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Frédéric Lavigne, Laurent Dumercy, Lucile Chanquoy, Brunissende Mercier & Françoise Vitu-Thibault

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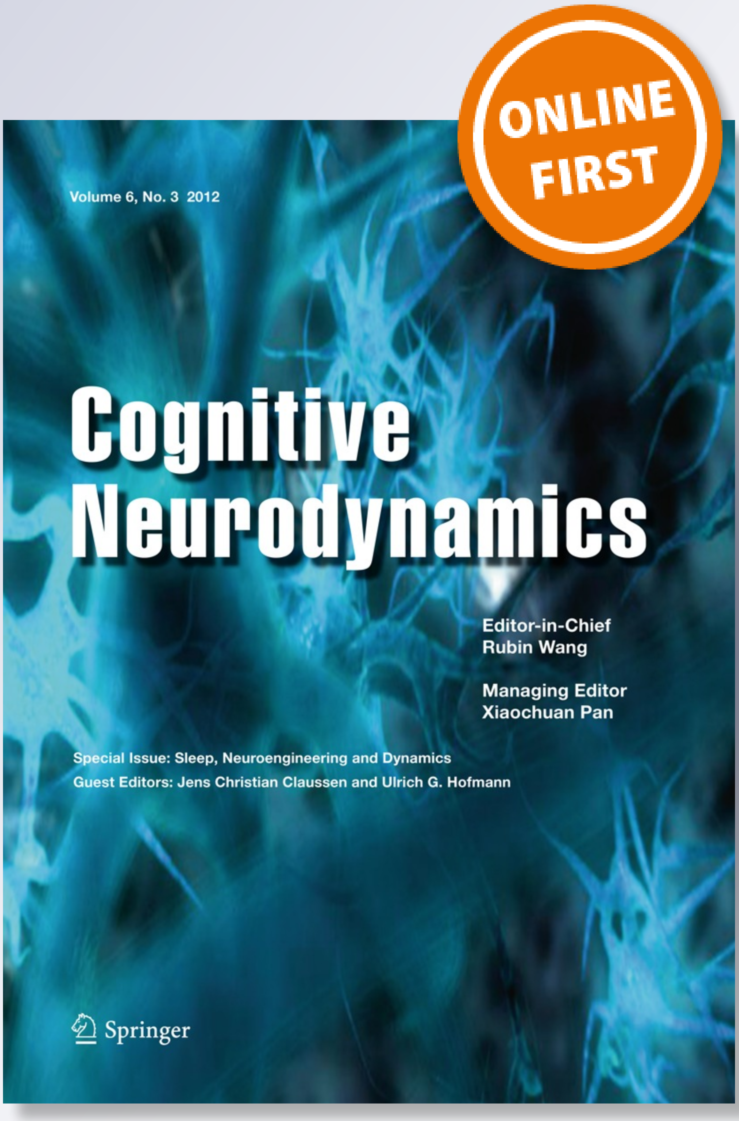

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RESEARCH ARTICLE

Dynamics of the semantic priming shift: behavioral experiments and cortical network model

Frédéric Lavigne · Laurent Dumercy ·
Lucile Chanquoy · Brunissende Mercier ·
Françoise Vitu-Thibault

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Abstract Multiple semantic priming processes between several related and/or unrelated words are at work during the processing of sequences of words. Multiple priming generates rich dynamics of effects depending on the relationship between the target word and the first and/or second prime previously presented. The experimental literature suggests that during the on-line processing of the primes, the activation can shift from associates to the first prime to associates to the second prime. Though the semantic priming shift is central to the on-line and rapid updating of word meanings in the working memory, its precise dynamics are still poorly understood and it is still a challenge to model how it functions in the cerebral cortex. Four multiple priming experiments are proposed that cross-manipulate delays and association strength between the primes and the target. Results show for the first time that association strength determines complex dynamics of the semantic priming shift, ranging from an absence of a shift to a complete shift. A cortical network model of spike frequency adaptive neuron populations is proposed to account for the non-continuous evolution of the priming shift over time. It allows linking the dynamics of the priming shift assessed at the behavioral level to the non-linear dynamics of the firing rates of neurons populations.

Keywords Multiple priming · Neural population · Priming dynamics · Spike frequency adaptation · Word meaning

Introduction

The processing of sequences of words requires dynamic recall of semantic knowledge, measured in real time at the behavioral level by semantic priming effects—that is, shorter response times to a target word (e.g., 'butter') when a preceding prime word is related (e.g., 'bread') than when it is unrelated (e.g., 'tree'; Meyer and Schvaneveldt 1971; Meyer et al. 1972). The processing of a prime in working memory increases the availability of targets in the long-term memory that are related in meaning. During processing of sequences of words, recall of knowledge requires the cognitive system to activate and handle multiple priming of associates to several primes in parallel in the working memory (Balota and Paul 1996). However, the working memory capacity is limited in terms of the number of items that can be activated simultaneously (see Cowan 2001). This implies a flexible updating of the representations activated as a function of new inputs, whilst maintaining the stability of these representations (see Artuso and Palladino 2011; Kessler and Meiran 2008; Morris and Jones 1990). As a consequence, to keep up the pace of processing the incoming sequence of primes, the cerebral cortex must be able to select in real time which associates to a prime prime and/or to a subsequent prime to activate, and which to deactivate in real time (see Whitney et al. 2009). The possibility for a semantic shift of activation of associates to a first prime to activation of associates to a second prime, and the description of its dynamics is a challenge for current network models, and the determinants of these dynamics are still to be tested experimentally.

F. Lavigne (✉) · L. Dumercy · L. Chanquoy · B. Mercier
Laboratoire Bases, Corpus, Langage - CNRS, Université de Nice-Sophia Antipolis, 24 Avenue des diables bleus, 06357 Nice Cedex 4, France
e-mail: lavigne@unice.fr

F. Vitu-Thibault
CNRS, Université d'Aix-Marseille, Marseille, France

Dynamics of the semantic priming shift

Multiple priming processes are analyzed by recording response times to a target (e.g., "tiger") that can be related to the two preceding primes that are sequentially presented (RR condition, e.g., "lion" and "stripes"), that are unrelated to the primes (UU condition, e.g., "fuel" and "shutter"), or that are related to the first prime (RU condition, e.g., "lion" and "shutter") or the second prime (UR condition, e.g., "fuel" and "stripes"). Multiple priming effects are calculated by subtracting reaction times in a given condition of primes-target relatedness (RR, RU, UR) from reaction times in the UU baseline condition (McNamara 1992). Semantic activation and selection corresponds to changes in the activation of RU associates to the first primes and/or activation of UR associates to the second prime. Investigating the dynamics of RU and UR priming effects when two primes are presented sequentially before the target requires to test for their magnitude as a function of the SOA1—that is the delay between prime1 and prime2 onsets—and the SOA2—that is the delay between prime2 and target onsets. When a single prime is involved, the SOA (Stimulus Onset Asynchrony) is assumed to describe a rapid and automatic stage of activation of the associates to the prime (short SOAs under 300 ms), followed by a slower stage of controlled processes of selection among the previously activated set of associates (Hutchison et al. 2001; Deacon et al. 1999; Neely 1976, 1977, 1991; Neely et al. 1989). The effects of SOA on multiple priming range from null to very important (e.g., Balota and Paul 1996; Chenery et al. 2004; Kandhadai and Federmeier 2007). A recent meta-analysis of multiple priming effects has pointed to the combined effects of SOA1 and SOA2 (Lavigne et al. 2011). While UR priming of associates to the second prime is reliable over a large range of SOAs, RU priming of associates to the first prime only appears when both SOAs are short or when SOA1 is longer than SOA2, but not when SOA2 is longer than SOA1. This points to the possibility for a semantic priming shift fort short SOA1 and increasing SOA2.

However, though meta-analyses allow for a summaries of the findings from many studies, they have drawbacks as well (see Durlack 1995). Meta-analyses are confronted with the file-drawer problem, wherein studies that report non-significant findings are less likely to be published. This leads to an underestimation of the probability of the type II error (i.e., failure to find a relationship despite its existence), which is a publication bias due to the fact that a larger number of studies that report significant findings are published (Durlack 1995). This could be the case for variables that lead to significant priming effects in some specific cases, such as RU priming that depends on the combination of SOAs. It's non-significance in the condition where there is a short SOA1 and a long SOA2 could have led to fewer publications about RU priming effects in this condition. Such a bias would affect the outcome of a meta-analysis by hiding non-significant findings regarding RU priming at some SOAs despite their interest. In addition, the different combinations of SOA1 and 2 in the meta-analysis came from different studies, and statistical constraints imposed a dichotomous partitioning of each SOA, defining four categories of short or long SOA1 or SOA2. These four categories do not capture the fine-grained dynamics of multiple priming processes, and the assessment of the effects of SOA1 and 2 relies on a meta-analysis and not on within study manipulations. The cross-manipulation of different SOA1 and 2 as within study variables have been tested only once and for a limited range of values (Lavigne and Vitu 1997), but through the manipulation of SOA2 only. As a consequence, the combined of SOA1 and 2 on multiple priming are still poorly understood, which points to the necessity to test for the effects of SOA1 and 2 as within study variables and for combinations of values of interest and not yet tested in the literature.

Effects of association strength

In addition to the effects of SOAs, Lavigne et al.'s (2011) meta-analysis revealed significant heterogeneity of RU priming within the categories of SOAs tested. This makes the effects of SOA alone unlikely. However, the determinants of such variability are still unknown and can only be the object of speculations based on the experimental literature on single priming. The magnitude of single priming effects is reported to vary with the strength of the prime-target association (Abernethy and Coney 1993; Frishkoff 2007; Hutchinson et al. 2003; Coney 2002; see Chiarello et al. 2003 for reviews). In a cortical network model of multiple priming (Lavigne et al. 2011), variations of the association between the first prime and the target led to variations in the magnitude of RU priming. However, our understanding of the semantic priming shift should not be grounded solely on model's predictions, but should rely on actual experimental data. We therefore propose here a first test of the effects of the strength of the association between each prime and the target in multiple priming protocols that also cross-manipulated SOAs as within study variables.

Layout of the experiments

The measure of the magnitude of UR and RU priming is key to calculating the priming shift. To investigate the dynamics of RU and UR priming, only a subset of combinations of SOAs could be tested experimentally. Some combinations were therefore selected that were of particular interest for the dynamics of the priming shift. The choice of values of SOA1 and 2 was guided toward ranges of SOAs not yet tested (Exp. 1, 3 and 4), or that corresponded to variable effects in the literature (Exp. 2). In addition, to test for the resistance of the model to small changes in SOAs and ISIs, the values selected for experiments 1, 3 and 4 to be modeled were slightly changed compared to simulations in the previous model by Lavigne et al. (2011). Finally, to test for the predictions of the model with the current experiments and the new matrix of different association strengths 1 and 2 in the current model, experiment 2 used the same values of SOAs and ISIs as in the previous model.

Experiment 1 (250 + 125) tested for the possibility that RU priming can arise and prevent from UR priming to arise at SOA2 shorter than SOA1. The literature reports significant UR priming for a wide range of SOAs, but for SOA2 equal to or longer than SOA1, and with prime2 durations longer than ISI2 (Angwin et al. 2005; Balota and Paul 1996; Chenery et al. 2004). The hypothesis that UR priming could not arise is based on model's prediction only in the case of very short SOA2 (125 ms, see Lavigne et al. 2011, figure 5C2). To decrease the activation of the UR associate by its related prime2, prime2 duration (50 ms) was set shorter than ISI2 (75 ms; absence of prime2) (p1 = 200 ms, ISI1 = 50 ms, p2 = 50 ms, ISI2 = 75 ms).

Experiment 2 (250 + 250) tested for the possible effects of association strength on RU and UR priming in a range of SOAs were results are variable and contradictory in the literature. When SOA1 and SOA2 are short and equal, RU effects vary from significant (e.g., Balota and Paul 1996) to non-significant (e.g., Masson et al. 1991; Masson 1995; Thérouanne and Denhière 2002). Lavigne et al.'s (2011) meta-analysis reveals an average RU effect size of 0.17 for short SOAs against 0.57 when SOA1 is longer than 300 ms. However, the possibility that variable results could be due to on variable association strengths used in the experiments is still unknown and relies only on simulations (Lavigne et al. 2011, Figure 5B2). Experiment 2 was therefore designed to test for the effects of association strength on the priming shift. To this aim we kept prime1 and ISI1 durations equal to those of experiment 1 (p1 = 200 ms, ISI1 = 50 ms), and took the same values, respectively, for prime2 and ISI2 durations (p2 = 200 ms, ISI2 = 50 ms).

Experiment 3 (250 + 850) tested for the possibility that a long SOA2 could deactivate RU associates during the long SOA2. The studies testing for RU priming for the range of short SOA1 and long SOA2 report non-significant effects (Kandhadai and Federmeier 2007, Exp. 1 and 2; Lavigne and Vitu 1997, Exp. 1 and 4; see Lavigne et al.'s 2011, meta-analysis 4). However, given the lack of experimental data available in the literature, and given that association strength has not been previously manipulated in multiple priming, the possibility for a complete deactivation of even strong RU associates remains an open question. To test for the effect of SOA2 alone, results of experiment 3 will be compared to those of experiment 2. To this aim SOA1 was kept equal in the two experiments (p1 = 200 ms, ISI1 = 50 ms) and SOA2 was increased to 850 ms in experiment 3. Given that the previous model simulated RU deactivation at long SOA2 by increasing prime2 duration—assumed to have a stronger effect than ISI2—we tested here the sole effect of time without stimulus by increasing ISI2 alone (p2 = 200 ms, ISI2 = 450 ms).

Experiment 4 tested for the possibility for RU priming to resist long SOA2 under the condition that SOA1 is also long (p1 = 850 ms, ISI1 = 0 ms, p2 = 850 ms, ISI2 = 0 ms). Some studies report that RU priming can resist long SOA2 if SOA1 is long enough (e.g., Angwin et al. 2005; Chenery et al. 2004; Davelaar and Coltheart 1975; Joordens and Becker 1997; McNamara 1992, 1994; Schvaneveldt and Meyer 1973; see Lavigne et al.'s 2011 meta-analysis 4; but see Fuentes and Santiago 1999; Fuentes et al. 1999). However, possible effects of strong associations between the prime1 and target are still to be confirmed. Experiment 4 was therefore designed to test for the possibility for combined RU and UR priming depending on association strength at long SOA1 and SOA2. To increase the possibility of combined activation of both RU and UR associates by their associates primes 1 or 2, primes durations were increased at the 850 ms SOAs durations with 0 ms ISIs.

Methods of the experiments

Participants

A total of 271 participants were involved in the four experiments for course credit at the University of Nice-Sophia Antipolis. All participants were native French speakers and had normal or corrected-to-normal visual acuity. Each participant took part in only one experiment.

Apparatus

Experiments were run on a computer using E-prime software to control stimulus presentation and to record participants' response times and errors. Participants were seated at 60 cm from a 15-inch PC monitor where stimuli were displayed.

Material

The material consisted of 96 word triplets (two word primes and a word target) and 96 pseudo-word triplets

(2 word primes and a pseudo-word target). All triplets were constructed on the basis of the relation between the two primes and the target words (free production norms in French: Kurzepa 2003; Cornuéjols 1999; Ferrand and Alario 1998). 96 word triplets were selected so that the target was related to each of the two primes, which were themselves unrelated. These 96 triplets corresponded to 4 groups of 24 triplets in which each prime could be either weakly (w) or strongly (s) related to the target. Association strength was calculated as being the percentage of production of a target word in relation to a given prime word among all participants. Average strength was of 33.1 % (between 15.7 and 92.1 %) for strong associates and 8.6 % (between 3.3 and 14.6 %) for weak associates. The choice for these ranges of strengths allowed to keep as many triplets as possible for the experiments. The combination of two association strengths and two primes generated four conditions of association strength within a triplet: (1) both primes strongly related to the target (ss, e.g., 'guitar' and 'harp' for 'string'); (2) the first prime strongly related and the second prime weakly related to the target (sw, e.g., 'bonnet' and 'pullover' for 'wool'); (3) the first prime weakly related and the second prime strongly related to the target (ws, e.g., 'cradle' and 'doll' for 'child') and both primes weakly related to the target (ww, e.g., 'cherry' and 'apricot' for 'pit').

Targets involved in the four conditions of association strength were controlled in lexical frequency (Lexique 3.5; New et al. 2004), that did not differ between the ss, ws, sw and ww conditions (mean frequencies of 90, 60, 145 and 95 occurrences per million, respectively; pairwise t tests $p > .05$). All primes and targets words were between 3 and 9 characters in length, and the lengths and frequencies of prime words did not differ between the four conditions of association strength.

In each of the 96 word triplets selected, the two primes were related to the target. By replacing the first, second, both or none of the primes in a triplet by an unrelated word—chosen among the set of primes related to other targets—each target could be embedded in four different combinations of relatedness between each prime and the target, thus defining four conditions of relatedness: (1) both primes related to the target (RR, e.g., 'hedgehog' and 'cactus' for 'spine'); (2) the first prime related and the second prime unrelated to the target (RU, e.g., 'hedgehog' and 'cherry' for 'spine'); (3) the first prime unrelated and the second prime related to the target (UR, e.g., 'doll' and 'cactus' for 'spine'); (4) both primes unrelated to the target (UU, e.g., 'cherry' and 'doll' for 'spine'). The primes 1 and 2 were related indirectly through their common associated target in the RR condition, but the absence of direct relation between them in any condition was controlled with the production norms.

The two independent variables of primes-target relatedness (RR, RU, UR, UU) and of association strength (ss, sw, ws, ww) were cross-manipulated in order to obtain 16 experimental conditions. Eight experimental lists of 96 word triplets and 96 pseudo-word triplets were created to counterbalance primes and targets across conditions of relatedness, so that each word appeared only once on the list of triplets presented to a participant. In half of the triplets on a list (96) the target was a bona fide French word. In the other half of the triplets (96) the target was a pseudo-word derived from a word by replacing one or two letters but constructed in accordance with the phonotactic constraints of French.

Design

A 4 × 4 factorial design was used, with relatedness (4: RR, RU, UR, UU) being manipulated as a within-participants and within-items variable, with associative strength (4: ss, sw, ws, ww) being manipulated as a within-participants and between-items variable, and with the prime's position being a random variable.

Task and procedure

Participants were tested individually in a soundproof room. They were told that in each trial three stimuli would be presented in a sequence at the center of the screen: two words in lower case lettering followed by a word or a pseudo-word in uppercase lettering. They were asked to perform a lexical decision task by responding as quickly and as accurately as possible with their dominant hand to indicate whether the third letter string was a French word (left click on the computer mouse) or not (right click). Sixteen practice trials were presented, followed by two experimental blocks of 96 trials, allowing a break between blocks. The order in which trials were presented was randomized and changed for each participant.

Protocol

Stimuli were displayed in 18 point Courier New in black font centered on a white background—with primes in lower-case lettering and targets in upper-case lettering. Each trial consisted of the following sequence of events: a blank screen for 800 ms, a visual warning signal made of three horizontally displayed asterisks for 200 ms, a blank screen for 400 ms; SOA1 corresponding to the presentation of the first prime for a duration p1, followed by the first inter-stimuli interval for a duration ISI1 (blank screen); SOA2 corresponding to the presentation of the second prime for a duration p2, followed by the second interval for a duration ISI2 (blank screen); finally, the target was presented for 240 ms, followed by a blank screen until the participant's response. Response times and errors were recorded for each participant's response.

Data analyses

Analyses of variance were performed on Response times (RT) with relatedness (RR vs. RU vs. UR vs. UU) as a within-participants and within-items variable, and with association strength as a within-participants and between-items variable. Trials where participants made errors were excluded from the analyses. A cut-off was set for each participant at ±2.5 SD units from each participant's mean RT on words, and outliers were excluded from the analyses. Data from participants who made errors more than 15 % of the time were also excluded from the analyses. To identify if the types of priming varied across the different combinations of SOAs, overall analyses were performed with the SOAs varying between experiments, as a between-participants and within-items variable. *p* values for participants analyses (p1) and items analyses (p2) are indicated as lesser than .01 or than .001, and exact *p* values are provided when greater than .01.

Overall results of the four experiments

Overall analyzes show main effects of relatedness (p1 < 0.0001; p2 < .0001), of association strength (p1 < .0001; p2 = .053) of SOAs (p1 = .024; p2 < .0001) and no significant interaction.

Planned comparisons show significant RR priming for strong RR associates (p1 < .01; p2 = .012) and for weak RR associates (p1 < .01; p2 = .015). This confirms results by Beeman et al. (1994) that showed that a target word (e.g., 'cut') can be primed even though it is only weakly related to the preceding primes (e.g., 'foot', 'cry' and 'glass'). Results indicate that priming in the RR condition does not interact with the SOAs (p1 = .82; p2 = .85).

Planned comparisons were performed on RU and UR priming. Given that in the RU and UR conditions the strength between the target and one related prime was considered (the first in RU priming and the second in UR priming), contrast analyses permitted to aggregate RU–ss and RU–sw to test for RU-s priming, RU-ws and RU-ww to test for RU-w priming, UR-ss and RU-ws to test for UR-s priming, and UR-sw and RU-ww to test for UR-w priming. This permitted to test RU and UR priming by using 12 items per conditions, by testing response times in the RU and UR conditions against response times on the same target items in the UU condition. Planned comparisons show significant effect for strong UR associates (p1 < .001; p2 < .001) and for weak UR associates (p1 = .036; p2 = .09), indicating that both strong and weak associates are primed in the UR condition. The interaction between UR priming and the SOAs is not significant (Fig. 1b). These results are in accordance with the stable magnitudes of RR priming (large magnitudes) and UR priming (medium magnitude) across SOA1 and 2, as reported by Lavigne et al.'s (2011) meta-analysis.

Turning to RU priming, planned comparisons show significant effects for strong RU associates (p1 < .01; p2 < .01) and for weak RU associates in the participant analysis (p1 = .032; p2 = .44). The interaction between the SOAs and RU priming of strong associates is significant by participants (p1 = .049; p2 = .16), with RU priming being stronger in Experiments 1 and 4 than in Experiments 2 and 3 (Fig. 1b). This result describes the time course of RU priming that increases at short SOA1 and 2, and decreases at longer SOA2. The sensitivity of RU priming to the combination of SOA1 and 2 could generate variations in the pattern of additivity, and also makes

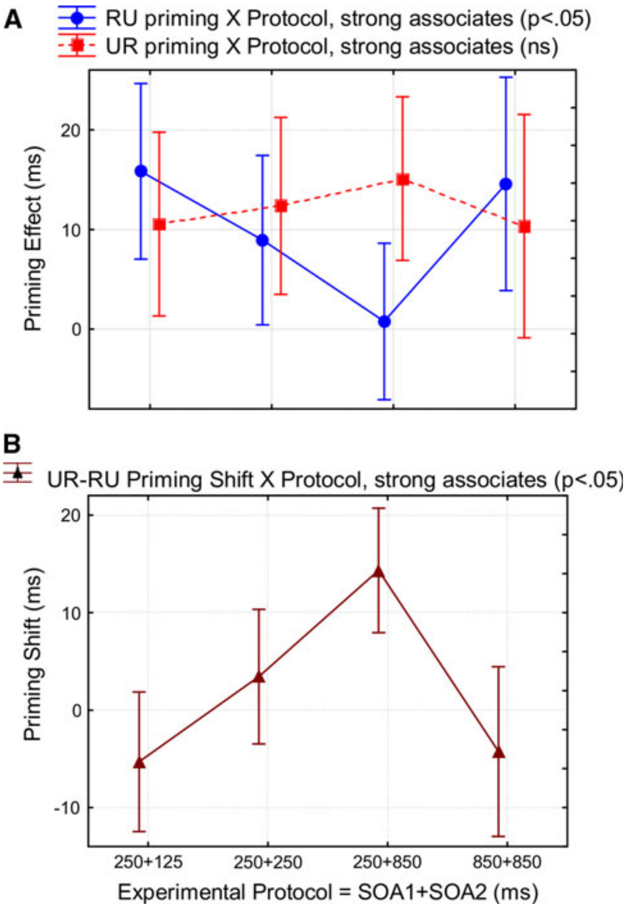


Fig. 1 **a** Significant variation of the magnitude of RU priming but not of UR priming of strong associates as a function of the protocols of the four experiments (250 + 125, 250 + 250, 250 + 850, 850 + 850). **b** Significant variation of the priming shift for strong associates as a function of the protocols (means and standard errors)

possible a semantic priming shift when compared to UR priming.

The general assumption regarding multiple priming is that the target receives converging sources of activation from the two related primes in the RR condition compared to the sum of the effects of one related and one unrelated prime (RU + UR). The experimental data available in the literature report variable patterns that cover the three types of converging activation: strictly additive (RR = RU + UR; Balota and Paul 1996; Chwilla and Kolk 2003; Lavigne and Vitu 1997, Exp. 1 and 4), under-additive (RR < RU + UR; Angwin et al. 2005; Chenery et al. 2004) and over-additive (RR > RU + UR; Chwilla and Kolk 2003, Exp. 2; Lavigne and Vitu 1997, Exp. 2 and 3). The overall results of the four experiments do not rule out the possibility of <1 ms strict additivity (i.e., RR = RU + UR; p1 = .43; p2 = .66). However, the magnitude of additivity interacts marginally with association strength (p1 = .092; p2 = .042) and with SOAs in the participant analysis (p1 = .070; p2 = .87), indicating that additivity is a variable measure of semantic activation. The pattern of additivity does not rely on the sole magnitudes of RU and UR priming but also on the magnitude of RR priming. For this reason, it is a less precise indicator of the dynamic changes in the type of associates activated during the SOA1 and 2.

To provide us with a detailed description of the dynamics of activation of associates to the sequence of primes, the priming shift was analyzed as a function of the protocols. The two-way interaction between the UR versus RU and the SOAs is marginally significant (p1 = .069; p2 = .049). The four current experiments provide us with a first-hand account of a priming shift for a same set of experimental material. In addition, planned comparisons indicate that the interaction between the shift and SOAs is significant for strong associates (p1 = .035; p2 = .016), indicating larger RU priming in Experiments 1 and 4 and a shift to larger UR priming in Experiments 2 and 3 (Fig. 1a). The priming shift will be further investigated by comparing the magnitudes of RU and UR priming in each experiment.

Results of experiment 1: 250 + 125

Experiment 1 involved 66 participants. Data from one participant whose responses consisted of more than 15 % errors were excluded from the analysis. Of the remaining 65 participants, the average error rate was 6.1 % and data from error trials were excluded from the analysis. A two-way ANOVA was performed on response times between the four conditions of relatedness and the four conditions of association strength (Table 1).

Table 1 Mean response time in ms (SD) in Experiment 1 (250 + 125) as a function of primes-target relatedness (RR, RU, UR, UU) and association strength (ss, sw, ws, ww)

	Association strength			
	ss	sw	ws	ww
Relatedness				
RR	590 (99)	589 (95)	584 (93)	598 (98)
RU	575 (81)	590 (95)	601 (102)	605 (99)
UR	584 (94)	604 (89)	599 (94)	596 (95)
UU	596 (93)	601 (87)	608 (91)	607 (100)

Results show a main effect of relatedness (p1 < 05; p2 = .1), an effect of association strength (p1 < .01; p2 < 05), and no significant interaction (p1 = .30; p2 = .15). Planned comparisons indicate significant priming effects in the RR condition (p1 < .01; p2 < .05; 13 ms effect), indicating that, according to the literature, the primes have time to activate their common associated target at short SOA1 and 2.

Regarding the semantic priming shift, the significant priming of strong RU associates (p1 < .05; p2 = .17; 17 ms effect) indicates that the total SOA between prime1 and target onset (= SOA1 + SOA2) of 375 ms is long enough to allow for RU priming, in accordance with Lavigne et al.'s (2011) meta-analysis. The current results emphasize that the pattern of RU priming depends on the prime1-target association strength, which had not been test in the literature. UR priming is non-significant (p1 < .1; p2 = .12; 7 ms effect) and smaller than RU priming of strong associates in the participants analysis (p1 < .05; p2 = .24). This result confirms the CN model's predictions of only weak UR priming at very short 125 ms SOA2, that were not tested in the literature before. Given that 125 ms is reported as long enough for single priming to occur (Perea and Rosa 2002; Rastle et al. 2000; Perea and Gotor 1997; Beauvillain and Segui 1983), the non-significant UR priming can be attributed to the processing of the first unrelated prime that could have impaired subsequent processing of the second prime. The RU priming larger than UR priming shows that the semantic priming shift has not occurred at 250 ms SOA1 and 125 ms SOA2. In addition, the current results indicate that the possibility for RU priming in this range of SO As rely on the strength of the prime1-target association.

Results of experiment 2: 250 + 250

Experiment 2 involved 74 participants. Data from four participants that consisted of more than 15 % errors were excluded from the analysis. On the remaining 70 participants, the average error rate was 3.1 %, and data from error trials were excluded from the analysis. A two-way

ANOVA was performed on response times between the four conditions of relatedness and the four conditions of association strength (Table 2).

Results show a main effect of relatedness ($p1 < .0001$; $p2 < .01$), no main effect of association strength ($p1 = .12$; $p2 < .05$) and no significant interaction ($p1 = .57$; $p2 = .18$). Planned comparisons show significant priming in the RR condition ($p1 < .001$; $p2 < .01$; 17 ms effect), indicating an activation of targets associated with both prime1 and 2 at 250 ms SOA1 & 2.

Regarding the semantic priming shift, the overall RU priming is smaller than the overall UR priming in the participant's analysis ($p1 < .05$; $p2 = 0.23$). This is confirmed by the combined significant UR priming ($p1 < .05$; $p2 < .05$; 9 ms effect) and non-significant RU priming ($p1 = .87$; $p2 = .13$; 1 ms effect). Analyzes as a function of association strength show that the priming of strong UR associates is significant ($p1 < .01$; $p2 < .05$; 12 ms effect) but not the priming of weak UR associates ($p1 = .33$; $p2 = .32$; 4 ms effect). The priming of strong RU associates is marginally significant ($p1 < .1$; $p2 < .05$; 9 ms effect) but not the priming of weak RU associates ($p1 = .17$; $p2 = .92$; −6 ms effect).

When comparing Experiments 1 and 2, the difference between RU and UR priming interacts with the SOAs in the participants analysis ($p1 < .05$; $p2 = .36$). RU priming is larger than UR priming in Experiment 1 and smaller than UR priming in Experiment 2, corresponding to a decrease of RU priming during the 250 ms SOA2 in Experiment 2. The 250 ms SOA2 is long enough for the unrelated prime2 to deactivate RU associates previously activated by the prime1 (Exp. 1). The marginally significant RU priming of strong associates indicates that the deactivation is not complete after 250 ms SOA2. This result is in accordance with the variable RU effects reported in the literature for this range of SOAs. A new result provided by Experiment 2 is that variable association strength between the prime1 and its RU associate can account for the variability of RU effects. This confirms predictions by the CN model of moderate overall RU priming at the 250 ms SOA1&2 (Lavigne et al. 2011, 15 ms effect in figure 5B2), that results from a 5 ms effect for weak RU associates (figure 5B1) and a 15 ms effect for strong associates (figure 5B3). To recapitulate, the pattern of RU and UR priming from Experiment 2 corresponds to a partial priming shift with partial activation of RU associates to the prime1 and stronger activation of UR associates to the prime2.

Results of experiment 3: 250 + 850

Experiment 3 involved 86 participants. Data from four participants that consisted of more than 15 % errors were excluded from the analysis. Of the remaining 82 participants, the average error rate was 5.1 % and data from error trials were excluded from the analysis. A two-way ANOVA was performed on response times between the four conditions of relatedness and the four conditions of association strength (Table 3).

Results show a main effect of relatedness ($p1 < .01$; $p2 < .05$), no effect of association strength ($p1 < .1$; $p2 = .48$) and no significant interaction ($p1 = .26$; $p2 = .56$). Planned comparisons indicate significant priming effects in the RR condition ($p1 < .01$; $p2 < .01$; 13 ms effect), indicating a reliability of RR priming over a large range of SOAs in accordance with the literature and previous model.

Regarding the priming shift, RU priming of strong associates is weaker than the overall UR priming of strong and weak associates ($p1 = .05$; $p2 = .056$). Priming effects are not significant in the RU condition ($p1 = .25$; $p2 = 0.51$; 5 ms effect). This is in accordance with the meta-analysis of the literature for this range of SOAs. The deactivation of RU associates for a SOA2 of 850 ms also extends the CN model predictions to SOA2 longer than 650 ms (Lavigne et al. 2011, Figure 5B&C2). RU priming is significant neither for strong associates ($p1 = .89$; $p2 = .40$; 1 ms effect) nor for weak associates ($p1 = 0.11$;

Table 2 Mean response time in ms (SD) in Experiment 1 (250 + 250) as a function of primes-target relatedness (RR, RU, UR, UU) and association strength (ss, sw, ws, ww)

	Association strength			
	ss	sw	ws	ww
Relatedness				
RR	607 (85)	615 (79)	611 (85)	609 (77)
RU	618 (72)	630 (84)	627 (88)	631 (78)
UR	612 (87)	626 (86)	617 (87)	617 (76)
UU	629 (77)	636 (85)	624 (80)	619 (85)

Table 3 Mean response time in ms (SD) in Experiment 3 (250 + 650) as a function of primes-target relatedness (RR, RU, UR, UU) and association strength (ss, sw, ws, ww)

	Association strength			
	ss	sw	ws	ww
Relatedness				
RR	609 (103)	615 (114)	600 (95)	603 (103)
RU	619 (108)	613 (106)	607 (106)	620 (102)
UR	597 (110)	615 (100)	607 (89)	619 (114)
UU	617 (109)	616 (120)	616 (104)	630 (118)

$p2 = .92$, 9 ms effect). This indicates that the SOA2 of 850 ms is long enough for even strong RU associates to become completely deactivated. Priming effects are significant in the UR condition ($p1 < .05$; $p2 = 0.14$). Priming of strong UR associates is significant ($p1 < .05$; $p2 < .1$; 15 ms effect) but not priming of weak UR associates ($p1 = .29$; $p2 = .10$; 6 ms effect). The complete deactivation of RU associates for a SOA2 of 850 ms is confirmed when comparing Experiments 1 and 3: strong RU associates were more activated than UR associates in Experiment 1, and became less activated than UR associates in Experiment 3 ($p1 < .01$; $p2 < 0.05$). The new results of Experiment 3 regards a partial priming shift depending on association strength, with complete deactivation of RU associates combined with the activation of strong UR associates.

Results of experiment 4: 850 + 850

Experiment 4 involved 45 participants. Data from one participant that consisted of more than 15 % errors were excluded from the analysis. Of the remaining 44 participants, the average error rate was 6.9 % and data from error trials were excluded from the analysis. A two-way ANOVA was performed on response times between the four conditions of relatedness and the four conditions of association strength (Table 4).

Results show a main effect of relatedness ($p1 < .01$; $p2 < .01$), an effect of association strength ($p1 = .013$; $p2 < .05$) and no significant interaction ($p1 = .94$; $p2 = .91$). Planned comparisons indicate significant priming effects in the RR condition ($p1 < .01$; $p2 < .001$; 20 ms effect), indicating again that RR priming occurs at all combinations of SOAs tested.

Regarding the priming shift by comparing Experiments 3 and 4, RU priming is of larger magnitude in Experiment 4 than in Experiment 3 in the participant analysis ($p1 < .05$; $p2 = .19$), while the change in UR priming is not significant ($p1 = .97$; $p2 = .61$).

Table 4 Mean response time in ms (SD) in Experiment 4 (850 + 850) as a function of primes-target relatedness (RR, RU, UR, UU) and association strength (ss, sw, ws, ww)

	Association strength			
	ss	sw	ws	ww
Relatedness				
RR	628 (107)	635 (113)	627 (100)	654 (117)
RU	633 (93)	640 (97)	648 (120)	650 (98)
UR	638 (97)	639 (101)	645 (108)	656 (111)
UU	645 (126)	657 (102)	659 (108)	661 (96)

In Experiment 4, RU and UR priming do not significantly differ ($p1 = .75$; $p2 = .32$). UR priming is marginally significant ($p1 < .1$; $p2 = .14$; 11 ms effect) and RU priming is significant ($p1 < .05$; $p2 < .05$; 13 ms effect). Priming of strong RU associates is marginally significant ($p1 < .1$; $p2 < .05$; 15 ms effect) but not priming of weak RU associates ($p1 = .20$; $p2 = .34$; 11 ms effect). The presence of RU priming at long SOA2 when SOA1 is also long is in accordance with previous meta-analysis. In addition, the dependence of RU priming on association strength extends predictions of the CN model made for SOAs of 650 ms (i.e., 80 ms RU effect for strong associates, Figure 5B3; and 0 ms effect for weak associates, Figure 5B1). Results of Experiments 4 show that association strength can account for the inter-studies variability of the effects reported in the literature.

To recapitulate, given that RU priming was canceled at the same long SOA2 of 850 ms in Experiment 3 as in Experiment 4, the presence of RU priming in Experiment 4 can be attributed to the long 850 ms SOA1 involved. The long SOA1 permits strong RU associates to become sufficiently activated to resist the 850 ms processing of the prime2. The current results provide us with a detailed picture of the dynamics of the priming shift, and also challenge models that aim at linking the dynamics of the behavioral effects to those of neural networks.

Methods of the cortical network model

Computational modeling of the cerebral cortex aims to link behavioral effects to the properties of neurons and their synaptic connections. The complex dynamics involved in RU priming is problematic in that it involves non-continuous activation of the target by its related prime1 followed by its deactivation during the processing of the unrelated prime2. A recent family of cortical network (CN) models has been proposed to account for the spike rate of neurons recorded in priming experiments on behaving monkeys. Two fundamental types of activities are reported during priming protocols involving a single prime picture preceding a related or unrelated target picture (e.g., Erickson and Desimone 1999; Sakai and Miyashita 1991; Rainer et al. 1999; Miller et al. 1996): retrospective activity—that is, increased firing rate of neurons coding for the prime during the ISI following its presentation—is believed to underlie activation of the prime in working memory; and prospective activity—that is, increasing firing rate, during the ISI, of neurons coding for the target yet to be presented (Naya et al. 2001, 2003; Yoshida et al. 2003; Fuster 2001; Rainer et al. 1999; Sakai and Miyashita 1991; Miyashita 1988; Miyashita and Chang 1988), sub-tending priming effects (Erickson and Desimone 1999).

Network architecture and neurons dynamics

We study a rate model of populations of excitatory neurons coding for the primes and targets (see Brunel and Wang 2001; Amit and Brunel 1997). We assume for simplicity that there are non-overlapping populations of excitatory neurons coding for distinct stimuli. The network includes multiple associated sets of neural populations (Fig. 2a).

Here, we use a mean-field approach describing the dynamics of populations of neurons dynamics by average firing rates obeying a standard Wilson-Cowan type equation. Excitatory neurons have a non-linear transfer function giving the firing rate versus the mean input current calculated as the sum of selective recurrent activities from the population and other populations in the network, selective external stimuli, spike frequency adaptation and non-selective feedback inhibition (Fig. 2b; see Lavigne et al. 2011). In the network, both a non-selective background state and selective attractors are present that correspond to single or multiple activated items. Spike frequency adaptation (SFA) corresponds to a rapid increase in the firing rate of neurons at input onset, followed by a progressive decrease in response to repeated (Baylis and Rolls 1987; Miller and Desimone 1994; Miller et al. 1993) or constant input (Puccini et al. 2006). At the network level, SFA leads to varying spike rate during retrospective activity of a neuron population that is coding for an input (Markram and Tsodyks 1996), and makes possible for the activation of items one after the other in specific sequences (Deco and Rolls 2005). This allows the population dynamics to match the non-continuous dynamics of multiple priming.

Synaptic matrix

We consider 99 objects stored in memory, organized in 33 groups of 3 associated items within a group. The synaptic matrix can have three different values, depending on the relationship between items encoded by the pre- and post-synaptic populations. The diagonal term (connections between neurons coding for the same item) has the maximum strength J1. Connections between populations coding for unrelated items have the minimum strength J0. To guarantee the generalization of the results of the model, the network architecture, population dynamics and the set of parameters used in this study were the same as in the previous model. However, in order to simulate the effects of different association strengths 1 and 2 tested in the experiments, the present CN model embedded a synaptic matrix in which connections between populations coding for related prime1 and 2 and the target could have to intermediate potentiation values Ja = J0 + a(J1 − J0) and Jb = J0 + b(J1 − J0), where a and b measure different association strengths1 and 2. Each parameter a and b take one of two values (low vs. high), which allows for the cross-manipulation of strength1 and 2. For simplicity, we write J1 = 1 and J0 = 0. In the case of a subset of the network with 9 objects, the synaptic matrix has the following form:

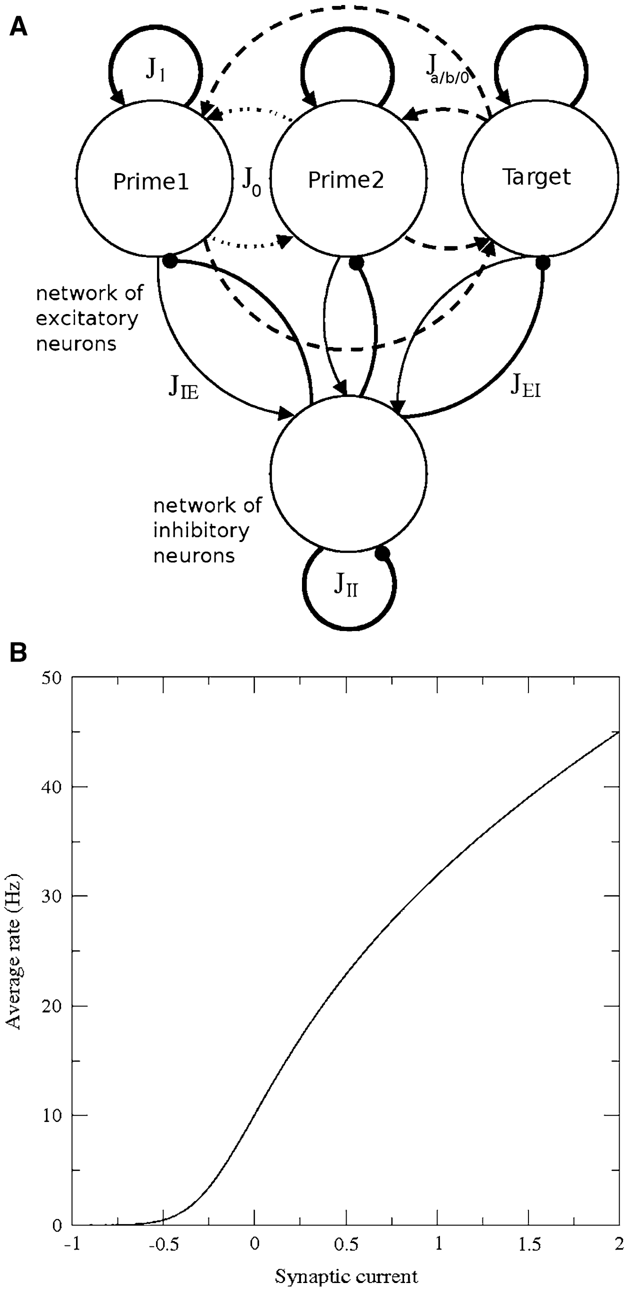


Fig. 2 **a** Architecture of the excitatory-inhibitory network: excitatory neurons are divided in 99 populations of neurons selective for distinct stimuli. For clarity, a group of 3 populations are displayed in the schema, that code for the two unrelated primes (J0) and the target that can be strongly or weakly related (Ja/Jb) or unrelated (J0) to the primes. Inhibitory neurons are non-selective. Synaptic strength is indicated by *line thickness* and type. **b** I-f curve described by the transfer function Φ

$$M_{i,j} = \begin{pmatrix} 1 & a & b & 0 & 0 & 0 & 0 & 0 & 0 \\ a & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ b & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & a & b & 0 & 0 & 0 \\ 0 & 0 & 0 & a & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & b & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & a & b \\ 0 & 0 & 0 & 0 & 0 & 0 & a & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & b & 0 & 1 \end{pmatrix} \quad (1)$$

Hence, for simulations, a target item (e.g., 3) is associated with 2 primes (e.g., 1 and 2), and each prime is related to the target. This allows for an analysis of different sequences of items corresponding to the different conditions of multiple priming: 1-2-3 for the RR condition, 1-4-3 for the RU condition, 4-1-3 for the UR condition and 4-7-3 for the UU condition. The values of association strengths a and b (high vs. low) were cross-manipulated to generate the four conditions of association strength1 and 2 (ss, sw, ws, ww).

Results of the cortical network model

Numerical simulations in the CN model used the same experimental protocols as those tested in the experiments (primes durations and ISIs defining SOAs), and tested the same experimental conditions of primes-target relatedness (RR, RU, UR and UU) for strong and weak primes-target associations (ss, sw, ws, ww). Electrophysiological studies in monkeys report correlation between spike rates and response times (Roitman and Shadlen 2002), as well as shorter reaction times on targets, and increased prospective activity of the corresponding neurons, when the targets are preceded by an associated prime (Erickson and Desimone 1999). On this basis, we take as the reaction time the time Tθ elapsed from target onset to the instant at which the mean firing rate of the corresponding neuron population crosses a threshold $v\theta$ for the first time (see Brunel and Lavigne 2009; Wong and Wang 2006; Wang 2002). The RR, RU and UR experimental conditions lead to specific recognition times, each subtracted to the one in the UU condition to calculate the corresponding priming effects. Tθ depends on the level of prospective activity of the neuron population coding for the target at target onset.

Rate dynamics and priming shift

The behavior of the CN model generating prospective activity of the target during the processing of the sequence of primes (Fig. 3a) depends on the conditions of relatedness and association strength embedded in the synaptic matrix, and on the specific protocol involved (Fig. 3b).

A trial begins with the network in a state of spontaneous activity. At prime1 onset, the corresponding neuron population reaches an elevated level of activity ('perceptive response'). The neuron population initially fires at a high frequency that then decreases according to spike frequency adaptation. The level of activation decreases after the prime1 offset but remains on retrospective activity above the level of spontaneous activity because of the strong excitatory feedback present through J1. This leads in turn to prospective activation of the population of neurons coding for its associate through Ja or Jb. At prime2 onset, the activity of neurons coding for prime2 increases, generating prospective activity of its associate during SOA2. Hence, at the time of the presentation of the target, the corresponding neuron population can exhibit variable levels of prospective activity depending on the condition of relatedness (RR, RU, UR, UU) and on association strengths 1 and 2. It also vary depending on the values of SOA1 and SOA2, during which SFA generates non-continuous changes in retrospective activity of the primes, and in turn in prospective activity of associated targets. The protocols of Experiments 2 and 3 are displayed in Fig. 3. Prospective activity of RU associates increases during SOA1 and begins to decreases during the 250 ms SOA2, while activity of UR associates increases. This leads to comparable RU and UR priming effects at target onset (Exp. 2; Figure 3A1). When SOA2 increases up to 850 ms like in Experiment 3, activity of RU associates decreases due to the increased activity of UR associates and to the effect of spike frequency adaptation. This leads at target onset to UR priming larger than RU priming, corresponding to the semantic priming shift (Exp. 3; Figure 3A2).

Across the four protocols, the model provides us with 32 values of multiple priming effects to compare to the corresponding 32 effects from the four experiments (Fig. 4a). The magnitudes of the effects generated by the model correlate significantly with those of the effects in the experiments ($r = 0.45$, $p < .01$, $\beta = 0.45$; Fig. 3a). In addition, the model generates the priming shift as a function of SOAs (Fig. 4b), that affects more largely the magnitude of RU priming (Fig. 4c) than the magnitude of UR priming (Fig. 4d).

Activation and interferences

Processes of activation and of interference are both reported in the experimental literature to develop through time and affect semantic priming (Coney 2002; Deacon et al. 1999; Kandhadai and Federmeier 2007; Lavigne and Vitu 1997; Neely 1976, 1977; Rastle et al. 2000). In the model, the non-selective inhibitory feedback proportional to the global level of activation of the items, sets a limit to the working memory system in which interference occurs when maximum

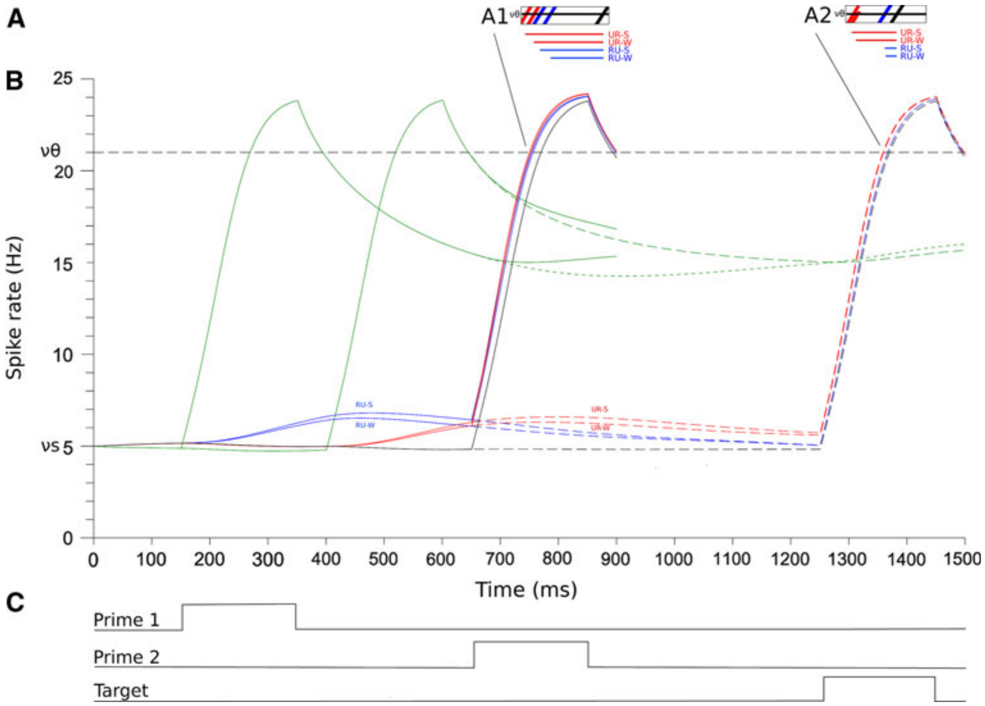


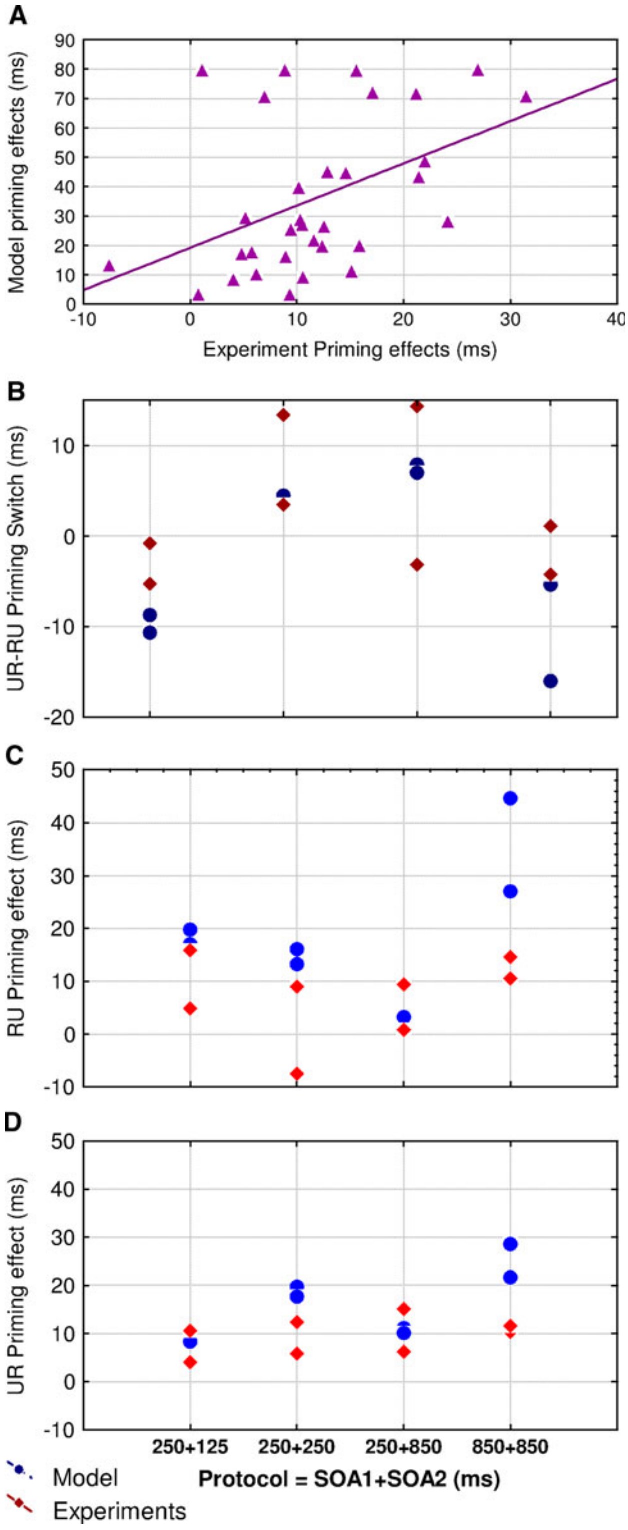
Fig. 3 **b** Spike rates of 7 neurons populations coding for the prime1 and prime2 (*green curves*), the strong and weak RU associates (*blues lines*), the strong and weak UR associates (*red curves*) and the unrelated target (*black curve*) (for clarity, the 92 other excitatory populations and inhibitory population are not displayed). Spikes rates are displayed as a function of time defined in protocol **c** corresponding to experiment 2 (250 + 250 SOAs) and experiment 3 (250 + 850 SOAs). **a** *Insets* A1 and A2 zoom on the crossing of the threshold for recognition by the spike rates of neurons populations for the two protocols. They show the magnitude of RU and UR priming effects for strong and weak associates (*horizontal color bars*) calculated as the difference between reaction times in the unrelated (TUU) and related conditions (TRU and TUR, respectively). Response times correspond to the time from target onset for target population activity to reach threshold $\nu\theta = 21$ Hz (*black horizontal dashed line*). **c** Experimental protocols 250 + 125 and 250 + 850 starting with prime1 presented for 200 ms, followed by 50 ms delay period with no selective input (ISI) defining a 250 ms SOA1; then the prime2 was presented for 200 ms followed by a 50 ms ISI (protocol 250 + 250) or for 200 ms followed by a 650 ms ISI (protocol 250 + 850 ms); finally the target was presented for 200 ms, followed by 50 ms with no selective input before the end of trial. (Color figure online)

capacity is reached (Cowan 2001; Amit et al. 2003; see Haarmann and Usher 2001 for a review). Therefore, the limit of the overall amount of activation implies a selection of which RU and/or UR associates are activated and which are not. The selection process relies on proactive interference—due to the activation of the prime1 and RU associates—on the processing of the subsequent UR associates to the prime2, and on retroactive interference—due to the activation of the prime2 and UR associates—on the processing of the previously activated RU associates to the prime1. In the RU condition, the first (related) prime activates its RU associates, and the second (unrelated) prime generates retroactive interference that is likely to cancel out previous activation of the RU associates. In addition, retroactive interference in the RU condition is usually reported to be stronger than proactive interference in the UR condition (Cowan 2001). This is the case in the model mainly because at prime2 onset, the perceptual response of the population coding for the prime2 is larger—and generates stronger feedback inhibition—than the retrospective activity of the prime1, as it is the case during the processing of sequences of items (see Amit et al. 2003). The different effects of proactive and retroactive interference on the level of activation of RU and UR associates are increased by the spike frequency adaptation of the rates of neurons populations, which makes possible the semantic priming shift between activation of RU associates to the prime1 and activation of UR associates to the prime2.

In protocol 1 (250 + 125), the 250 ms SOA1 is long enough to allow for the prime1 to activate its strong RU associate, while the 125 ms SOA2 is too short to allow for the prime2 to activate its UR associate, corresponding to an absence of priming shift.

In protocol 2 (250 + 250), the 250 ms SOA2 is long enough to allows for the prime2 to activate its strong UR associate, which generates retroactive interference that decreases but does not cancel out the previous activation of RU associates (17 ms and 13 ms priming of strong and weak associates, respectively), corresponding to a partial priming shift.

In protocol 3 (250 + 850), the 850 ms SOA2 allows for activation of the UR associate and the related retroactive



◀ **Fig. 4** **a** Correlation between the 32 mean priming effects recorded in the experiments and the 32 priming effects predicted by the model, for the same four combinations of SOA1 + SOA2 and the same 8 combinations of relatedness and primes-target association strengths (RR-ss, RR-sw, RR-ws, RR-ww, RU-s, RU-w, UR-s, UR-w) (correlation coefficient $r = 0.45$, $p < 0.01$). **b** Semantic priming shift (UR-RU), **c** RU priming effects and **d** UR priming effects as a function of the four experimental protocols (SOA1 + SOA2). Mean values of the effects for strong and weak associates are displayed for the experiments (*red rhombus*) and for the model (*blue circles*). (Color figure online)

interference completely cancels out activation of the weak and strong RU associates to the prime1 (<5 ms effects), corresponding to a complete priming shift.

In protocol 4 (850 + 850), the long SOA1 allows for the activated RU associates to resist retroactive interference generated during the 850 ms SOA2. As a consequence, strong RU and UR associates are co-active, corresponding to a partial priming shift.

Discussion

The four experiments presented here were designed to test the dependence of the priming shift on association strength1 and 2—whose effects were not tested before—for a range of SOA1 and 2—whose values were not yet cross-manipulated. SOA1 and 2 were cross-manipulated across the four experiments, which allows extending results of the meta-analysis to ranges of SOAs not tested previously in the literature. In addition, this first manipulation of association strength in multiple priming experiments provides us with new data on the dynamics of multiple priming as a function of association strength. The results highlight that a semantic priming shift can occur during the processing of sequences of words, and that it can be only partial depending on association strength. The combined experimental and modeling approaches allow to precisely link the dynamics of the priming shift and of the spike rates of spike frequency adaptive populations of cortical neurons.

Integration in mixed meanings

Neither priming nor the priming shift are all or none phenomenons, but rather evolve in time. As a consequence, the meaning related to the sequence of primes at a given time depends on the type of associates activated as a function of the primes themselves and evolves dynamically. Results of the experiments and of the model converge to indicate the possibility for simultaneous activation of associates to the first prime, to the second prime, or to both primes. The resulting meaning related to the sequence of primes at a given time can then range from a 'single meaning' of either the first or second prime—through activation of all or part of its associates (cases of absent or complete priming shift, respectively)—to an 'integrated meaning' of the two primes—through the activation of common associates (case of RR priming; Balota and Paul 1996; Beeman et al. 1994; Whitney et al. 2011).

Through the cross-manipulation of associations strengths 1 & 2, the present results points to the possibility for an intermediate case of simultaneous activation of the strong RU and UR associates to each of the primes (cases of partial priming shift in the RU/UR conditions). This intermediate case could corresponds to a 'double meaning' within which associates of the two primes co-exist though they are not related together. It could also correspond to an 'integrated meaning' of the two primes if their RU and UR associates were able to activate their own common associates to make a link between the two primes. Indirect associations between a single prime and a target are reported to allow for activation and priming effects in the experimental literature and in cortical network models of single priming (McNamara and Altarriba 1988; Kiefer et al. 1998, 2005; Kischka et al. 1996; see Brunel and Lavigne 2009 for a review and model). In single priming, indirect (step2) associations are reported to generate priming. They could therefore subtend the activation of associates to the RU and UR associates to the primes, and then make possible meaning integration by indirectly linking the two primes through common indirect associates. The test for this possibility would require manipulating a condition where the two primes do not have a direct common associate (step1 RR condition) but have and indirect common associate (step2 RR condition). To our knowledge, step2 associations have not yet been tested in multiple priming paradigms. Further, the modeling of meaning integration through activation of common indirect associates to the two primes would require synaptic matrices embedding not only the primes and target but also their associates.

The choice for a rather simple matrix in the current research permitted to clearly understand the respective levels of activation of the items during a protocol. The cortical network model allows for large variations in the number of associates to each item tested in a multiple priming protocol (i.e., each prime and the target), leading to more complex pattern of connectivity between items in more realistic semantic networks. Here we made no assumption on possible different patterns of connectivity between the items tested and their associates, and considered that each prime in the protocol had one target associate. In the case of a larger number of associates, these associates to the primes would be activated and increase the level of inhibitory feedback, which in turn would decrease activation of the target tested. This effect of a larger number of associates could be counter-balanced by a weaker inhibitory feedback—through inhibitory synapses—and/or smaller values of association strength—through excitatory synapses. The later case was tested by Brunel and Lavigne (2009) in a cortical network model of single priming, in which the number of associates to the prime was varied in the synaptic matrix (varying the prime's set size; see Nelson et al. 1991 for experiments). The model was in accordance with experiments, showing that priming effects decrease with set size and increase with association strength (Brunel and Lavigne 2009; Fig. 4b, red and black curves). The complexity of the semantic network varied through the number of associates to the prime changed quantitatively the magnitude of priming effects but not qualitatively their rank of magnitude (i.e., the curves do not cross). In the current model of multiple priming, changes in the number of associates to the primes would change the absolute magnitude of priming effects quantitatively, but not the relative magnitudes of RR, RU and UR effects qualitatively.

In the case of spike frequency adaptive neurons, the non-linearity of the variations of priming effects with time could generate new patterns of multiple priming when step2 associates are used and/or with different numbers of associates to the primes. The current study focuses on the simplest case of connectivity matrix to more clearly analyze the effects of association strength. However, the experimental test of different types of connectivity in multiple priming is a next step to further develop models of priming.

Neural coding of concepts

Computing of the behavior of single populations is a simplification compared to the coding of items by large groups of individual neurons. However, by simplifying the stochastic behavior of large groups of neurons in terms of simpler dynamics of the populations, the mean field approach has the great advantage of allowing a mathematically tractable analysis of attractor states in the network and a clear descriptions of the average levels of activity of the different populations involved in a protocol. Thanks to the mathematical work of physicists, the mean field approach roots the average firing rates of populations to the individual spike rates of individual neurons—through the analysis of network architecture and of the transfer function—according to the biophysics of individual neurons, membrane and receptors' time constants, specific values of potentiation within the synaptic matrix, random noise, etc. (e.g., Amit and Brunel 1997; Brunel and Latham 2003). In that sense the populations' rates may be interpreted as representing pools of spiking neurons in an asynchronous regime (Wennekers and Palm 2009). Previous studies have pointed to the close link between the mean field approach and models of individual integrate and fire neurons. They propose a mean field analysis of the effects of parameters at the neuronal level, such as the ratios of different receptors, their differential gain in different types of neurons, and spike frequency adaptation, on the attractor states of populations of neurons corresponding to retrospective activity in working memory (e.g., Brunel and Wang 2001) and prospective activity (e.g., Mongillo et al. 2003; Lavigne and Darmon 2008; Lavigne et al. 2011). In the current study, a challenge to the model was to tackle the effects of association strength put in evidence by the experiments on the dynamics of multiple priming effects and the priming shift. We note here that the dynamics of populations are slower than the ones of individual neurons and display specific properties (such as sustained retrospective and prospective activities) that emerge from the connectivity matrix between neurons (association strengths, see Amit and Brunel 1997). In a first step, the mean field approach is appropriate to better analyze the effects of cross-variations of associations strengths while keeping other parameters fixed. This approach can nevertheless allow, in a second step, to test for the effects of neurons parameters such as gain modulation of receptors on perturbations of multiple priming (see, e.g., Lavigne and Darmon 2008).

Regarding the neural coding of items in the model, neurophysiological data point to the existence of a distributed coding of items by populations of neurons (Gross 2002; Quiroga et al. 2008). A consequence is the possibility for a given neuron to code for more than one item, and a coding of items by overlapping populations of neurons (see Bowers 2009). In the current study, the choice for non-overlapping populations was guided by the need for a straightforward analysis of the effects of association strengths between clearly separated populations, under the assumption that neuronal coding is sparse (Booth and Rolls 1998). This choice was not imposed by the mean field approach itself. Contrary to localist models were items are coded by single nodes (Anderson 1976, 1983a, b; Collins and Loftus 1975; Collins and Quillian 1969), the mean field approach is compatible with neurons coding for several items in memory and populations overlap, as in distributed models (Lerner et al. in press, 2010; Ursino et al. 2011; Cree et al. 1999; Becker et al. 1997; Masson 1995; Plaut 1995; Moss et al. 1994). Such overlap has been the object of studies on in cortical network models and would not change qualitatively the effects observed here (Romani et al. 2006; Curti et al. 2004). In a mean field model, overlap between populations coding for different items would have increase the average potentiation between populations and generate activation between these populations in addition to association strength. The effect of overlap added to the one of association strength would make populations activities noisier and more difficult to interpret. However overlap is a central question for models of semantic priming, and its precise effects on multiple priming will be a further development of the model.

We emphasize here that overlap in a cortical network model is random and that neurons do not code a priori for features shared by semantically related concepts (see Brunel and Lavigne 2009, for a discussion). This allows for classical hebbian learning based on the sole cooccurrence of items without a priori labeling of features of concepts. In addition to hebbian learning, Lerner et al.'s (in press, 2010) model embeds short-term synaptic plasticity that decreases synaptic efficacy with its activity (Loebel and Tsodyks 2002). This allows for random jumps to occur between correlated patterns, or latching dynamics (Treves 2005) that can account for single priming effects between a prime and a target. Lerner et al.'s studies suggest that short-term depression could also contribute to the dynamic of multiple priming and of the priming shift with spike frequency adaptation. In a cortical network model, short-term depression has been reported to reproduce the statistics of firing rates during retrospective activity (i.e., spike rates and coefficient of variation of the interspike interval; Barbieri and Brunel 2007). A further step toward modeling the priming shift would therefore rely on the investigation of the effects of short-term synaptic depression, which could decrease the activation of the target by its related prime with time. A consequence could be a time-dependent decrease of priming in the RU condition, and also to limit the maximum magnitude of priming effects and diminish the over-estimation of RR priming effects by the current model. The promising perspective of latching dynamics are still to be modeled in a cortical network model of multiple priming to test for the possible link between the time constant of short-term depression at the synaptic level and the one of RU priming at the behavioral level.

Further investigation of the dynamics of multiple priming could combine modeling of population overlap and short-term potentiation, and the experimental test of the hypothesis of meaning integration through indirect associations in more complex semantic network.

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