

1 **Relational learning of exclusive-or combinations by baboons (*Papio papio*):**
2 **Behavioral assessment and computational model**

3
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8 **Abstract**

9 Previous research has shown that learning exclusive-or (XOR) combinations of stimuli is a
10 difficult enterprise for primates, but this research leaves unclear the exact learning process.
11 Indeed, learning of combinations of stimuli according to an XOR rule can be based on either
12 simple information provided by any single stimulus or on relational information provided by
13 combinations of stimuli. One reason for this is that complying with an XOR rule can be
14 achieved by rote learning of the four triplets of pieces of information that independently
15 comprise an XOR. However, XOR combinations entail relational information that can be
16 beneficial to the learning process. To study how this relational information can be used by
17 learners, we used a serial response time task involving triplets of discs displayed sequentially
18 on a screen according to XOR combinations with a group of Guinea baboons (*Papio papio*).
19 We found that the baboons used the relational information to predict stimuli in the series. This
20 was indicated by a decrease in response times for the third stimulus that benefited from
21 relational information from the first and second stimuli. A bio-inspired model of the cerebral
22 cortex reproduces these patterns of response times and points to the limits of classical
23 Hebbian learning. We conclude that the learning of exclusive-or combinations in monkeys is
24 not based on the simple memorization of independent cases but is driven by complex
25 combinatorial relational learning.
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28 **Keywords**

29 Combination rule – cortical network – priming – exclusive or – XOR
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32 **Running title**

33 Relational learning of XOR combinations

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36 **Acknowledgments**

37 We are grateful to Gianluigi Mongillo for comments and discussion of a previous version of
38 the manuscript. F. L. was supported by a grant from the CNRS and the Université Nice
39 Sophia Antipolis.

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48 **1. Introduction**

49 Prediction of future stimuli is central for the adaptation of behavior to the environment
50 (DeLong, Urbach, & Kutas, 2005). When prediction can be based on a rule, it sometimes
51 requires to learn complex combinations of stimuli (Miller, 1999; Bunge, Kahn, Wallis, Miller,
52 & Wagner, 2003; Wallis & Miller, 2003; Muhammad, Wallis, & Miller, 2006; Lavigne,
53 Avnaïm, & Dumercy, 2014). A paradigmatic complex rule is the exclusive-OR (also named
54 XOR, see Minsky & Papert, 1969; see Figure 1A). For instance, the rule "square XOR black"
55 corresponds to "square OR black but not both" in natural language. In this example, in which
56 the positive examples (● and □) have nothing in common, the learner often finds it very
57 difficult to consider these objects as belonging to the same category.

58 Combinations of stimuli according to an XOR rule can be learned by preschool children
59 (Mathy, Friedman, Couren, Laurent, & Millot, 2015), by adults (Bourne, 1970; Bruner,
60 Goodnow, & Austin, 1956; Bradmetz & Mathy, 2008; Feldman, 2000; Feldman, 2006;
61 Hovland, 1966; Lafond, Lacouture, & Mineau, 2007; Mathy & Bradmetz, 2004; Nosofsky,
62 Gluck, Palmeri, McKinley, & Gauthier, 1994; Vigo, 2006) and by non-human animals
63 (Wallis, Anderson & Miller, 2001; Baker, Behrmann, & Olson, 2002; Wallis & Miller, 2003).
64 For instance, Baker, Behrmann, and Olson (2002) used an XOR task in an
65 electrophysiological study with Rhesus macaques (*Macaca mulatta*). Learning of XOR
66 combinations was long and effortful as it required several thousands of training trials. After
67 training, selective cell responses in the infero-temporal cortex arose from conjunctive
68 encoding whereby two parts of a stimulus together exerted greater influence on neuronal
69 activity than predicted by the additive influence of each part considered individually. In a
70 behavioral study, Smith, Minda, and Washburn (2004) assessed the ability of four monkeys to
71 learn a variety of problems using shapes as stimuli. The monkeys could learn to solve XOR
72 problems, but this learning was more difficult for monkeys than for humans and more difficult
73 for the XOR problems than for other problems requiring simpler rules (e.g., ● and ■). Two
74 other studies on learning of XOR combinations of visual forms confirmed that learning of
75 XOR combinations is within the scope of ability of monkeys (Anderson, Peissig, Singer &
76 Sheinberg, 2006; Smith, Coutinho & Couchman, 2011). Taken together, these results suggest
77 that the learning of XOR combinations by nonhuman primates is possible but very difficult.
78 Notably, all of these studies used discrimination tasks involving visual stimuli that differed in

79 shape or color. We will discuss the possibility that such tasks might promote forms of case-
80 based learning while minimizing the need for learning the XOR combinations. Here, we
81 address the question of the nature of learning of XOR combinations based solely on the
82 relationships between stimuli in experimental trials.

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/ Figure 1 /

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86 *Simple and relational information in learning XOR combinations*

87 Learning combinations of stimuli and responses according to an XOR rule requires taking
88 into account of the combinations of stimuli but not of their intrinsic properties. For example,
89 let's consider that both ■□ and □■ are negative examples while ■■ and □□ are positive
90 examples. In that case, neither of the two stimulus properties taken alone (color on the left,
91 color on the right) is diagnostic, a feature that is typical of the XOR. One solution is to
92 memorize one subclass by rote memory by considering that the two stimuli of the positive
93 category (■■ and □□) are independent, that is, without relying on any commonality
94 between the two stimuli. Another way to learn an XOR is to acquire additional information
95 that can simplify the categorization process, using the available relational information to
96 describe the positive subcategory (e.g., "similar color = positive category"). According to this
97 strategy, the values of the attributes are no longer important. Regardless of whether the right
98 and left colors are black or white, the important characteristic is that they are identical. Such a
99 rule-based process to produce the rule "similar color = positive" seems beneficial to learning
100 because it is simple. The least effective alternative strategy is based on feature similarity¹,
101 given that 1) there is no critical feature in each class and 2) the positive examples are less
102 similar to one another than to either of the two negative examples (this odd statistical density
103 can be measured by a simple within- and between-category distance ratio; see Homa, Rhoads,
104 & Chambliss, 1979; Sloutsky, 2010). In the XOR, the disjunction undermines the role of
105 similarity in subserving learning (Goldstone, 1994), and the acquisition of such a concept
106 might question models that use feature similarity as a metric of the psychological space (e.g.,

¹ We do not refer here to the similarity that must be computed to describe the relational information in the XOR, such as "similar color = positive category"; this requires, at minimum, perception of the absence of entropy in similar pairs of colors. We refer here to the similarity that is computed between the four stimuli, which would indicate that the average similarity between the negative examples and the positive examples (i.e., 1 feature in common) is larger than the similarity between the examples of the same category (zero features in common). This inevitably makes the similarity-based models such that judging the similarity between examples does not simplify the learning process.

107 Estes, 1994; Kruschke, 1992; Medin & Schaffer, 1978; Nosofsky, 1984; Nosofsky, Gluck,
108 Palmeri, McKinley, & Gauthier, 1994). A more global issue related to the current study is that
109 although both classes of models (rule-based and similarity-based) rate the XOR as the most
110 difficult 2D logical structure, neither of them is clearly able to decompose the process of
111 learning an XOR.

112 One problem with using stimuli such as ■□ and □■ is that the learner might notice that
113 the stimulus is negative if there is only one black square. This is due to the fact that one
114 stimulus is made of two separate parts (■□ = ■ + □) that vary on only one dimension (here
115 the color) across the repeated feature (here square). Thus, such a task involves a numerical
116 facilitation due to the possibility to simply count the number of black squares. These stimuli
117 must by all means be avoided in studying whether relational information can be learned. This
118 problem has been overcome by using compound stimuli such as ●, ○, ■, and □ that employ
119 shapes and colors (these dimensions are considered as canonical in the categorization
120 literature; see Love & Markman, 2003; Mathy & Bradmetz, 2011). Here, the stimuli are
121 considered compound because two features, shape and color, are combined within a single
122 stimulus (● = ‘circle’ + ‘black’). An XOR combination for these shapes would be *black XOR*
123 *square* (meaning "black OR square but not both" in natural language). Such an XOR rule
124 requires the learner to consider that ■ and ○ are negative examples whereas ● and □ are
125 positive ones (e.g., Minda, Desroches, & Church, 2008; see Smith, Minda, & Washburn, 2004
126 on animal learning). In this example, in which (again) the positive examples have no feature
127 in common, the simple information provided by one feature of the stimulus (shape or color) is
128 not sufficient to properly categorize the stimulus. This makes the XOR a particularly long and
129 difficult construction to learn. The difficulty encountered by participants in artificial learning
130 settings of this type may be because the dimensions involved in the XOR (square *vs.* circle
131 and black *vs.* white) are much less important than the relationship between them (“black OR
132 square but not both”). The combinations can be learned by use of the relational information
133 between dimensions of the stimuli, which in the XOR corresponds to capturing the mutual
134 information that is due to the redundancy among the features (Shannon, 1948; Garner, 1962,
135 Fass, 2006; Mathy, 2010). A consequence of this is that efficient learning of XOR
136 combinations of stimuli requires learning the relational information provided by the
137 combination of the stimuli. However, compound stimuli are not optimal to study how
138 relational information is acquired. Compound stimuli hinder studying how this relational

139 information is used because participants can learn the four stimuli independently in a case-
140 based fashion. For example, one participant first associates ● with the positive category, then,
141 independently, ○ with the negative category, then, independently, ■ with the negative
142 category and finally □ with the positive category, without taking into account of the existing
143 combinations between features (e.g. the rule itself: black XOR square). Therefore, these
144 stimuli cannot be used to observe how relational information is used.

145 To overcome both numerical facilitation due to repeated features and compound stimuli,
146 we chose to study the XOR by use of a serial response time task (Nissen & Bullemer, 1987)
147 with sequences of three spatial stimuli (positions on a screen). One advantage in these
148 sequences is that the third stimulus is not predictable based on the first or second stimulus
149 alone, whereas it is predictable based on the combination of the first and second stimuli. This
150 paradigm clearly allows better studying how relational information is used in real time by
151 learners. The aim of the present study was twofold: (1) to investigate to what extent relational
152 information is effectively used to learn XOR combinations of stimuli and (2) to model on-line
153 synaptic learning of both simple information provided by a single stimulus and relational
154 information provided by a combination of two stimuli in a network model.

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166 **2. Experiment**

167 *Sequential learning and sequential processing of XOR combinations*

168 In the current study, we were particularly interested in the learning of the relational
169 structure in XOR combinations by participants who could not rely on either previous learning
170 of other XOR combinations or on language experience. We therefore chose a group of non-

171 human primates (Guinea baboons, *Papio papio*). Taking into account reports of the learning
172 of XOR combinations by monkeys (Wallis, Anderson & Miller, 2001; Baker et al., 2002;
173 Wallis & Miller, 2003), the protocol used in the present study aimed to disentangle the
174 learning of simple information and the learning of relational information necessary to process
175 XOR combinations. This was achieved by presenting sequences of three stimuli such that the
176 second stimulus was not predictable based on simple information provided by the first
177 stimulus alone, whereas the third stimulus was predictable based on the relational information
178 provided by the combination of the first and second stimuli (see Figures 1B and 1C). We used
179 a serial response time task in which the participant is required to respond to sequences of
180 stimuli that appear one-by-one at various locations on a computer screen. This permits the
181 decomposition of the learning process by using sequences of positions that represent separate
182 dimensions (Minier, Fagot, & Rey, 2015). In this task, non-human primates are required to
183 touch a target (a red disc) that appears on a touch-screen at nine possible positions (see Figure
184 1D). Once the target has been touched, it disappears and re-appears at a different position. On
185 each trial, the monkeys simply had to touch the successive positions (here, the three
186 successive positions involved in the four XOR sequence combinations) to receive a reward
187 after a given number of touches. Using this experimental paradigm, Minier et al. (2015) found
188 that when monkeys were exposed to concatenations of three regular sequences (defined by
189 their positions on the screen, e.g., 4-7-3, 1-9-6, 5-8-2), their transition times (TT; response to
190 a position following a preceding one) decreased more rapidly for the third element of the to-
191 be-learned sequence (i.e., 3, 6, or 2) than for the second element of the sequence. The
192 decrease in TT relative to the second element (i.e., 7, 9, or 8) indicated that the third element
193 benefited from richer contextual and predictable information than the second element (i.e., 3
194 was predicted by the co-occurrence of 4-7, whereas 7 was only predicted by 4). This additive
195 effect of prediction is consistent with the results in humans, in which a given word stimulus is
196 primed more strongly when preceded by two words related to it than when related to only one
197 of the preceding words (Lavigne et al., 2011 for a meta-analysis and model). However, one
198 possibility in Minier et al.'s study as well as in priming studies in human is that the two first
199 stimuli can be used independently to predict the third stimulus. Although non-human primates
200 can use statistical cues to learn a predictable motor sequence (Heimbauer, Conway,
201 Christiansen, Beran, & Owren, 2012; Locurto, Dillon, Collins, Conway, & Cunningham,
202 2013; Locurto, Gagne, & Natile, 2010; Procyk, Ford Dominey, Amiez, & Joseph, 2000), the

203 question remains as to whether they use relational information provided by combinations of
204 stimuli. The present study seeks to test this possibility using a design in which a third stimulus
205 can be predicted only by the combination of the first two stimuli. The XOR structure is
206 particularly informative for addressing the learning of relational information in comparison to
207 the learning of simple information.

208 To implement the XOR structure in a spatial task, we exposed monkeys to the following
209 four regular sequences defined according to XOR combinations of positions (see Figures 1B
210 and 1C): 1-2-4, 7-2-9, 1-8-9 and 7-8-4. To parallel examples in the Introduction, the rule here
211 is 1 XOR 8 gives 4, that is 1 OR 8 but not both gives 4. These precise sequences were chosen
212 because TT between the different positions in these random sequences did not differ and
213 therefore could not bias TT during the processing of XOR combinations. As shown in Figure
214 1B, the first and second positions *taken alone* do not predict the third position because they
215 are *not* systematically followed by a given position (e.g., 7 can be followed by 2 or 8, and 2
216 can be followed by 4 or 9). Due to the lack of predictability of position two from position one,
217 the exact second position of a triplet could not be learned (i.e., no decrease of TT on positions
218 2 or 8 should be observed; see the model section). Similarly, the third position of a triplet
219 cannot be learned if the monkeys only takes into account the immediate information provided
220 by the second position (i.e., 4 or 9 can indeed be preceded either by 2 or 8). The only way to
221 predict the third position of a triplet is to consider the mutual information provided by the first
222 *and* second positions taken together (i.e., if the sequence begins with 7 followed by 2, then 9
223 will appear). We hypothesized that if monkeys are able to learn relational information, they
224 should be able to predict the third position (e.g., 7-2-9). Our key prediction is that a true
225 learning process of these typical XOR combinations should be associated with a decrease of
226 TT2 from the second to the third position but not with a decrease of TT1 from the first to the
227 second position.

228 *Participants*

229 Ten female and seven male Guinea baboons (*Papio papio*, age range 3–15.5 years) from
230 the CNRS primate facility in Rousset, France were tested in this study. The monkeys were
231 part of a social group of 25 individuals living in a 700-m² outdoor enclosure containing
232 climbing structures connected to two experimental indoor areas containing the test equipment
233 (see below). Water was provided *ad libitum* during the test, and the monkeys received their
234 normal food ratio of fruits every day at 5 PM.

235

236 *Apparatus*

237 This experiment was conducted using a computer-learning device based on the voluntary
238 participation of baboons (for details, see Fagot & Bonte, 2010). The baboons were implanted
239 with RFID microchips and had free access to 10 automatic operant conditioning learning
240 devices. Whenever a monkey entered a test chamber, it was identified by its microchip and
241 the system was prompted to resume the trial list at the place at which the subject left it at its
242 previous visit. The experiment was controlled by a software test program written by JF using
243 E-prime (Version 2.0 professional, Psychology Software Tools, Pittsburgh, PA, USA)

244

245 *Procedure*

246 The screen was divided into nine equidistant positions represented by white crosses on a
247 black background (see Figure 1C). A trial began with the presentation of a fixation cross at
248 the bottom of the screen. After the baboon touched it, the fixation cross disappeared and the
249 nine crosses were displayed, one of them being replaced by the target, a red disc. When the
250 target was touched, it disappeared and was replaced by the cross. The next position in the
251 sequence was then replaced by the red disc until the end of the sequence was reached. A
252 reward (a drop of dry wheat) was provided at the end of a sequence of three touches. To learn
253 the task, the baboons initially received 1-item trials that were rewarded after one touch, after
254 which the number of touches in a trial was progressively increased to three. If the baboon
255 touched an inappropriate location (incorrect trial) or failed to touch the screen within 5 sec
256 after the red disc appeared (aborted trial), a green screen was displayed for 3 sec as a marker
257 of failure. Aborted trials were not counted as trials and were therefore presented again, while
258 incorrect trials were not. The elapsed time between the appearance of the red disc and the
259 baboon's touch of this disc was recorded as the TT for each item of the sequence.

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261 To control for the motor difficulty of the sequences to be produced, each baboon was first
262 tested with a series of 504 random sequences of three positions chosen among 9 (without
263 repetition of a position in a sequence). We doubled the 504 possibilities to obtain 1008
264 sequences and removed 8 sequences randomly to yield an arbitrary set of 1000 sequences. On
265 the basis of these random trials, a baseline measure for all possible transitions from one
266 position to another was computed by calculating the mean TT for each transition (e.g., from

267 position 2 to 7) and for each monkey, yielding a 9×9 matrix of mean TT (calculated over the
268 entire group of monkeys, Table 2).

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270 After these random trials, each monkey was exposed to 4000 trials, each involving one of
271 four possible regular sequences. These four 3-item regular sequences were carefully
272 constructed so that the mean TTs of their first and second transitions would not differ
273 statistically based on the baseline measurements obtained for these transitions during the
274 random trials. Because we were interested in the evolution of TT on the first and second
275 transitions in the triplets within the regular sequences, a computer program was developed to
276 find the smallest TT differences between these transitions within the random trials. The
277 following set of four triplets emerged from that selection: 7-2-9, 7-8-4, 1-2-4, and 1-8-9 (see
278 Figure 1, right panel). Baseline TT for the first transitions (i.e., 7-2, 7-8, 1-2, and 1-8) were
279 410, 420, 429, 399 ms, respectively (average: 414.6 ms; SD = 34.8). Baseline TT for the
280 second transitions (i.e., 2-9, 8-4, 2-4, and 8-9) were 409, 418, 432, 403 ms, respectively
281 (average: 415.4 ms; SD = 30.8).

282

283 3. Results

284 We analyzed the evolution of the first and second TT in each sequence (corresponding to
285 Transition 1 and Transition 2, respectively) by dividing the 4000 trials into 10 successive
286 blocks of 400 trials. Incorrect trials (0.7 % of the entire data set) were discarded for statistical
287 analyses, as were all correct TT greater than 2.5 standard deviations from the mean computed
288 for each subject (2.6 % of the trials). The mean TT per transition type (first vs. second), per
289 block and per monkey was then computed and analyzed using statistical tests (Figure 2 and
290 Table 1).

291

292 / Figure 2/

293 / Table 1 /

294

295 We first ran a 2 (Transitions) by 10 (Blocks) repeated measures ANOVA on mean TT and
296 found a significant effect of Transition ($F(1, 16) = 9.8, p = 0.06, \eta^2_p = .38$), TT1 being slower
297 than TT2, no significant effect of Block ($F(9, 144) < 1$), and a significant interaction between
298 Transition and Block ($F(9, 144) = 9.0, p < .001, \eta^2_p = .36$). More importantly, we found a

299 significant linear polynomial contrast for the interaction ($F(1, 16) = 26.9, p < .001, \eta^2_p = .63$),
300 with a large amount of the variance accounted for, showing the increasing difference between
301 the two TT with block number.

302

303 Finally, we analyzed the results using Generalized Linear Mixed Models (GLMM) using
304 the R software and the package lme4, and we followed the procedure recommended by Zuur
305 et al. (2009). To get a more normal distribution of the results, we used the inverse of the
306 reaction time as the dependent variable. We also included the individuals as a random variable
307 with a random intercept and a random slope depending on the number of blocks of trials
308 performed (continuous variable) to account for the repeated measurements. Based on the
309 design of the experiment, we chose to include an interaction between the number of blocks
310 performed and the transition (categorical variable) as explanatory variables. We found a
311 significant interaction between the number of blocks performed and the type of transition
312 (GLMM, $t = 4.957, p < .001$; $\beta = 3.211e-05, SE = 6.478e-06$). For the first transition, the
313 inverse of the reaction time significantly decreased by an estimated $-1.567e-05$ per block (SE
314 $= 6.618e-06, t = -2.368, p = 0.025$). For the second transition, the inverse of the reaction time
315 significantly increased by an estimated $1.644e-05$ per block (SE $= 6.618e-06, t = 2.484, p =$
316 0.0191).

317

318 To anticipate our conclusion, the observed decrease in TT2 supports the idea that the
319 triplets were not simply learned by rote, a process that would have produced similar decreases
320 in TT1 and TT2. Thus, the present results show that the relational structure of the XOR was
321 learned by the monkeys. Effectively, the monkeys used the two first positions to predict the
322 third position, a process that is sufficient to account for the decrease in TT2 and that also
323 accounts for the constant TT1. The next section presents an account of the learning of simple
324 and relational information in XOR combinations.

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328 **4. Computational Model**

329 Electrophysiological experiments provide evidence about the neural activity in the cerebral
330 cortex when monkeys are presented with a first stimulus that predicts an upcoming second

331 stimulus. After pairs of stimuli are learned, two main types of selective neuronal activity are
332 triggered by the presentation of the first stimulus. First, some neurons respond strongly to the
333 presentation of the first stimulus and maintain an elevated firing rate after its offset
334 (Miyashita, 1988; Miyashita & Chang, 1988; Fuster & Alexander, 1971). This retrospective
335 activity is believed to underlie short-term maintenance of the first stimulus in working
336 memory. Second, some neurons exhibit an increasing firing rate during the delay period prior
337 to the presentation of the second stimulus and respond strongly to the presentation of the
338 second stimulus. This prospective activity is believed to underlie the prediction of the second
339 stimulus (Naya, Yoshida, & Miyashita, 2001, 2003; Naya, Yoshida, Takeda, Fujimichi, &
340 Miyashita, 2003; Yoshida, Naya, & Miyashita, 2003; Erickson & Desimone, 1999; Rainer,
341 Rao, & Miller, 1999; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999; Sakai &
342 Miyashita, 1991). Prospective activity is an important mechanism subtending priming
343 processes and prediction based on previously learned knowledge (Brunel & Lavigne, 2009;
344 Lavigne et al., 2011; Lerner, Bentin, & Shriki, 2012; Lerner & Shriki, 2014). Biologically
345 inspired models of the cerebral cortex have shown that retrospective activity can be
346 reproduced assuming that Hebbian learning increases the efficacy of synapses between
347 neurons coding for the stimulus (Amit & Brunel, 1997, Brunel 1996; Amit, Bernacchia, &
348 Yakovlev, 2003). Furthermore, models have also shown that prospective activity can arise
349 after some level of learning of the pair of stimuli that increases the synaptic efficacy between
350 neurons coding for the first stimulus and neurons coding for the second stimulus (Brunel,
351 1996; Mongillo, Amit, & Brunel, 2003; see Lavigne & Denis, 2001, 2002; Lavigne, 2004).
352 Prospective activity has been reported as a predictor of response times during the processing
353 of sequences of two stimuli (Mongillo, Amit, & Brunel, 2003; Brunel & Lavigne, 2009; see
354 also Wang, 2002, 2008; Salinas, 2008; Soltani, & Wang, 2010; see Lerner et al., 2012; Lerner
355 & Shriki, 2014) and of three stimuli (Lavigne et al., 2011, 2012, 2013).

356 Pair associations can be learned through Hebbian learning, according to which the
357 activity of the pre- *and* post-synaptic neurons (e.g. coding for the first and second stimuli,
358 respectively) leads to long-term potentiation of the synapse (LTP; Bliss & Lømo, 1973; Bliss
359 & Collingridge, 1993). Conversely, the activity of the pre- *or* post-synaptic neuron leads to
360 long-term depression of the synapse (LTD; e.g., Kirkwood & Bear, 1994). However, although
361 Hebbian learning allows to associate stimuli in pairs, predicting a third stimulus according to
362 XOR combinations requires taking into account the relational information provided by the

363 two first stimuli, that is taking into account of the triplet of stimuli. Learning of XOR
364 combinations of three stimuli is a non-linearly separable problem that points to the limits of
365 classical Hebbian learning of pairs only. Learning of XOR combinations requires models
366 involving either additional neurons (see Rigotti et al., 2010a, 2010b, 2013; Bourjailly &
367 Miller, 2011a,b, 2012) or new learning algorithms (Lavigne et al., 2014 for a discussion and
368 model).

369 We present here a new learning algorithm in which potentiation or depression of a
370 synapse ij between two neurons, post-synaptic i and pre-synaptic j , depends on the activity of
371 these neurons, as in classical Hebbian learning, but also on the activity of a third pre-synaptic
372 neuron k . In the case of the sequential learning of XOR combinations, let us consider a typical
373 sequence KJI as the first, second and third positions, respectively (to match the classical
374 notation of synaptic efficacies used below). We use a biologically realistic inter-synaptic (IS)
375 learning algorithm of a synapse (e.g., ij) as a function of the activity of neurons i and j as well
376 as of other neurons (e.g., k) (Govindarajan, Israely, Huang, & Tonegawa 2011; also see
377 Govindarajan, Kelleher, & Tonegawa, 2006; see Lavigne et al., 2014). This IS learning rule
378 involves a Hebbian component that allows learning of pairs and an IS component that allows
379 learning of triplets (Appendix A). In the case of XOR combinations, IS learning associates
380 two positions (e.g., IJ) depending on another position (e.g., K).

381

382 *Modeling synaptic learning and activations in memory*

383 The design of the experiment permitted linking the processing of simple information vs.
384 relational information to variable levels of learning of the XOR combinations. Based on the
385 learned synaptic efficacies between populations of neurons coding for the positions, a
386 minimal model of activation between populations of neurons coding for the positions permits
387 reproduction of the data with a restricted number of parameters (Okun, 2015). The present
388 model is based on a simple network in which populations of neurons code for Positions stored
389 in memory. Here, $n = 9$ populations of neurons code for the nine Positions used in the
390 experiment with monkeys. No *a priori* knowledge of the structure of the stimuli is given to
391 the network through any pre-wiring of the network (see Lavigne et al., 2014; Bernacchia, La
392 Camera, & Lavigne, 2014 for discussion). Hence the populations are all connected together
393 with the same initial value of synaptic efficacy and learning relies solely on the sequences of
394 Positions.

395 Following computational models that have emphasized the critical role played by
396 synaptic connectivity on the level of prospective activity (e.g., Mongillo, Amit, & Brunel,
397 2003) and response times (Brunel and Laviigne, 2009), the present model investigates to what
398 extent IS learning generates TT during learning of XOR combinations. TT are simulated on
399 the second stimulus depending only on the simple information provided by the first stimulus
400 (i.e., the learned association between the pair of stimuli one and two) and on the third stimulus
401 depending on the relational information provided by the first two stimuli (i.e., learned
402 association between the triplet of stimuli one, two, and three).

403

404 *Learning of XOR combinations*

405 The Hebbian and IS learning rules apply at each learning trial of XOR sequences. We
406 consider here that the populations of neurons coding for items presented in a trial exhibit
407 increased retrospective activity when the corresponding stimulus is displayed (Miyashita,
408 1988; Miyashita & Chang, 1988; Fuster & Alexander, 1971). As has been reported for the
409 prefrontal cortex (Miller, Erickson, & Desimone, 1996; Takeda, Naya, Fujimichi, Takeuchi,
410 & Miyashita, 2005), when several stimuli are displayed successively, different populations of
411 neurons coding for those stimuli are active simultaneously. A direct consequence of this is
412 that in each learning trial, three populations of neurons (each of which codes for one of the
413 three positions displayed in that trial) exhibit an increased level of retrospective activity.
414 These neuronal populations will be considered active for that trial, whereas the other six
415 populations will be considered inactive. The combinations of populations that are active or
416 inactive change from trial to trial according to the sequences of positions displayed. For
417 simplicity, we consider here that when a population is active or inactive all of the neurons of
418 this population are in the same state. According to the Hebbian and IS learning rules, LTP or
419 LTD occurs at each synapse on a trial-by-trial basis according to the activities of the
420 populations connected by this synapse. The calculated synaptic efficacies are then taken as the
421 average efficacies of the populations of neurons coding for the stimuli.

422 The simulations follow the two phases of our experiment. During the first phase of the
423 experiment, random sequences of three positions are presented, and three populations of
424 neurons are active together (e.g., 7-2-9, 7-8-4, 1-2-4, etc.). Given that the monkeys were
425 exposed to all possible combinations of triplets, this phase generates equal values of synaptic
426 efficacy between the nine populations of neurons that code for the nine Positions. These initial

427 values of efficacy have a Hebbian component $J_{ij}(0)$ and an IS component $J_{ij}^k(0)$ (Equations
428 (4) and (8)). $J_{ij}(0)$ and $J_{ij}^k(0)$ were computed according to Brunel et al.'s (1998) Equation
429 (15) under the condition of infinite and slow learning. Efficacy depends on the instant
430 probabilities of potentiation/depression and on the average probability that the synapse has
431 been potentiated and/or depressed during the monkey's exposure to the random sequences
432 (here $J_{ij}(0)=\frac{1}{3}$ and $J_{ij}^k(0)=\frac{1}{7}$). During the second phase, specific sequences of positions
433 corresponding to the XOR rule were displayed, and learning occurred. This is modeled using
434 the initial values $J_{ij}(0)$ and $J_{ij}^k(0)$. These values are updated at each learning trial according
435 to the LTP and LTD equations described above. The resulting efficacy of the synapses thus
436 depends on the number of times two specific Positions were presented together in the same
437 trial (Figure 3A). The efficacy values have an increased or decreased probability of being
438 potentiated as a function of the number of times LTP or LTD occurred during learning of the
439 sequences (Figure 3B).

440 Hebbian learning potentiates/depresses synapses between populations coding for
441 positions proportionally to the number of times the two positions are presented in the
442 same/different trials (J_{ij} , shown in light orange in Figures A and B). For example, positions 7
443 and 2 occur together in one of the four sequences (LTP of the 7-2 synapse), and they occur
444 separately in two of the four sequences (LTD of the 7-2 synapse). According to Equation (A1)
445 (see Brunel et al.'s (1998) Equation (15), the efficacy of the 7-2 synapse converges to

446 $\frac{q_P^+}{q_P^+ + 2q_P^-} = \frac{1}{3}$ ($q_P^- = q_P^+$). The same occurs for synapses 7-9, 2-9, 1-2, 1-4, etc.

447 IS learning potentiates/depresses synapses in proportion to the number of times the three
448 positions are present in the same/different trials (J_{ij}^k , shown in dark orange in Figures 3A and
449 3B). For example, positions 7, 2 and 9 occur together in one of the four sequences (LTP of the
450 7-2 synapse when 9 is present), and there is no trial in which two positions (e.g., 7 and 2)
451 occur without the third (e.g., 9). According to Equation (A2), when 9 is present, the efficacy

452 of the 7-2 synapse converges to $\frac{q_T^+}{q_T^+ + 0q_T^-} = 1$ ($q_T^- = q_T^+$). The same occurs for synapses 1-

453 2 when 4 is present and for synapses 1-8 when 9 is present, etc.

454

455

456

457

458 *Activations and Transition Time 1*

459 Consistent with the prospective activity reported in neurophysiological studies in
 460 monkeys, the Position receiving an input (e.g., $K = 7$) generates prospective activity for all
 461 associated Positions (i.e., $J = 2$ or 8) irrespective of the Position that will actually follow in the
 462 sequence (e.g., $J = 2$ if the trial corresponds to the sequence 7-2-9). The simulation of
 463 Transition times for a given trial KJI relies on the level of activation received by the second
 464 input (Transition 1 from input 1, K , to input 2, J) (Figure 3C, D). The first Position, K ,
 465 activates the population coding for it (e.g., $K = 7$) at a value A_k (here, $A_k = 10$).
 466 Neurophysiological experiments in monkeys have shown that the response time to a given
 467 stimulus is inversely proportional to the level of activity of neurons coding for this stimulus at
 468 the stimulus onset (Roitman & Shadlen, 2001) and can be related to prospective activity
 469 (Erickson & Desimone 1999). Similarly, computational modeling studies use the level of
 470 prospective activity of neurons as a predictor of response time (Brunel & Lavigne, 2009;
 471 Wong & Wang, 2006; Wang, 2002; see also the diffusion models of reaction time described
 472 in Ratcliff, 1978, 2006 and in Ratcliff, Gomez, & McKoon, 2004). Hence, in the model,
 473 response time for the second Position, corresponding to Transition time 1, is inversely
 474 proportional to the prospective activity of the population coding for the second Position² (see
 475 Appendix B). In the present model, simulations of the activations and of the corresponding
 476 Transition time 1 were run after each learning trial (Figure 3D, blue line). The results show
 477 that Transition time 1 decreased only slightly (6 ms) over the forty learning trials. This is due
 478 to the very slow increase in the efficacy of synapse jk , which potentiates once and depresses
 479 twice every four trials, converging to the value $1/3$. This is due to the XOR rule in which the
 480 first Position (e.g., 7) predicts different possible second Positions (i.e., 2 or 8).

481

482 *Activations and Transition Time 2*

² This mechanism of activation is consistent with the results of priming studies in humans showing that the processing time for a word stimulus is shortened when the word is preceded by a word that is associated in memory (e.g., Meyer & Schvaneveldt, 1971, 1976; see Neely, 1991; Brunel & Lavigne, 2009; Lavigne et al., 2011 for reviews).

483 During the processing of sequences of the three Positions KJI , population i receives
484 combined activation from populations j and k . The prospective activity of population i is
485 proportional to the total synaptic efficacy (Hebbian and IS components) between population i
486 and populations j and k . Following the first input ($K = 7$), the second input ($J = 2$), for which
487 Transition time 1 is recorded, activates population j , which codes for the second Position, at a
488 value A_j (here $A_j = A_k = 10$). The combined activities of populations k and j , which code for
489 the first and second Positions, respectively, generate prospective activity of the associated
490 populations. According to the learned pairs, $K = 7$ activates associated Positions 2, 8, 4 and 9,
491 whereas $J = 2$ activates associated Positions 1, 7, 4 and 9. In addition, the combination of
492 Positions $K = 7$ and $J = 2$ activates associated Position 9 through stronger efficacies J_{ijk} due to
493 IS learning. In agreement with neurophysiological studies that show that the integration of
494 inputs is multiplicative for synapses within a same dendritic branch (Koch, Poggio, & Torre,
495 1983; Mel, 1992, 1993; Polsky, Mel, & Schiller, 2004; see Spruston, 2008; Poirazi & Mel,
496 2001), the integration of the input generated by the IS component of synapses (within a same
497 branch) is multiplicative in the present model (see Appendix B). Here, the IS learning rule
498 makes possible greater activation of the correct Position $I = 9$ following processing of
499 Positions 7 and 2 compared to the activation of other Positions (1, 8 and 4) that are associated
500 with 7 and 2 in pairs but not in a triplet.

501

502 TT2 for the third Position was recorded after each learning trial (Figure 3D, red line).
503 The results show that Transition time 2 continuously decreased (with a reduction of 30 ms)
504 during learning over the forty trials. Transition time 2 therefore diverges from Transition time
505 1 during learning. This is due to the IS component J_{ij}^k of the efficacy of synapse ij when k is
506 present. This component increases more rapidly than the Hebbian component J_{ij} because it
507 potentiates once every four trials and never depresses (thus converging to a value of 1). This
508 is due to the XOR rule, for which the combination of the first and second Positions (7 and 2)
509 predicts only one possible third Position (9). The multiplicative integration of the input
510 activities of populations k (7) and j (2) by population i (9) increases the activation of i when it
511 is learned in a triplet compared to when it is not. IS learning generates the divergence of the
512 two curves T1 and T2 (blue and red lines). Note that when IS learning and multiplicative
513 integration are removed, leaving only Hebbian learning and additive integration of the inputs,
514 Transition time 2 no longer diverges from Transition time 1. This reminds that simple

515 Hebbian learning between pairs of Positions does not allow learning of XOR combinations.

516

517 **5. Discussion**

518 The purpose of the present study was to investigate the respective contributions of simple
519 information and of relational information during learning of XOR combinations. The
520 experimental task required monkeys to associate two different outcome positions (4 and 9)
521 with combinations of four initial positions (1, 2, 7 and 8). For each sequence of three positions
522 (e.g., 7, 2 → 9), Position 1 and Position 2 can each be followed by two different positions (4
523 or 9). Position 1 alone therefore predicts a given Position 2 with probability $\frac{1}{2}$ and a given
524 Position 3 with probability $\frac{1}{2}$, whereas Position 2 alone also predicts a given Position 3 with
525 probability $\frac{1}{2}$. However, Positions 1 and 2 taken together predict Position 3 with probability
526 1. In other words, because simple information provided by either the first or second position is
527 not predictive of the third position, the relational information provided by the first two
528 positions must be learned to predict the third position (for instance, 7, 2 → 9). This is typical
529 of relational information, which is maximal in XOR combinations. One concurrent way of
530 dealing with the task is to learn in a case-based fashion each of the four triplets separately.
531 This mode of learning would have led to a general decrease of TT1 and TT2 because of the
532 non-null probability of Position 2 given Position 1 (TT1) as well as Position 3 given Position
533 2 (TT2). On the contrary, our results show that TT2 decrease during learning but not TT1.
534 This indicates that the relational information provided by the combination of Positions 1 and 2
535 is learned progressively over time to better predict Position 3. This enhanced performance is
536 in clear contrast with the absence of a decrease in Transition Time 1 (from Position 1 to
537 Position 2), which involves information that cannot be predicted unambiguously. Whereas the
538 monkeys' performance on the first transition did not improve with the number of trials, their
539 performance on the second transition (as shown by the decrease of TT2 as the number of trials
540 increased) benefited from the relational information contained in the first two items of the
541 sequence.

542 The learning of simple information provided by stimuli and of relational information
543 provided by combinations of stimuli can be modeled by a biologically inspired inter-synaptic
544 learning rule in which a given synapse is potentiated or depressed according to the activities
545 of two neurons pre- and post-synaptic and that of a third neuron that is pre-synaptic to this
546 synapse. This new learning algorithm is based on inter-synaptic learning mechanisms that

547 have been reported in neurophysiological studies (see Govindarajan et al., 2012) and modeled
548 at the level of individual synapses (Lavigne et al., 2014). The inter-synaptic learning
549 algorithm proposed here applies at the level of synapses between populations of neurons
550 coding for the different stimuli and takes into account the potentiation/depression of synapses
551 between two stimuli as a function of a third stimulus involved in an XOR combination. The
552 inter-synaptic synaptic learning rule has a classical Hebbian component that relies on the
553 potentiation/depression of synapses as a function of the activity of two pre- and post-synaptic
554 populations. This component potentiates synapses between a first and a second population,
555 allowing the first population to activate and predict the second. In learning XOR
556 combinations of three positions, learning of the first transition is supported by LTP
557 mechanisms in $1/4^{\text{th}}$ of the trials (when the two Positions are present in the same trial) and by
558 LTD in half of the trials (when the two Positions do not occur in the same trial); nothing
559 occurs in $1/4^{\text{th}}$ of the trials (when neither of the two Positions occurs in a single trial). As a
560 result of this proportion of LTP ($1/4$) and LTD ($3/4$), the efficacy of synapses converges to
561 $1/3$. Given that Transition Time 1 can benefit only from simple information coded by the
562 association between Positions 1 and 2 that is encoded in low values of synaptic efficacy, it
563 hardly decreases with learning. However, in the learning model, this absence of improvement
564 in Transition 1 does not mean that no learning occurred between Positions 1 and 2. Due to the
565 XOR structure of the experiment, learning was impaired by the co-occurrence of inconsistent
566 associations involving the same positions (e.g., because 7 was alternatively and randomly
567 followed by 2 or 8, it could not be used to predict the next position in the sequence). Hebbian
568 learning between pairs of stimuli is therefore not sufficient for learning XOR combinations.

569 The IS learning rule also has a specific IS component that potentiates a synapse as a
570 function of the activity of three populations of neurons. This component potentiates a synapse
571 between two populations and a third, allowing the combined activity of two populations to
572 activate and predict a third. In learning XOR combinations of three positions, learning of the
573 second transition is supported by IS LTP mechanisms in every trial (when the three Positions
574 are present in the same trial) and by IS LTD in none of the trials (because three given
575 Positions are always in a same trial and two of them are never presented with a different third
576 position). Due to this proportion of IS LTP ($1/1$) and IS LTD ($0/4$), the combination of the
577 first two positions predicts exactly which third Position will appear. Learning of the
578 combinations is apparent as a decrease in Transition Time 2; this learning is not possible

579 through Hebbian learning alone but requires IS learning between the three positions taken
580 together.

581 The proposed model provides a simple framework that can be used to link behavioral data
582 recorded in monkeys with synaptic learning. During on-line learning of XOR combinations of
583 stimuli, LTP and LTD determine the efficacy values between populations of neurons coding
584 for the different Positions. The synaptic matrix generated by learning determines the
585 activation between Positions during learning trials. The presentation of a Position activates the
586 neuronal population coding for that Position (i.e., retrospective activity). The activated
587 population, in turn, activates populations coding for Positions associated with the first one
588 (i.e., prospective activity) according to the learned efficacy values. The level of activation of a
589 given Population can be used as a predictor of Transition Time to the Position it codes for.
590 The present framework of IS learning provides a generalized understanding of the effects of
591 statistical regularities on the processing of sequences according to the simple information
592 shared between pairs of stimuli (Minier et al., 2015) and according to the relational
593 information between groups of stimuli (Wallis et al., 2001, 2003; Baker et al., 2002).

594 Overall, we show that baboons can rapidly learn XOR combinations using relational
595 information between triplets of stimuli in temporal sequences and that a bio-inspired model of
596 the cerebral cortex reproduces the patterns of transition times and points to the limits of
597 classical Hebbian learning.

598

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815

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818

819 **Appendix A**

820 *Hebbian learning*

821 In the present model, learning occurs on plastic synapses that connect the nine
822 populations of excitatory neurons that code for the nine different stimuli (positions) presented
823 in the sequences. The plastic synapses are assumed to be binary with two discrete states: a
824 potentiated and a depressed state. During learning trials, synapses ij are updated as a function
825 of the activity of the post- and pre-synaptic neurons i and j . On each trial, the presence (or
826 not) on the screen of a position I drives the state of neuron i coding for I to V_i . The state of
827 neuron i is in retrospective activity if position I is present and in spontaneous activity if I is
828 not present. The presence or absence of Position I in a trial is described as a binary string $\xi_i \in$
829 $\{0; 1\}$.

830

831 In rewarded trials in which the monkey points to the correct positions, LTP and LTD
832 have been reported to occur in association with rewarded responses (Soltani & Wang, 2006)
833 and are dependent on dopamine modulation of synaptic plasticity (Reynolds, Hyland, &
834 Wickens, 2001; Reynolds & Wickens, 2002; see also Centonze et al., 1999; Calabresi et al.,
835 1992a). In the present simulation, the XOR consists of four combinations of three positions K ,
836 J and I . We consider the possibility of long-term potentiation (LTP) or long-term depression
837 (LTD) of a synapse ij (from neuron j to neuron i) to depend on the presentation (or not) in the
838 same trial of positions J and I , coded by the pre-synaptic activity of neuron j and the post-
839 synaptic activity of neuron i , respectively. According to classical Hebbian learning (Hebb,
840 1949; Bliss and Lomo, 1973; Bliss and Collingridge, 1993; Kirkwood and Bear, 1994), if
841 positions J and I are displayed in the same trial, synapse ij between neuron j and neuron i
842 potentiates; otherwise, it depresses (and identically for synapse ji). Learning therefore occurs
843 at synapses between neurons i , j and k through successive trials corresponding to the
844 combinations of the three positions.

845

846 Following Brunel et al.'s (1998) formalism of LTP and LTD describing probabilistic
847 synaptic modification (Amit & Fusi, 1994; Brunel et al., 1998; Fusi, 2002; Fusi et al., 2005),
848 LTP of synapse ij occurs under the condition that the two populations j and i are active in the
849 same trial (*i.e.*, when positions J and I are present in the same trial). When pair LTP occurs,

850 synapse ij in the Down state has an instant probability q_P^+ of being switched to the Up state.
 851 As a result, the synapses have probability a_{ij} of being potentiated:

852

$$853 \quad a_{ij} = q_P^+ \xi_i \xi_j \quad (1)$$

854

855 LTD of synapse ij occurs under the condition that one neuron is active and the other is
 856 inactive. When LTD occurs, synapse ij in the Up state has an instant probability q_H^- of being
 857 switched to the Down state (we take here $q_P^- = q_P^+ = 0.1 \times 10^{-3}$). As a result, the synapse has
 858 probability b_{ij} of being depressed:

859

$$860 \quad b_{ij} = q_P^- [\xi_i (1 - \xi_j) + \xi_j (1 - \xi_i)] \quad (2)$$

861

862 Hebbian learning is calculated at each learning step as the probability J_{ij} of potentiating
 863 synapse ij .

864

865

866 In the case of Hebbian learning, the probability that no change occurs is:

867

$$868 \quad \lambda_{ij} = 1 - a_{ij} - b_{ij} \quad (3)$$

869

870 Brunel et al. (1998) have shown that the probability J_{ij} of potentiating the synapse ij at time T
 871 can be calculated using a_{ij} and b_{ij} , without further changes along the learning protocol:

872

$$873 \quad J_{ij}(T) = \sum_{t=1}^T a_{ij}(t) \prod_{s=t+1}^T \lambda_{ij}(s) + J_{ij}(0) \prod_{s=1}^T \lambda_{ij}(s) \quad (4)$$

874

875 Each $a_{ij}(t)$ in the sum $\sum_{t=1}^T a_{ij}(t)$ corresponds to a probability that the synapse is potentiated for

876 a given stimulus presented at time $t < T$ when neurons i and j are both active. Each term in the

877 sum is weighted by the probability $\prod_{s=t+1}^T \lambda_s$ that no transition occurs during the trials following
878 the potentiation between time $t+1$ and time T . This left-hand side of Equation (4) corresponds
879 to actual ‘learning’ of the synapse through successive potentiation and (or) depression. In the
880 right-hand side of Equation (A2), $J_{ij}(0)$ is the initial value of the potentiation of the Hebbian
881 component of the synapse before learning the XOR sequences. $J_{ij}(0)$ is weighted by the
882 probability $\prod_{s=1}^T \lambda_s$ that no transition occurs during all the trials between the beginning of
883 learning and time T . This product decays with the increasing number of learning trials and
884 corresponds to a progressive ‘forgetting’ of past trials by the synapse.

885

886 The initial value $J_{ij}(0)$ is defined by the successive cases of potentiation and depression of the
887 synapse during ‘the exposition to the random sequences of positions that preceded learning of
888 the XOR sequences.

889

890 *Inter-synaptic (IS) learning*

891 The formalism proposed here takes into account that during the learning of sequence
892 KJI learning occurs at synapse ij between two neurons i and j coding for two positions in a s
893 equence according to the activity of a third neuron k that codes for the third position in the
894 same sequence. Such an IS learning rule describes LTP or LTD of synapse ij as a function of
895 the activity of the post- and pre-synaptic neurons i and j , respectively, and of a third neuron
896 also, pre-synaptic neuron k .

897

898 In IS learning, LTP of synapse ij occurs under the condition that the three neurons i, j
899 and k are active during a trial in which the three positions K, J and I are displayed. In that
900 case, a synapse in the Down state has an instant probability q_T^+ of being switched to the Up
901 state. As a result, the synapse has the probability a_{ij}^k of being potentiated:

902

$$903 \quad a_{ij}^k = q_T^+ \xi_i \xi_j \xi_k \quad (5)$$

904

905 In IS learning, LTD of synapse ij occurs under the condition in which the two neurons i

906 and j are active and the third neuron is inactive. In that case, a synapse in the Up state has an
 907 instant probability q_{IS}^- of being switched to the Down state (as for the Hebbian component,
 908 we take here $q_T^- = q_T^+ = 0.3 \times 10^{-3}$). As a result, the synapse has probability b_{ij}^k of being
 909 depressed:

$$910$$

$$911 \quad b_{ij}^k = q_T^- [\xi_i \xi_j (1 - \xi_k) + \xi_i \xi_k (1 - \xi_j) + \xi_j \xi_k (1 - \xi_i)] \quad (6)$$

912

913 IS learning is calculated at each learning step as the probability J_{ij} of potentiating the
 914 synapse ij (see Equation A4 in Appendix A).

915

916

917 In the case of IS learning, the probability that no change occurs is:

$$918$$

$$919 \quad \lambda_{ij}^k = 1 - a_{ij}^k - b_{ij}^k \quad (7)$$

920

921 As in Equation A1, the resulting values of potentiation of the IS component J_{ijk} between two
 922 neurons i and j as a function of a third neuron k becomes:

$$923$$

$$924 \quad J_{ij}^k(T) = \sum_{t=1}^T a_{ij}^k(t) \prod_{s=t+1}^T \lambda_{ij}^k(s) + J_{ij}^k(0) \prod_{s=1}^T \lambda_{ij}^k(s) \quad (8)$$

925

926 At each learning trial, the total efficacy of a synapse is updated as a Hebbian component J_{ij}
 927 and an IS component J_{ij}^k .

928

929 **Appendix B**

930 *Transition Times 1*

931 The level of prospective activity of population j coding for J is proportional to the total
 932 synaptic efficacy between population k and j :

$$933$$

$$934 \quad A_{jk} = (J_{jk} + J_{jk}^i) A_k \quad (9)$$

935

936 J_{jk} is the Hebbian component and J_{jk}^i is the IS component of the total efficacy of synapse jk .

937 The activity generated by the input (e.g., $K = 7$) among all associated populations is regulated

938 by an inhibitory activity that is proportional to the total activity of all $n = 9$ activated

939 populations (Amit & Brunel, 1997; Brunel, 1996):

940

$$941 \quad Inh_1 = I_1 \sum_{i=1}^n A_i \quad (10)$$

942

943 This inhibition is global and unselective, that is it applies to all populations. It is then
944 subtracted to the prospective activity of each population after the first input.

945 The resulting prospective activity for each population then allow to compute a response time

946 on the to-be-predicted population ($J = 2$) when it is presented in the sequence (Transition time

947 1, blue line in Figure 3D). In the model, response time on the second Position ($J = 2$)

948 following the first Position ($K = 7$) corresponds to Transition time 1:

949

$$950 \quad TT_1 = \frac{r}{A_{jk}} \quad (11)$$

951

952 Here $r = 940$ simply gives TT of equivalent magnitude as in the experimental data.

953

954 *Transition Times 2*

955 The level of prospective activity of population i coding for I is proportional to the total

956 synaptic efficacy between population i and k and i and j . The resulting activation of

957 population i by j and k is:

$$958 \quad A_{i,jk} = J_{ij} A_j + J_{ik} A_k + \left(\frac{J_{ij}^k A_j + J_{ik}^j A_k}{2} \right)^m \quad (12)$$

959

960 Here $m = 3$ is a multiplicative factor of the inputs coming from the IS component of the

961 synapse, that gives a gain of TT2 of equivalent magnitude as in the experimental data.

962

963 As was the case after the first input K , the activity generated by the two inputs K and J among
964 the populations associated to K and J is regulated by an inhibitory activity that is proportional
965 to all $n = 9$ activated populations. A new value of inhibition is subtracted to the prospective
966 activity of each population:

967

$$968 \quad Inh_2 = I_2 \sum_{i=1}^n A_i \quad (13)$$

969

970 Response time on the third Position ($I = 9$) following the first two Positions ($K = 7$ and $J = 2$)
971 now corresponds to Transition time 2:

972

$$973 \quad TT_2 = \frac{r}{A_{i,jk}} \quad (14)$$

974

975

976

977

977

978 **Figures legends**

979

980 *Figure 1: A.* Exclusive-or relations using a truth table. *B.* Exclusive-or relations can also
981 describe specific sequences of three of six items (indicated by the colored arrows). *C.*
982 Exclusive-or relations using spatial positions. The items in the sequences are positions on a
983 screen arranged according to four regular patterns (shown in cyan, purple, green, and pink)
984 used to implement the XOR relationships. Arrows and numbers are displayed for illustrative
985 purposes. The regularities in the combinations of positions are used to compute the relational
986 information between the positions. *D.* Representation of a trial in the experimental setup.
987 Monkeys were required to touch three red discs displayed successively at three positions
988 according to one of the four sequences of the XOR (the three discs are displayed together only
989 in the figure). The first two discs are shown in dotted red lines, and the third disc is displayed
990 as in the experiment. The sequence is indicated by the two green arrows displayed here for
991 illustrative purposes only.

992

993 *Figure 2.* Mean response times across trials as a function of transition type and block number.
994 Each block corresponds to 400 successive trials (100 of each sequence). Error bars represent
995 +/- one standard error after the response times were collapsed by monkey and block number.
996 The black dashed line represents the grand average TT computed across the random trials of
997 the first phase.

998

999 *Figure 3: A.* Synaptic efficacies J_{ij} and J_{ij}^k associated with the nine positions as a function of
1000 the sequences of three positions involved in the learning trials. For clarity, the Figure displays
1001 efficacies in one direction only for Positions 7, 2 and 9 (green arrows); these positions are
1002 involved in one of the four XOR trials (i.e., 7-2-9, 7-8-4, 1-2-4, and 1-8-9). Efficacies are also
1003 reported for position 4, which occurs with positions 7 (purple arrow) and 2 (cyan arrow) in
1004 different trials (i.e., 7-8-4 and 1-2-4, respectively), and for position 3 (gray arrow), which is
1005 not involved in any XOR trial. Efficacies shown in dark orange (J_{ij}^k) correspond to trials in
1006 which the corresponding Positions are presented together, leading to LTP of the synapse.
1007 Efficacies shown in light orange (J_{ij}) correspond to trials in which the corresponding

1008 Positions are not presented together, leading to LTD of the synapse. **B.** Evolution of synaptic
1009 efficacies J_{ij} and J_{ij}^k as a function of the number of trials with LTP and the number of trials
1010 with LTD (shown in the same colors as in A ; ten blocks of 4 XOR sequences). The evolution
1011 of synapse efficacy is displayed for synapses that are affected by different numbers of cases of
1012 LTP and LTD: 1) for Hebbian learning involving one LTP and 2 LTD (light orange, solid
1013 line); 2) for Hebbian learning involving zero LTP and two LTD (light orange, dotted line); 3)
1014 for IS learning involving one LTP and zero LTD (dark orange, full line); and 4) for IS
1015 learning involving zero LTP and one LTD (dark orange, dotted line). **C.** Activations A_{ij} and
1016 A_{ij}^k of populations coding for the nine Positions and for the XOR trial 7-2-9: 7 is the first input
1017 (gray disc), 2 is the second input (blue disc), on which Transition time 1 is recorded (Figure
1018 3D, blue line), and 9 is the third input (red disc), on which Transition time 2 is recorded
1019 (Figure 3D, red line). For clarity, Figure 3C presents only activations of the same Positions
1020 shown in Figure 3A. The total activation has two components, A_{ij}^k (dark orange) and A_{ij}
1021 (light orange), that correspond to different values of efficacy J_{ij}^k and J_{ij} (shown in the same
1022 colors; see text). **D.** Evolution of Transition time 1 (from Position 7 to 2, blue line) and of
1023 Transition time 2 (from Position 2 to 9, red line) as a function of the number of learning trials.
1024

1024

1025 **Table legend**

	Monkey #																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
r1	0,26	0,94	-0,28	0,04	0,77	0,44	0,55	0,62	-0,10	0,75	0,15	-0,48	-0,20	0,81	-0,01	-0,02	0,21
p1	0,47	0,00	0,43	0,91	0,01	0,21	0,10	0,06	0,79	0,01	0,68	0,16	0,58	0,00	0,99	0,96	0,56
r2	0,06	0,65	-0,58	0,23	0,22	-0,40	0,14	-0,28	-0,92	-0,16	-0,76	-0,89	-0,80	0,74	-0,75	-0,32	-0,33
p2	0,86	0,04	0,08	0,53	0,53	0,25	0,70	0,43	0,00	0,67	0,01	0,00	0,01	0,01	0,01	0,37	0,36
diff 1-2	39	26	33	90	-9	50	29	-11	-8	49	30	-27	37	3	9	10	17

1026

1027 *Table 1:* For each monkey, correlation between block number and TT as a function of
 1028 Transition Type is shown. Note: r1, correlation for Transition 1; p1, p value for r1; likewise
 1029 for Transition 2. The last line indicates the mean difference between the two types of
 1030 transitions across blocks. Correlations r1 shown in bold indicate a positive correlation, and p1
 1031 values shown in bold are those that are significant. Correlations r2 shown in bold are negative.

1032

1033

1 st Element in Transition	2 nd Element in Transition								
	1	2	3	4	5	6	7	8	9
1	-	429	429	423	368	396	440	399	405
2	531	-	442	432	371	398	458	391	409
3	527	421	-	437	379	389	453	390	408
4	515	418	431	-	368	403	431	384	418
5	507	401	417	409	-	377	431	384	395
6	529	421	429	426	356	-	443	377	399
7	506	410	441	407	368	408	-	420	423
8	523	401	419	418	359	386	441	-	403
9	508	408	420	427	356	378	457	394	-

1034 *Table 2:* Mean response times for each of the 72 possible transitions calculated from the 1000
 1035 random trials, over the entire group of baboons

1036

1037

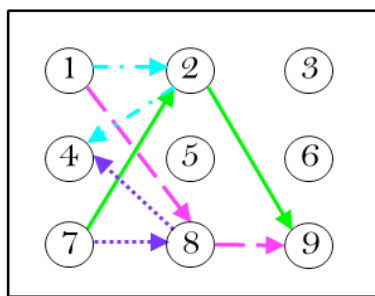
A. XOR truth table

Input 1	Input 2	→	XOR
0	0	→	0
0	1	→	1
1	0	→	1
1	1	→	0

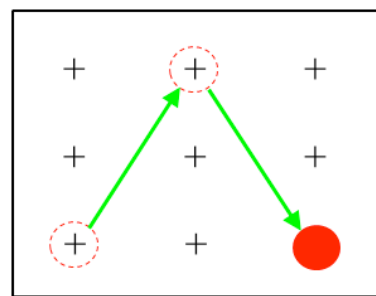
B. XOR combinations

Stim 1	Stim 2	→	Stim 3
1	2	→	4
7	2	→	9
1	8	→	9
7	8	→	4

C. Sequences of combinations

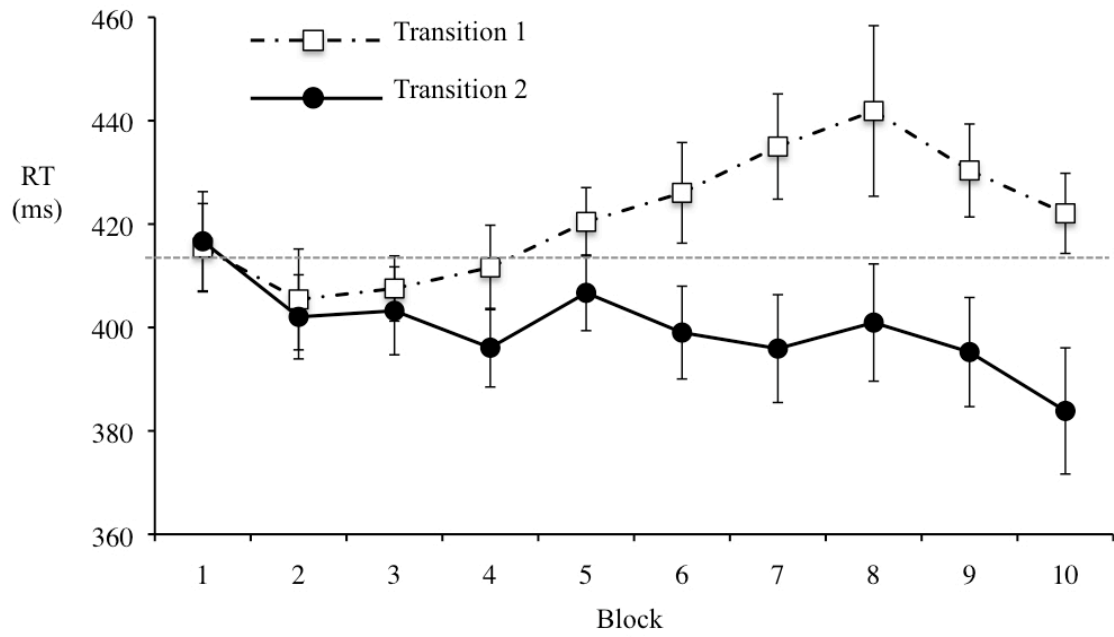


D. Example of a single trial



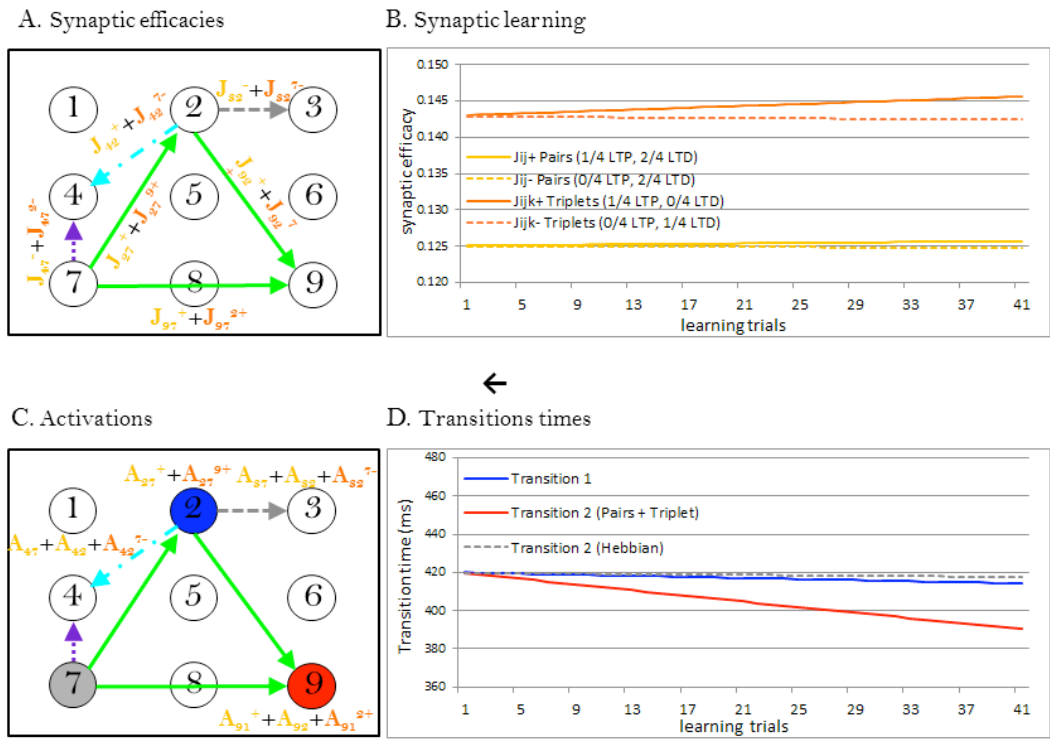
1038
1039

1039
1040 Fig. 2
1041



1042
1043

1043
1044 Fig. 3



1045