–638, Springer
- 352 10 Kirkham, N.Z. *et al.* (2002) Visual statistical learning in infancy: Evidence for a
353 domain general learning mechanism. *Cognition* 83, B35–B42
- 354 11 Bulf, H. *et al.* (2011) Visual statistical learning in the newborn infant. *Cognition*
355 121, 127–132
- 356 12 Endress, A.D. and Mehler, J. (2009) The surprising power of statistical learning:
357 When fragment knowledge leads to false memories of unheard words. *J. Mem.*
358 *Lang.* 60, 351–367
- 359 13 Saffran, J.R. and Thiessen, E.D. (2007) Domain-General Learning Capacities. In
360 *Blackwell Handbook of Language Development* (Hoff, E. and Shatz, M., eds), pp.
361 68–86

- 362 14 Hauser, M.D. *et al.* (2001) Segmentation of the speech stream in a non-human
363 primate: Statistical learning in cotton-top tamarins. *Cognition* 78, B53–B64
- 364 15 Toro, J.M. and Trobalón, J.B. (2005) Statistical computations over a speech
365 stream in a rodent. *Percept. Psychophys.* 67, 867–875
- 366 16 Conway, C.M. and Christiansen, M.H. (2005) Modality-constrained statistical
367 learning of tactile, visual, and auditory sequences. *J. Exp. Psychol. Learn. Mem.*
368 *Cogn.* 31, 24–39
- 369 17 Conway, C.M. and Christiansen, M.H. (2006) Statistical learning within and
370 between modalities: pitting abstract against stimulus-specific representations.
371 *Psychol. Sci.* 17, 905–912
- 372 18 Mitchel, A.D. and Weiss, D.J. (2011) Learning across senses: Cross-modal
373 effects in multisensory statistical learning. *J. Exp. Psychol. Learn. Mem. Cogn.* 37,
374 1081–1091
- 375 19 Misyak, J.B. and Christiansen, M.H. (2012) Statistical learning and language: An
376 individual differences study. *Lang. Learn.* 62, 302–331
- 377 20 Redington, M. and Chater, N. (1996) Transfer in artificial grammar learning: A
378 reevaluation. *J. Exp. Psychol. Gen.* 125, 123–138
- 379 21 Tunney, R.J. and Altmann, G.T.M. (1999) The transfer effect in artificial grammar
380 learning: Reappraising the evidence on the transfer of sequential dependencies.
381 *J. Exp. Psychol. Learn. Mem. Cogn.* 25, 1322–1333
- 382 22 Emberson, L.L. *et al.* (2011) Timing is everything: changes in presentation rate
383 have opposite effects on auditory and visual implicit statistical learning. *Q. J. Exp.*
384 *Psychol. (Hove).* 64, 1021–1040
- 385 23 Johansson, T. (2009) Strengthening the case for stimulus-specificity in artificial
386 grammar learning: no evidence for abstract representations with extended
387 exposure. *Exp. Psychol.* 56, 188–197
- 388 24 Sigman, M. and Gilbert, C.D. (2000) Learning to find a shape. *Nat. Neurosci.* 3,
389 264–269
- 390 25 Sjöström, P.J. *et al.* (2008) Dendritic excitability and synaptic plasticity. *Physiol.*
391 *Rev.* 88, 769–840
- 392 26 Samson, R.D. *et al.* (2010) Computational models of reinforcement learning: the
393 role of dopamine as a reward signal. *Cogn. Neurodyn.* 4, 91–105

- 394 27 Chen, L. and Vroomen, J. (2013) Intersensory binding across space and time: a
395 tutorial review. *Atten. Percept. Psychophys.* 75, 790–811
- 396 28 Recanzone, G.H. (2009) Interactions of auditory and visual stimuli in space and
397 time. *Hear. Res.* 258, 89–99
- 398 29 Sams, M. *et al.* (1993) The Human Auditory Sensory Memory Trace Persists
399 about 10 sec: Neuromagnetic Evidence. *J. Cogn. Neurosci.* 5, 363–70
- 400 30 Fiser, J. and Aslin, R.N. (2001) Unsupervised statistical learning of higher-order
401 spatial structures from visual scenes. *Psychol. Sci. a J. Am. Psychol. Soc. / APS*
402 12, 499–504
- 403 31 Fiser, J. and Aslin, R.N. (2002) Statistical learning of higher-order temporal
404 structure from visual shape sequences. *J. Exp. Psychol. Learn. Mem. Cogn.* 28,
405 458–467
- 406 32 Mitchel, A.D. *et al.* (2014) Multimodal integration in statistical learning: Evidence
407 from the McGurk illusion. *Front. Psychol.* 5, 407
- 408 33 Morein-Zamir, S. *et al.* (2003) Auditory capture of vision: Examining temporal
409 ventriloquism. *Cogn. Brain Res.* 17, 154–163
- 410 34 Tyll, S. *et al.* (2011) Thalamic influences on multisensory integration. *Commun.*
411 *Integr. Biol.* 4, 378–381
- 412 35 Basura, G.J. *et al.* (2012) Multi-sensory integration in brainstem and auditory
413 cortex. *Brain Res.* 1485, 95–107
- 414 36 Patterson, K. *et al.* (2007) Where do you know what you know? The
415 representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8,
416 976–987
- 417 37 Romanski, L.M. and Hwang, J. (2012) Timing of audiovisual inputs to the
418 prefrontal cortex and multisensory integration. *Neuroscience* 214, 36–48
- 419 38 Altmann, G.T.M. *et al.* (1995) Modality independence of implicitly learned
420 grammatical knowledge. *J. Exp. Psychol. Learn. Mem. Cogn.* 21, 899–912
- 421 39 Fedorenko, E. and Thompson-Schill, S.L. (2014) Reworking the language
422 network. *Trends Cogn. Sci.* 18, 120–126
- 423 40 Turk-Browne, N.B. *et al.* (2009) Neural evidence of statistical learning: efficient
424 detection of visual regularities without awareness. *J. Cogn. Neurosci.* 21, 1934–
425 45

- 426 41 Bischoff-Grethe, A. *et al.* (2000) Conscious and unconscious processing of
427 nonverbal predictability in Wernicke's area. *J. Neurosci.* 20, 1975–1981
- 428 42 McNealy, K. *et al.* (2006) Cracking the language code: neural mechanisms
429 underlying speech parsing. *J. Neurosci.* 26, 7629–7639
- 430 43 Karuza, E.A. *et al.* (2013) The neural correlates of statistical learning in a word
431 segmentation task: An fMRI study. *Brain Lang.* 127, 46–54
- 432 44 Schapiro, A.C. *et al.* (2014) The Necessity of the Medial-Temporal Lobe for
433 Statistical Learning. *J. Cogn. Neurosci.* 26, 1736–1747
- 434 45 Cohen, N.J. and Eichenbaum, H. (1993) *Memory, Amnesia, and the Hippocampal*
435 *System*, MIT Press.
- 436 46 Eichenbaum, H. (2013) Memory on time. *Trends Cogn. Sci.* 17, 81–88
- 437 47 Bornstein, A.M. and Daw, N.D. (2012) Dissociating hippocampal and striatal
438 contributions to sequential prediction learning. *Eur. J. Neurosci.* 35, 1011–23
- 439 48 Shohamy, D. and Turk-Browne, N.B. (2013) Mechanisms for widespread
440 hippocampal involvement in cognition. *J. Exp. Psychol. Gen.* 142, 1159–70
- 441 49 Papanicolaou, A.C. *et al.* (2002) The Hippocampus and Memory of Verbal and
442 Pictorial Material. *Learn. Mem.* 9, 99–104
- 443 50 Poppenk, J. *et al.* (2013) Long-axis specialization of the human hippocampus.
444 *Trends Cogn. Sci.* 17, 230–40
- 445 51 McClelland, J.L. *et al.* (1995) Why there are complementary learning systems in
446 the hippocampus and neocortex: insights from the successes and failures of
447 connectionist models of learning and memory. *Psychol. Rev.* 102, 419–457
- 448 52 Azab, M. *et al.* (2014) Contributions of human hippocampal subfields to spatial
449 and temporal pattern separation. *Hippocampus* 24, 293–302
- 450 53 O'Reilly, R.C. *et al.* (2011) Complementary Learning Systems. *Cogn. Sci.* 38,
451 1229–1248
- 452 54 Rolls, E.T. (2013) The mechanisms for pattern completion and pattern separation
453 in the hippocampus. *Front. Syst. Neurosci.* 7, 74
- 454 55 Poldrack, R.A. *et al.* (2005) The neural correlates of motor skill automaticity. *J.*
455 *Neurosci.* 25, 5356–5364

- 456 56 Roux, F. and Uhlhaas, P.J. (2014) Working memory and neural oscillations:
457 alpha-gamma versus theta-gamma codes for distinct WM information? *Trends*
458 *Cogn. Sci.* 18, 16–25
- 459 57 Knowlton, B.J. *et al.* (1992) Intact Artificial Grammar Learning in Amnesia:
460 Dissociation of Classification Learning and Explicit Memory for Specific Instances.
461 *Psychol. Sci.* 3, 172–179
- 462 58 Reber, A.S. (1996) *Implicit Learning and Tacit Knowledge: An Essay on the*
463 *Cognitive Unconscious*, Oxford University Press.
- 464 59 Arciuli, J. and Simpson, I.C. (2012) Statistical learning is related to reading ability
465 in children and adults. *Cogn. Sci.* 36, 286–304
- 466 60 Frost, R. *et al.* (2013) What predicts successful literacy acquisition in a second
467 language? *Psychol. Sci.* 24, 1243–52
- 468 61 Misyak, J.B. *et al.* (2010) On-line individual differences in statistical learning
469 predict language processing. *Front. Psychol.* 1, 31
- 470 62 Armstrong, B.C. and Plaut, D.C. (2013) , Simulating overall and trial-by-trial
471 effects in response selection with a biologically-plausible connectionist network. ,
472 in *Proceedings of the 35th Annual Conference of the Cognitive Science Society*,
473 pp. 139–144
- 474 63 Flöel, A. *et al.* (2009) White matter integrity in the vicinity of Broca’s area predicts
475 grammar learning success. *Neuroimage* 47, 1974–1981
- 476 64 Matzel, L.D. *et al.* (2000) Synaptic efficacy is commonly regulated within a
477 nervous system and predicts individual differences in learning. *Neuroreport* 11,
478 1253–1258
- 479 65 Thiessen, E.D. *et al.* (2013) The extraction and integration framework: a two-
480 process account of statistical learning. *Psychol. Bull.* 139, 792–814
- 481 66 Hagmann, P. *et al.* (2010) White matter maturation reshapes structural
482 connectivity in the late developing human brain. *Proc. Natl. Acad. Sci.* 107,
483 19067–19072
- 484 67 Thiessen, E.D. and Pavlik, P.I. (2013) iMinerva: a mathematical model of
485 distributional statistical learning. *Cogn. Sci.* 37, 310–43
- 486 68 Reeder, P.A. *et al.* (2013) From shared contexts to syntactic categories: The role
487 of distributional information in learning linguistic form-classes. *Cogn. Psychol.* 66,
488 30–54

- 489 69 Marcus, G.F. *et al.* (2007) Infant rule learning facilitated by speech. *Psychol. Sci.*
490 18, 387–391
- 491 70 Gomez, R.L. *et al.* (2000) The basis of transfer in artificial grammar learning.
492 *Mem. Cognit.* 28, 253–263
- 493 71 Elman, J.L. (1990) Finding structure in time. *Cogn. Sci.* 14, 179–211
- 494 72 Carreiras, M. *et al.* (2014) The what, when, where, and how of visual word
495 recognition. *Trends Cogn. Sci.* 18, 90–98
- 496 73 Sutskever, I. *et al.* (2008) The Recurrent Temporal Restricted Boltzmann
497 Machine. *Neural Inf. Process. Syst.* 21, 1601–1608
- 498 74 Laszlo, S. and Armstrong, B.C. (2014) PSPs and ERPs: Applying the dynamics of
499 post-synaptic potentials to individual units in simulation of temporally extended
500 Event-Related Potential reading data. *Brain Lang.* 132C, 22–27
- 501 75 Laszlo, S. and Plaut, D.C. (2012) A neurally plausible Parallel Distributed
502 Processing model of Event-Related Potential word reading data. *Brain Lang.* 120,
503 271–281
- 504 76 Lambon Ralph, M.A. *et al.* (2011) Finite case series or infinite single-case
505 studies? Comments on “Case series investigations in cognitive neuropsychology”
506 by Schwartz and Dell (2010). *Cogn. Neuropsychol.* 28, 466–74
- 507 77 Di Bono, M.G. and Zorzi, M. (2013) Deep generative learning of location-invariant
508 visual word recognition. *Front. Psychol.* 4, 635
- 509 78 Hinton, G.E. and Salakhutdinov, R.R. (2006) Reducing the dimensionality of data
510 with neural networks. *Science (80-)*. 313, 504–507
- 511 79 Orbán, G. *et al.* (2008) Bayesian learning of visual chunks by human observers.
512 *Proc. Natl. Acad. Sci.* 105, 2745–2750
- 513 80 Aslin, R.N. and Newport, E.L. (2012) Statistical learning: From acquiring specific
514 items to forming general rules. *Curr. Dir. Psychol. Sci.* 21, 170–176
- 515 81 Plaut, D. and Behrmann, M. (2011) Complementary neural representations for
516 faces and words: A computational exploration. *Cogn. Neuropsychol.* 28, 251–275
- 517 82 McClelland, J.L. and Rogers, T.T. (2003) The parallel distributed processing
518 approach to semantic cognition. *Nat. Rev. Neurosci.* 4, 310–22
- 519 83 Gebhart, A.L. *et al.* (2009) Statistical learning of adjacent and nonadjacent
520 dependencies among nonlinguistic sounds. *Psychon. Bull. Rev.* 16, 486–490

- 521 84 Kidd, E. (2012) Implicit statistical learning is directly associated with the
522 acquisition of syntax. *Dev. Psychol.* 48, 171–184
- 523 85 Kaufman, S.B. *et al.* (2010) Implicit learning as an ability. *Cognition* 116, 321–340
- 524 86 Christiansen, M.H. *et al.* (2012) Similar Neural Correlates for Language and
525 Sequential Learning: Evidence from Event-Related Brain Potentials. *Lang. Cogn.*
526 *Process.* 27, 231–256
- 527 87 Petersson, K.M. *et al.* (2012) What artificial grammar learning reveals about the
528 neurobiology of syntax. *Brain Lang.* 120, 83–95
- 529 88 McGurk, H. and MacDonald, J. (1976) Hearing lips and seeing voices. *Nature*
530 264, 746–748
- 531 89 Xia, M. *et al.* (2013) BrainNet Viewer: A Network Visualization Tool for Human
532 Brain Connectomics. *PLoS One* 8, e68910

533

534 **BOX 1: Generalization and transfer in statistical learning**

535 A key aspect of learning is to be able to apply knowledge gained from past
536 experiences to novel input. In some studies of SL, for example, participants are first
537 presented with a set of items generated by a pre-defined set of rules, and then in a
538 subsequent test phase asked to distinguish unseen items generated by these rules (i.e.
539 “grammatical items”) from another set of novel items that violate these rules (i.e.
540 “ungrammatical items”). If they are able to correctly classify the unseen items as
541 “grammatical” or “ungrammatical” at above chance levels, generalization from seen
542 items to the novel exemplars is assumed.

543 Many scientists initially interpreted successful generalization as evidence that the
544 participants had acquired the rules used to generate the stimuli and applied them to the
545 novel stimuli. However, several studies have shown that participants’ performance at
546 test can be readily explained by sensitivity to so-called “fragment” information,

547 consisting of distributional properties of subparts of individual items [16]. Consider a
548 hypothetical novel test item, ABCDE, which consists of various bigram (AB, BC, CD,
549 DE) and trigram (ABC, BCD, CDE) fragments. The likelihood of a participant endorsing
550 this test item as grammatical will depend on how frequently these bigram and trigram
551 fragments have occurred in the training items. If a test item contains a fragment that has
552 not been seen during training, then participants will tend to reject that item as
553 ungrammatical (see [68]) . Thus, generalization in SL is often, if not always, driven by
554 local stimulus properties and overall judgements of similarity, rather than the extraction
555 of abstract rules.

556 Another possible way in which past learning could be extrapolated to new input is
557 through the transfer of regularities learned in one domain to another (e.g., from visual
558 input to auditory input). Although early studies appeared to support cross-modal transfer
559 (e.g., [58,69]), more recent studies have shown that there is little, or no evidence for
560 transfer effects, once learning during test based on repetition or simple fragment
561 information is taken into account (e.g., [20,21,70]).

562 Generalization and transfer significantly differ in their contribution to theories of
563 learning. Whereas generalization has been demonstrated in SL studies—which is
564 important for the application of SL to language—there is little evidence of cross-modal
565 transfer, likely because of the substantial differences in neurobiological characteristics
566 of the visual, auditory and somatosensory cortices.

567

568 **BOX 2: Advancing SL Theory via Computational Modeling**

569 Computational modeling serves an important dual role in providing a quantitative

570 account of observed empirical effects, and in generating novel predictions to guide
571 empirical research (e.g., [67,71,72]). Within our framework, such modeling should
572 reflect the relevant neural hardware of sensory cortices, elucidating what distributional
573 properties are tracked by neural networks, as well as how [40,56,73]. It should also
574 make direct contact with neural measures as opposed to focusing strictly on behavioral
575 end-states (see [72,74,75] for discussion).

576 The development of explicit models allows for the parametric variation of different
577 aspects of the SL system, including the contributions of different learning mechanisms,
578 different brain regions, as well as of the quality and nature of the representations in
579 different parts of the system (Figure 1). This allows the probing of the model's ability to
580 account not only for group-averaged effects, but also for individual differences (see Box
581 3; [76]), and to establish how and why variation in different aspects of the system
582 modulate overall performance.

583 Recent advances in “deep” neural networks have also enabled interesting
584 insights into the effects of allowing intermediate representations to emerge as a function
585 of learning [77,78], as opposed to being explicitly stipulated. This relates directly to the
586 issues of modality and stimulus specificity that currently challenge SL theories. For
587 instance, representations closer to the sensory cortices are learned earlier and are
588 more strongly shaped by the specific characteristics of individual stimuli. This contrasts
589 with higher-order (but possibly modality specific) areas that operate on these early
590 sensory representations, and which can detect commonalities in higher-order statistics
591 despite little similarity in the surface properties or lower-order statistical relationships
592 amongst the stimuli (for related work using a Bayesian approach, see [79]). This

593 predicts that SL tasks that involve stimuli whose relationships are only detectable in
594 higher-order statistics should be more likely to show at least some generalization
595 relative to early sensory regions, which are predicted to exhibit stronger stimulus-
596 specificity (for a related proposal see [80]). For instance, the purpose of some brain
597 regions is primarily to distinguish between highly-similar complex inputs (e.g., visual
598 expertise areas such as the putative fusiform face area; [81]), or to transmit similar
599 outputs to multiple brain regions regardless of the source of its input (e.g., the semantic
600 memory system; [82]). Such a model is also able to account for stimulus specificity in
601 some higher-order domains and predict the possibility of generalization in others.

602

603 **BOX 3: Mapping individual trajectories in statistical learning.**

604 The present theoretical approach outlines a methodology for investigating
605 individual performance in SL tasks by orthogonally manipulating the experimental
606 parameters affecting encoding efficacy on the one hand, and parameters related to
607 efficiency in registering distributional properties, on the other. In general, manipulations
608 that center on input encoding parameters (temporal presentation rate, number of items
609 in a spatial configuration, stimuli complexity, etc.), will probe individual abilities in
610 encoding stimuli in a given modality. In contrast, manipulations that center on
611 transitional probabilities (i.e., the likelihood of Y following X, given the occurrence of X),
612 types of statistical contingencies (e.g., adjacent or non-adjacent), etc., will probe the
613 relative efficiency of a person's computational ability for registering distributional
614 properties (see [6] for manipulation of transitional probabilities in a Serial Reaction Time
615 task). Such parametric experimental designs would reveal, for any given individual,

616 specific patterns of interaction of two main factors driving SL, outlining how their joint
617 contribution determines his/her performance on a specific task. Figure 1 presents
618 hypothetical plots of the performance of two individuals following such parametric
619 manipulations. The figure illustrates differential trajectories of individual sensitivities to
620 either type of manipulation. This experimental approach has the additional promise of
621 revealing systematic commonalities or differences in sensitivity to various types of
622 distributional properties across domains or modalities.

623 A possible extension of this line of research would incorporate the impact of prior
624 knowledge on SL. The process of encoding representations of any continuous input is
625 dependent on the characteristics of the representational space for a given individual.
626 Thus, encoding an input of continuous syllabic elements (e.g., [12]) is different than
627 encoding a sequence of non-linguistic novel sounds (e.g., [83]), affecting SL efficacy.
628 This could generate significant individual differences in SL in domains such as
629 language, where individuals differ significantly in their linguistic representations (e.g.,
630 vocabulary size, number of languages spoken).

631 Note that most current research on individual differences in SL focuses on
632 predicting general cognitive or linguistic abilities from performance in SL tasks [19,59–
633 61,84,85] or showing similar neural correlates within subjects for SL and language
634 [86,87]. Investigating the various facets of performance in SL, as outlined above, is a
635 necessary further step to describe and explain the specific sources of potential
636 correlations between SL test measures and the cognitive functions they are aimed to
637 predict. Identifying these sources would, in turn, allow researchers to refine predictions
638 and generate well-defined *a priori* hypotheses.

639

640 **BOX 4: Outstanding questions**

641 • To what degree are high-level cognitive SL effects and low-level sensorimotor SL
642 effects modulated by the partially shared SL systems (e.g., hippocampus, basal
643 ganglia, inferior frontal gyrus) versus modality-specific systems?

644 • Can a better understanding of low-level cellular and systems neurobiology guide
645 theoretical advance by predicting the specific types of information that a brain
646 region will be most suited to encode and, consequently, the types of statistical
647 learning that may take place?

648 • To what degree does variability in the quality and nature of an individual's
649 modality-specific representations of individual stimuli, and variability in sensitivity
650 to the dependencies between stimuli, explain individual differences in SL
651 experiments?

652 • To what degree are the modality-specific and partially-shared neural processing
653 systems that underlie SL modulated by experience versus neuronal maturation
654 throughout development?

655

656 GLOSSARY

657 **Amodal representations.** “Amodal” representations are typically taken to be “abstract”
658 in the sense that they are not bound by specific sensory features (e.g., visual or
659 auditory). Apart from the problem of defining a theoretical construct in terms of what it is
660 not, the neurobiological evidence for such representations is scarce.

661 **Artificial Grammar Learning (AGL).** In a typical AGL experiment, participants are
662 exposed to sequences generated by a miniature grammar. Participants are only
663 informed about the rule-based nature of the sequences after the exposure phase, when
664 they are asked to classify a new set of sequences, some of which follow the grammar
665 while others do not. AGL is also considered to be a kind of implicit learning task.

666 **Generalization.** Refers to extension of learned statistical structure to unseen stimuli,
667 typically from within the same modality or stimulus domain.

668 **Internal Representation.** In neurobiological terms, an internal representation of a
669 stimulus is the pattern of neural activity evoked by a stimulus in a brain region (or
670 network of brain regions).

671 **McGurk effect.** The McGurk effect [88] illustrates the potentially complex interactions
672 between two conflicting streams of information from the auditory and visual modalities.
673 For instance, if a video of an individual pronouncing /ga/ is combined with the sound
674 /ba/, a listener will tend to hear /da/ because the sound /da/ is most consistent with the
675 visually-perceived positions of the lips and with the auditorily-perceived sound.

676 **Modality.** The sensorimotor mode in which the stimulus was presented (e.g., vision,
677 audition, touch). One modality may contain several sub-modalities (e.g., visual motion,
678 color), each of which is subserved by distinct neuroanatomy.

679 **Multimodal representations.** Representations that form when information from two or
680 more modalities are integrated in a representational space and associated brain region
681 (or network of regions). Importantly, these representations are, therefore, not “amodal”.

682 **Transfer.** A broader type of extension of learned knowledge than generalization, and
683 refers to the application of learned regularities to novel domains and/or modalities.

684

685

686 Acknowledgments

687 This paper was supported by The Israel Science Foundation (Grant 217/14 awarded to Ram
688 Frost), by the NICHD (RO1 HD 067364 awarded to Ken Pugh and Ram Frost, and PO1 HD
689 01994 awarded to Haskins Laboratories), and by a Marie Curie IIF award (PIIF-GA-2013-
690 627784 awarded to Blair C. Armstrong).

691

692

693 **Figure 1 – Theoretical Model of Statistical Learning**

694

695

696

697 Schematic representation of the processing of distributional information in the visual, auditory,
698 and somatosensory cortex, for unimodal and multimodal events. Different encoded
699 representations of continuous input presented in time or space result in task-stimulus specificity,
700 in spite of similar computations and contributions from partially shared neurocomputational
701 networks.

702

703 Figure 2 - Key Neural Networks involved in Visual and Auditory Statistical Learning

704

705

706

707 Key brain regions associated with domain-general (blue), and lower- and higher-level auditory (green)
708 and visual (red) modality-specific processing and representation, plotted on a smoothed ICBM152
709 template brain. The depicted regions are not intended to constitute an exhaustive set of brain regions
710 subserving each domain. C = Cuneus, FG = Fusiform Gyrus, STG = Superior Temporal Gyrus, IPL =
711 Inferior Parietal Lobule, H = Hippocampus, T = Thalamus, CA = Caudate, IFG = Inferior Frontal Gyrus.
712 Generated with the BrainNet Viewer [89].

713

714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733

Box 2 - Figure I – Candidate computational architecture for explaining and predicting the neural and behavioural data pertaining to statistical learning

Depiction of candidate SL model architecture. In this model, visual and auditory sensory input are first encoded and processed in pools of units (neurons) that code for low-level sensory features (e.g., sound frequency, edge orientation). These pools then project to higher-level visual and auditory areas which are better suited for detecting higher-order statistics and developing more sophisticated representations (e.g., of objects or syllables). Bimodal representations may also be learned in an area that receives inputs from both modalities. All of these modality-specific and bimodal areas also project to and receive feedback from shared representation and memory modulation systems. Arrows denote connections that send representations from one pool to another; blue lines denote connections that can either send representations, modulate processing, or both. Note that this figure is not intended to be exhaustive: other representations (e.g., low-level audio-visual) are assumed to be part of a more complete model, as is the coding of more detailed sensory information inputs (e.g., color, shape, movement, taste, smell).

734 **Box 3 - Figure I - Predicted empirical results illustrating how stimulus encoding and**
735 **transitional probability shape individual differences**

736

737

738

739

740 The two graphs above present hypothetical data from two participants and illustrates how the ability to
741 detect regularities and to encode inputs may be separated experimentally. Panel A demonstrates the
742 manipulation of rate of presentation and shows that whereas Participant 1 performs well even in relatively
743 fast rates, Participant 2 shows no learning when stimuli are presented at or above a rate of one per 600
744 ms. Panel B displays the manipulation of transitional probabilities. Here the rate of presentation is the
745 same across all 5 tasks, but transitional probabilities vary from 0.6 to 1. The results show that Participant
746 2, who performs above chance in the test even when the transitional probabilities between elements are
747 low, is more efficient in detecting probabilities than Participant 1.

748