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

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Abstract

Previous research has shown that learning exclusive-or (XOR) combinations of stimuli is a difficult enterprise for primates, but this research leaves unclear the exact learning process. Indeed, learning of combinations of stimuli according to an XOR rule can be based on either simple information provided by any single stimulus or on relational information provided by combinations of stimuli. One reason for this is that complying with an XOR rule can be achieved by rote learning of the four triplets of pieces of information that independently comprise an XOR. However, XOR combinations entail relational information that can be beneficial to the learning process. To study how this relational information can be used by learners, we used a serial response time task involving triplets of discs displayed sequentially on a screen according to XOR combinations with a group of Guinea baboons (*Papio papio*).

We found that the baboons used the relational information to predict stimuli in the series. This was indicated by a decrease in response times for the third stimulus that benefited from relational information from the first and second stimuli. A bio-inspired model of the cerebral cortex reproduces these patterns of response times and points to the limits of classical Hebbian learning. We conclude that the learning of exclusive-or combinations in monkeys is not based on the simple memorization of independent cases but is driven by complex combinatorial relational learning.

Keywords

Combination rule – cortical network – priming – exclusive or – XOR

Running title
Relational learning of XOR combinations

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1. Introduction

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

Combinations of stimuli according to an XOR rule can be learned by preschool children (Mathy, Friedman, Couren, Laurent, & Millot, 2015), by adults (Bourne, 1970; Bruner, Goodnow, & Austin, 1956; Bradmetz & Mathy, 2008; Feldman, 2000; Feldman, 2006; Hovland, 1966; Lafond, Lacouture, & Mineau, 2007; Mathy & Bradmetz, 2004; Nosofsky, Gluck, Palmeri, McKinley, & Gauthier, 1994; Vigo, 2006) and by non-human animals (Wallis, Anderson & Miller, 2001; Baker, Behrmann, & Olson, 2002; Wallis & Miller, 2003). For instance, Baker, Behrmann, and Olson (2002) used an XOR task in an electrophysiological study with Rhesus macaques (Macaca mulatta). Learning of XOR combinations was long and effortful as it required several thousands of training trials. After training, selective cell responses in the infero-temporal cortex arose from conjunctive encoding whereby two parts of a stimulus together exerted greater influence on neuronal activity than predicted by the additive influence of each part considered individually. In a behavioral study, Smith, Minda, and Washburn (2004) assessed the ability of four monkeys to learn a variety of problems using shapes as stimuli. The monkeys could learn to solve XOR problems, but this learning was more difficult for monkeys than for humans and more difficult for the XOR problems than for other problems requiring simpler rules (e.g., ● and □). Two other studies on learning of XOR combinations of visual forms confirmed that learning of XOR combinations is within the scope of ability of monkeys (Anderson, Peissig, Singer & Sheinberg, 2006; Smith, Coutinho & Couchman, 2011). Taken together, these results suggest that the learning of XOR combinations by nonhuman primates is possible but very difficult. Notably, all of these studies used discrimination tasks involving visual stimuli that differed in
shape or color. We will discuss the possibility that such tasks might promote forms of case-based learning while minimizing the need for learning the XOR combinations. Here, we address the question of the nature of learning of XOR combinations based solely on the relationships between stimuli in experimental trials.

/ Figure 1 /

*Simple and relational information in learning XOR combinations*

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

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\(^1\) 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.
One problem with using stimuli such as □ and □ is that the learner might notice that the stimulus is negative if there is only one black square. This is due to the fact that one stimulus is made of two separate parts (□ = ■ + □) that vary on only one dimension (here the color) across the repeated feature (here square). Thus, such a task involves a numerical facilitation due to the possibility to simply count the number of black squares. These stimuli must by all means be avoided in studying whether relational information can be learned. This problem has been overcome by using compound stimuli such as ●, ○, ■, and □ that employ shapes and colors (these dimensions are considered as canonical in the categorization literature; see Love & Markman, 2003; Mathy & Bradmetz, 2011). Here, the stimuli are considered compound because two features, shape and color, are combined within a single stimulus (● = ‘circle’ + ‘black’). An XOR combination for these shapes would be black XOR square (meaning "black OR square but not both" in natural language). Such an XOR rule requires the learner to consider that ■ and ○ are negative examples whereas ● and □ are positive ones (e.g., Minda, Desroches, & Church, 2008; see Smith, Minda, & Washburn, 2004 on animal learning). In this example, in which (again) the positive examples have no feature in common, the simple information provided by one feature of the stimulus (shape or color) is not sufficient to properly categorize the stimulus. This makes the XOR a particularly long and difficult construction to learn. The difficulty encountered by participants in artificial learning settings of this type may be because the dimensions involved in the XOR (square vs. circle and black vs. white) are much less important than the relationship between them (“black OR square but not both”). The combinations can be learned by use of the relational information between dimensions of the stimuli, which in the XOR corresponds to capturing the mutual information that is due to the redundancy among the features (Shannon, 1948; Garner, 1962, Fass, 2006; Mathy, 2010). A consequence of this is that efficient learning of XOR combinations of stimuli requires learning the relational information provided by the combination of the stimuli. However, compound stimuli are not optimal to study how relational information is acquired. Compound stimuli hinder studying how this relational
information is used because participants can learn the four stimuli independently in a case-based fashion. For example, one participant first associates • with the positive category, then, independently, ○ with the negative category, then, independently, ■ with the negative category and finally □ with the positive category, without taking into account of the existing combinations between features (e.g. the rule itself: black XOR square). Therefore, these stimuli cannot be used to observe how relational information is used.

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

2. Experiment

Sequential learning and sequential processing of XOR combinations

In the current study, we were particularly interested in the learning of the relational structure in XOR combinations by participants who could not rely on either previous learning of other XOR combinations or on language experience. We therefore chose a group of non-
human primates (Guinea baboons, *Papio papio*). Taking into account reports of the learning of XOR combinations by monkeys (Wallis, Anderson & Miller, 2001; Baker et al., 2002; Wallis & Miller, 2003), the protocol used in the present study aimed to disentangle the learning of simple information and the learning of relational information necessary to process XOR combinations. This was achieved by presenting sequences of three stimuli such that the second stimulus was not predictable based on simple information provided by the first stimulus alone, whereas the third stimulus was predictable based on the relational information provided by the combination of the first and second stimuli (see Figures 1B and 1C). We used a serial response time task in which the participant is required to respond to sequences of stimuli that appear one-by-one at various locations on a computer screen. This permits the decomposition of the learning process by using sequences of positions that represent separate dimensions (Minier, Fagot, & Rey, 2015). In this task, non-human primates are required to touch a target (a red disc) that appears on a touch-screen at nine possible positions (see Figure 1D). Once the target has been touched, it disappears and re-appears at a different position. On each trial, the monkeys simply had to touch the successive positions (here, the three successive positions involved in the four XOR sequence combinations) to receive a reward after a given number of touches. Using this experimental paradigm, Minier et al. (2015) found that when monkeys were exposed to concatenations of three regular sequences (defined by their positions on the screen, e.g., 4-7-3, 1-9-6, 5-8-2), their transition times (TT; response to a position following a preceding one) decreased more rapidly for the third element of the to-be-learned sequence (i.e., 3, 6, or 2) than for the second element of the sequence. The decrease in TT relative to the second element (i.e., 7, 9, or 8) indicated that the third element benefited from richer contextual and predictable information than the second element (i.e., 3 was predicted by the co-occurrence of 4-7, whereas 7 was only predicted by 4). This additive effect of prediction is consistent with the results in humans, in which a given word stimulus is primed more strongly when preceded by two words related to it than when related to only one of the preceding words (Lavigne et al., 2011 for a meta-analysis and model). However, one possibility in Minier et al.’s study as well as in priming studies in human is that the two first stimuli can be used independently to predict the third stimulus. Although non-human primates can use statistical cues to learn a predictable motor sequence (Heimbauer, Conway, Christiansen, Beran, & Owren, 2012; Locurto, Dillon, Collins, Conway, & Cunningham, 2013; Locurto, Gagne, & Nutable, 2010; Procyk, Ford Dominey, Amiez, & Joseph, 2000), the
question remains as to whether they use relational information provided by combinations of stimuli. The present study seeks to test this possibility using a design in which a third stimulus can be predicted only by the combination of the first two stimuli. The XOR structure is particularly informative for addressing the learning of relational information in comparison to the learning of simple information.

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

Participants

Ten female and seven male Guinea baboons (Papio papio, age range 3–15.5 years) from the CNRS primate facility in Rouset, France were tested in this study. The monkeys were part of a social group of 25 individuals living in a 700-m² outdoor enclosure containing climbing structures connected to two experimental indoor areas containing the test equipment (see below). Water was provided ad libitum during the test, and the monkeys received their normal food ratio of fruits every day at 5 PM.
This experiment was conducted using a computer-learning device based on the voluntary participation of baboons (for details, see Fagot & Bonfante, 2010). The baboons were implanted with RFID microchips and had free access to 10 automatic operant conditioning learning devices. Whenever a monkey entered a test chamber, it was identified by its microchip and the system was prompted to resume the trial list at the place at which the subject left it at its previous visit. The experiment was controlled by a software test program written by JF using E-prime (Version 2.0 professional, Psychology Software Tools, Pittsburgh, PA, USA).

Procedure

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

To control for the motor difficulty of the sequences to be produced, each baboon was first tested with a series of 504 random sequences of three positions chosen among 9 (without repetition of a position in a sequence). We doubled the 504 possibilities to obtain 1008 sequences and removed 8 sequences randomly to yield an arbitrary set of 1000 sequences. On the basis of these random trials, a baseline measure for all possible transitions from one position to another was computed by calculating the mean TT for each transition (e.g., from...
position 2 to 7) and for each monkey, yielding a $9 \times 9$ matrix of mean TT (calculated over the entire group of monkeys, Table 2).

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

3. Results

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

We first ran a 2 (Transitions) by 10 (Blocks) repeated measures ANOVA on mean TT and found a significant effect of Transition ($F(1, 16) = 9.8, p = 0.06, \eta^2_p = .38$), TT1 being slower than TT2, no significant effect of Block ($F(9, 144) < 1$), and a significant interaction between Transition and Block ($F(9, 144) = 9.0, p < .001, \eta^2_p = .36$). More importantly, we found a
significant linear polynomial contrast for the interaction \( F(1, 16) = 26.9, p < .001, \eta^2_p = .63 \), with a large amount of the variance accounted for, showing the increasing difference between the two TT with block number.

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

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

### 4. Computational Model

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

Pair associations can be learned through Hebbian learning, according to which the activity of the pre- and post-synaptic neurons (e.g. coding for the first and second stimuli, respectively) leads to long-term potentiation of the synapse (LTP; Bliss & Lømo, 1973; Bliss & Collingridge, 1993). Conversely, the activity of the pre- or post-synaptic neuron leads to long-term depression of the synapse (LTD; e.g., Kirkwood & Bear, 1994). However, although Hebbian learning allows to associate stimuli in pairs, predicting a third stimulus according to XOR combinations requires taking into account the relational information provided by the
two first stimuli, that is taking into account of the triplet of stimuli. Learning of XOR combinations of three stimuli is a non-linearly separable problem that points to the limits of classical Hebbian learning of pairs only. Learning of XOR combinations requires models involving either additional neurons (see Rigotti et al., 2010a, 2010b, 2013; Bourjailly & Miller, 2011a,b, 2012) or new learning algorithms (Lavigne et al., 2014 for a discussion and model).

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

**Modeling synaptic learning and activations in memory**

The design of the experiment permitted linking the processing of simple information vs. relational information to variable levels of learning of the XOR combinations. Based on the learned synaptic efficacies between populations of neurons coding for the positions, a minimal model of activation between populations of neurons coding for the positions permits reproduction of the data with a restricted number of parameters (Okun, 2015). The present model is based on a simple network in which populations of neurons code for Positions stored in memory. Here, $n = 9$ populations of neurons code for the nine Positions used in the experiment with monkeys. No a priori knowledge of the structure of the stimuli is given to the network through any pre-wiring of the network (see Lavigne et al., 2014; Bernacchia, La Camera, & Lavigne, 2014 for discussion). Hence the populations are all connected together with the same initial value of synaptic efficacy and learning relies solely on the sequences of Positions.
Following computational models that have emphasized the critical role played by synaptic connectivity on the level of prospective activity (e.g., Mongillo, Amit, & Brunel, 2003) and response times (Brunel and Lavigne, 2009), the present model investigates to what extent IS learning generates TT during learning of XOR combinations. TT are simulated on the second stimulus depending only on the simple information provided by the first stimulus (i.e., the learned association between the pair of stimuli one and two) and on the third stimulus depending on the relational information provided by the first two stimuli (i.e., learned association between the triplet of stimuli one, two, and three).

**Learning of XOR combinations**

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

The simulations follow the two phases of our experiment. During the first phase of the experiment, random sequences of three positions are presented, and three populations of neurons are active together (e.g., 7-2-9, 7-8-4, 1-2-4, etc.). Given that the monkeys were exposed to all possible combinations of triplets, this phase generates equal values of synaptic efficacy between the nine populations of neurons that code for the nine Positions. These initial
values of efficacy have a Hebbian component $J_\theta^H(0)$ and an IS component $J_\theta^K(0)$ (Equations 4 and 8). $J_\theta^H(0)$ and $J_\theta^K(0)$ were computed according to Brunel et al.'s (1998) Equation (15) under the condition of infinite and slow learning. Efficacy depends on the instant probabilities of potentiation/depression and on the average probability that the synapse has been potentiated and/or depressed during the monkey’s exposure to the random sequences (here $J_\theta^H(0)=\sqrt{3}$ and $J_\theta^K(0)=\sqrt{7}$). During the second phase, specific sequences of positions corresponding to the XOR rule were displayed, and learning occurred. This is modeled using the initial values $J_\theta^H(0)$ and $J_\theta^K(0)$. These values are updated at each learning trial according to the LTP and LTD equations described above. The resulting efficacy of the synapses thus depends on the number of times two specific Positions were presented together in the same trial (Figure 3A). The efficacy values have an increased or decreased probability of being potentiated as a function of the number of times LTP or LTD occurred during learning of the sequences (Figure 3B).

Hebbian learning potentiates/depresses synapses between populations coding for positions proportionally to the number of times the two positions are presented in the same/different trials ($J_\theta^H$, shown in light orange in Figures A and B). For example, positions 7 and 2 occur together in one of the four sequences (LTP of the 7-2 synapse), and they occur separately in two of the four sequences (LTD of the 7-2 synapse). According to Equation (A1) (see Brunel et al.’s (1998) Equation (15), the efficacy of the 7-2 synapse converges to

$$q_\theta^+ / q_\theta^+ + 2q_\theta^- = \sqrt{3} \quad (q_\theta^- = q_\theta^+)$$

The same occurs for synapses 7-9, 2-9, 1-2, 1-4, etc.

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

$$q_\theta^+ / q_\theta^+ + 0q_\theta^- = 1 \quad (q_\theta^- = q_\theta^+)$$

The same occurs for synapses 1-2 when 4 is present and for synapses 1-8 when 9 is present, etc.
Activations and Transition Time 1

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

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

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

5. Discussion

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

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

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

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

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


Appendix A

Hebbian learning

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

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

Following Brunel et al.’s (1998) formalism of LTP and LTD describing probabilistic synaptic modification (Amit & Fusi, 1994; Brunel et al., 1998; Fusi, 2002; Fusi et al., 2005), LTP of synapse $ij$ occurs under the condition that the two populations $j$ and $i$ are active in the same trial (i.e., when positions $J$ and $I$ are present in the same trial). When pair LTP occurs,
synapse $ij$ in the Down state has an instant probability $q_p^+$ of being switched to the Up state. As a result, the synapses have probability $a_{ij}$ of being potentiated:

$$a_{ij} = q_p^+ \xi_i \xi_j$$  \hspace{1cm} (1)

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

$$b_{ij} = q_p^- \left[ \xi_i (1-\xi_j) \xi_j (1-\xi_i) \right]$$  \hspace{1cm} (2)

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

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

$$\lambda_{ij} = 1 - a_{ij} - b_{ij}$$  \hspace{1cm} (3)

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

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

Each $a_{ij}(t)$ in the sum $\sum_{t=1}^{T} a_{ij}(t)$ corresponds to a probability that the synapse is potentiated for a given stimulus presented at time $t < T$ when neurons $i$ and $j$ are both active. Each term in the
sum is weighted by the probability $\prod_{s=t+1}^{T} \lambda_s$ that no transition occurs during the trials following the potentiation between time $t+1$ and time $T$. This left-hand side of Equation (4) corresponds to actual ‘learning’ of the synapse through successive potentiation and (or) depression. In the right-hand side of Equation (A2), $J_{ij}(0)$ is the initial value of the potentiation of the Hebbian component of the synapse before learning the XOR sequences. $J_{ij}(0)$ is weighted by the probability $\prod_{s=1}^{T} \lambda_s$ that no transition occurs during all the trials between the beginning of learning and time $T$. This product decays with the increasing number of learning trials and corresponds to a progressive ‘forgetting’ of past trials by the synapse.

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

Inter-synaptic (IS) learning

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

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

$$a^k_{ij} = q^+_T \xi_i \xi_j \xi_k$$

In IS learning, LTD of synapse $ij$ occurs under the condition in which the two neurons $i$
and \( j \) are active and the third neuron is inactive. In that case, a synapse in the Up state has an instant probability \( q_{IS}^- \) of being switched to the Down state (as for the Hebbian component, we take here \( q_{T}^- = q_{T}^+ = 0.3 \times 10^{-3} \)). As a result, the synapse has probability \( b_{ij}^k \) of being depressed:

\[
b_{ij}^k = q_T^{-} \left[ \xi_j \xi_i (1 - \xi_k) + \xi_i \xi_k (1 - \xi_j) + \xi_j \xi_k (1 - \xi_i) \right] \tag{6}
\]

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

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

\[
\lambda_{ij}^k = 1 - a_{ij}^k - b_{ij}^k \tag{7}
\]

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

\[
J_{ij}^k(t) = \sum_{t=1}^{T} \sum_{s=1}^{T} a_{ij}^k(t) \prod_{r=t+1}^{T} \lambda_{ij}^k(s) J_{ij}^k(0) \prod_{r=1}^{T} \lambda_{ij}^k(s) \tag{8}
\]

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

**Appendix B**

*Transition Times 1*

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

\[
A_{jk} = (J_{jk} + J_{jk}^i) A_k \tag{9}
\]
$J_{jk}$ is the Hebbian component and $J'_{jk}$ is the IS component of the total efficacy of synapse $jk$.

The activity generated by the input (e.g., $K = 7$) among all associated populations is regulated by an inhibitory activity that is proportional to the total activity of all $n = 9$ activated populations (Amit & Brunel, 1997; Brunel, 1996):

\[ \text{Inh}_i = I_i \sum_{i=1}^{n} A_i \]  \hspace{1cm} (10)

This inhibition is global and unselective, that is it applies to all populations. It is then subtracted to the prospective activity of each population after the first input. The resulting prospective activity for each population then allow to compute a response time on the to-be-predicted population ($J = 2$) when it is presented in the sequence (Transition time 1, blue line in Figure 3D). In the model, response time on the second Position ($J = 2$) following the first Position ($K = 7$) corresponds to Transition time 1:

\[ TT_i = \frac{r}{A_{jk}} \]  \hspace{1cm} (11)

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

**Transition Times 2**

The level of prospective activity of population $i$ coding for $I$ is proportional to the total synaptic efficacy between population $i$ and $k$ and $i$ and $j$. The resulting activation of population $i$ by $j$ and $k$ is:

\[ A_{i,j,k} = J_{ij}A_j + J_{ik}A_k + \left( \frac{J_{ij}A_j + J_{ik}A_k}{2} \right)^m \]  \hspace{1cm} (12)

Here $m = 3$ is a multiplicative factor of the inputs coming from the IS component of the synapse, that gives a gain of TT2 of equivalent magnitude as in the experimental data.
As was the case after the first input $K$, the activity generated by the two inputs $K$ and $J$ among the populations associated to $K$ and $J$ is regulated by an inhibitory activity that is proportional to all $n = 9$ activated populations. A new value of inhibition is subtracted to the prospective activity of each population:

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

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

$$TT_2 = \frac{r}{A_{i,j,k}}$$  \hspace{1cm} (14)
Figures legends

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

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

Figure 3: A. Synaptic efficacies \( J_y \) and \( J_y^k \) associated with the nine positions as a function of the sequences of three positions involved in the learning trials. For clarity, the Figure displays efficacies in one direction only for Positions 7, 2 and 9 (green arrows); these positions are 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 reported for position 4, which occurs with positions 7 (purple arrow) and 2 (cyan arrow) in different trials (i.e., 7-8-4 and 1-2-4, respectively), and for position 3 (gray arrow), which is not involved in any XOR trial. Efficacies shown in dark orange (\( J_y^k \)) correspond to trials in which the corresponding Positions are presented together, leading to LTP of the synapse. Efficacies shown in light orange (\( J_y \)) correspond to trials in which the corresponding
Positions are not presented together, leading to LTD of the synapse. B. Evolution of synaptic efficacies $J_y$ and $J_y^k$ as a function of the number of trials with LTP and the number of trials with LTD (shown in the same colors as in A; ten blocks of 4 XOR sequences). The evolution of synapse efficacy is displayed for synapses that are affected by different numbers of cases of LTP and LTD: 1) for Hebbian learning involving one LTP and 2 LTD (light orange, solid line); 2) for Hebbian learning involving zero LTP and two LTD (light orange, dotted line); 3) for IS learning involving one LTP and zero LTD (dark orange, full line); and 4) for IS learning involving zero LTP and one LTD (dark orange, dotted line). C. Activations $A_y$ and $A_y^k$ of populations coding for the nine Positions and for the XOR trial 7-2-9: 7 is the first input (gray disc), 2 is the second input (blue disc), on which Transition time 1 is recorded (Figure 3D, blue line), and 9 is the third input (red disc), on which Transition time 2 is recorded (Figure 3D, red line). For clarity, Figure 3C presents only activations of the same Positions shown in Figure 3A. The total activation has two components, $A_y^k$ (dark orange) and $A_y$ (light orange), that correspond to different values of efficacy $J_y^k$ and $J_y$ (shown in the same colors; see text). D. Evolution of Transition time 1 (from Position 7 to 2, blue line) and of Transition time 2 (from Position 2 to 9, red line) as a function of the number of learning trials.
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diff 1-2  | 30 | 26 | 33 | 90 | -9 | 50 | 29 | -11 | -8 | 49 | 30 | -27 | 37 | 3 | 9 | 10 | 17 |

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

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<td>356</td>
<td>378</td>
<td>457</td>
<td>394</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 2: Mean response times for each of the 72 possible transitions calculated from the 1000 random trials, over the entire group of baboons.
A. XOR truth table

<table>
<thead>
<tr>
<th>Input 1</th>
<th>Input 2</th>
<th>→ XOR</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>→ 0</td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>→ 1</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>→ 1</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>→ 0</td>
</tr>
</tbody>
</table>

B. XOR combinations

<table>
<thead>
<tr>
<th>Stim 1</th>
<th>Stim 2</th>
<th>→ Stim 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>→ 4</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>→ 9</td>
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<tr>
<td>1</td>
<td>8</td>
<td>→ 9</td>
</tr>
<tr>
<td>7</td>
<td>8</td>
<td>→ 4</td>
</tr>
</tbody>
</table>

C. Sequences of combinations

D. Example of a single trial
Fig. 2

RT (ms)

1 2 3 4 5 6 7 8 9 10

Block

Transition 1
Transition 2
Fig. 3

A. Synaptic efficacies

B. Synaptic learning

C. Activations

D. Transitions times