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ERP correlates of priming in language and stimulus equivalence: Evidence of similar N400 effects in absence of semantic content



Angel Tabullo *,1, Alberto Yorio 1, Silvano Zanutto 1, Alejandro Wainselboim 1,2

Instituto de Medicina y Biología Experimental, Conicet, Vuelta de Obligado 2490 (C1428ADN), Buenos Aires, Argentina

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ABSTRACT

Semantic priming has been widely observed at both behavioral and electrophysiological levels as reductions in response times and N400 magnitudes respectively. However, the possibility that stimulus relations derived from associative learning elicit N400 priming effects comparable to those found in language has not been properly addressed yet. Equivalence relations emerge after establishing a set of arbitrary and intra-experimentally defined relations through associative learning, thus allowing the study of derived stimulus relations in the absence of semantic content. The present study aimed to compare ERP correlates of priming in semantically related words and pseudowords related through equivalence. We found similar behavioral and N400 effects when comparing unrelated vs related prime-target pairs in language and stimulus equivalence tasks, suggesting that priming engages at least partially overlapping neural mechanisms in both contexts. In addition, we found a posteriorly distributed late positivity in the semantic priming task only, which may be reflecting language-specific processing.

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1. Introduction

One of the most characteristic and widely studied phenomena in semantic processing is the semantic priming effect (Meyer and Schvaneveldt, 1971; Neely, 1977, 1991). In a typical semantic priming study, the response to a target word (for instance, recognizing that it is an actual word, in lexical decision tasks) is facilitated by the previous presentation of a semantically related "prime" word (e.g. "tiger-lion"). This effect can be observed at a behavioral level as a decrease in mean response latencies when comparing semantically related and unrelated (e.g. "table-lion") word pairs. At a neurophysiological level, eventrelated potential (ERP) correlates of semantic priming consist in reductions of the N400 ERP (Bentin et al., 1985; Rugg, 1985; Holcomb, 1988). The N400 is a negativity that typically occurs between 200 and 600 ms after a critical or target word, has a posteriorly distributed topography, and has been shown to be highly sensitive to semantic relations between words (Kutas and Hillyard, 1984, for a review see Kutas and Federmeier, 2011). Related word pairs in semantic priming tasks generate smaller N400 effects than unrelated ones (Kounios and Holcomb, 1992; Holcomb and Anderson, 1993), and a lesser N400 decrease can also be found in indirectly related words (such as the pair "stripes-lion", which is connected through the commonly related word "tiger") (Kiefer et al., 1998; Kreher et al., 2006; Weisbrod et al., 1999). Although N400 priming effects were originally observed in linguistic contexts, several lines of evidence indicate that this modulation can be elicited by any potentially meaningful stimulus, like pictures (Barrett and Rugg, 1990; Holcomb and McPherson, 1994; Ganis et al., 1996), faces (Barrett et al., 1988; Barrett and Rugg, 1989; Olivares et al., 1999), environmental sounds (Van Petten and Rheinfelder, 1995), or even pseudowords (orthographically legal, but meaningless, letter strings) that have been associated with meaningful sentence contexts (Borovsky et al., 2012, 2013; Mestres-Missé et al., 2007). Moreover, one study (Mestres-Missé et al., 2007) showed that those pseudowords can facilitate real words related to the sentences in which they were learned, resulting in N400 priming. Another study indicated that these N400 modulations could not be due to increased familiarity with the intially novel stimuli, since no changes in N400 effects were found after repeated exposure to pseudowords (Bermúdez-Margaretto et al., 2014). According to these results, N400 effects would only be modulated by semantic processing. On the other hand, recent studies (Rhodes and Donaldson, 2007; Ortu et al., 2013) have suggested that N400 priming effects depend on associative links between words (i.e. the co-occurrence of words according to language usage and the subject's previous experience) and not on the overlap of semantic features or conceptual relations per se.

One possibility that has not been systematically addressed yet is that stimulus associations in the absence of semantic content or meaningful context can elicit N400 priming effects similar to those observed in language. A potentially useful paradigm to analyze such a question is stimulus equivalence (Sidman, 1971; Sidman and Tailby, 1982), which has

^{*} Corresponding author at: INCIHUSA, CCT – Mendoza, Av. Ruiz Leal s/n (5500), Ciudad de Mendoza, Mendoza, Argentina. Tel.: +54 261 524 4348; fax: +54 261 524 4001.

E-mail address: angeltabullo@ibyme.conicet.gov.ar (A. Tabullo).

¹ Tel.: +54 11 4783 2869x235; fax: +54 11 4786 2564.

² Present Address: INCIHUSA, CCT — Mendoza, Av. Ruiz Leal s/n (5500), Ciudad de Mendoza, Mendoza, Argentina. Tel.: +54 261 524 4348; fax: +54 261 524 4001.

been widely applied in the field of Experimental Analysis of Behavior (Barnes-Holmes et al., 2004; Sidman, 1994; Rehfleldt, 2011). An equivalence relation is established when, after training a series of arbitrary relations between a set of stimuli, new untrained stimulus relations emerge, which verify the criteria of mathematic and logic equivalence. The initial or baseline relations are usually trained as successive conditional discriminations using the matching-to-sample (MTS) procedure, although stimulus pairs can also become associated with Pavlovian conditioning, in the absence of reinforcement contingencies (Leader et al., 2000). During MTS training, a stimulus (for instance, A1) is presented as sample, and several (at least two) others are presented as comparison stimuli (for instance, B1 and B2). Only the selection of the correct comparison stimulus is reinforced, and after a number of trials, subjects are capable of choosing stimulus B1 in the presence of A1 and B2 in the presence of A2, thus establishing two stimulus-stimulus relations (A1-B1 and A2-B2). If additional relations B1-C1 and B2-C2 are trained, a new set of untrained associations emerge, which can be tested through unreinforced MTS trials. These tests include: symmetry (the reversal of the trained baseline relations, such as B-A and C-B), transitivity (relations between two stimuli linked to a common one, like A-C given A–B and B–C) and the combination of symmetry and transitivity, or synthetically, "equivalence" (C-A). Reflexivity (the relation of each stimulus with itself, like A-A, B-B or C-C) can also be verified, but is seldom tested in practice. If the subject passes these tests, it means that an equivalence relation has been formed. Each set of equivalence-related stimuli is called an "equivalence class". In the previous example, MTS training would have resulted in the formation of two three-stimulus equivalence classes: A1-B1-C1 and A2-B2-C2. It should be noted that the derived relations of symmetry, transitivity and their combination (the abbreviated test for equivalence) are defined as a function of the baseline trained relations. In the previous example, where A-B and B-C relations are trained, the comparison stimuli (B) from one set of baseline relations (A–B) serves as sample stimuli for the other set (B–C). This training structure is known as "linear series protocol" (Saunders and Green, 1999). In this case, symmetry relations are defined as B-A and C-B, transitivity as A-C and the combination of symmetry and transitivity as C-A. However, it is also possible to train all baseline relations using the same sample stimuli for each set (for instance: A-B; A-C). This structure is known as "sample-as-node" or "one-to-many" protocol (Saunders and Green, 1999). In this case, symmetry would be defined as B-A and C-A, and the combination of symmetry and transitivity as: B-C and C-B, while the relation of transitivity could not be analyzed independently (B-C implies both symmetry relation B-A and trained relation A-C, C-B implies both symmetry relation C-A and trained relation A-B) (see Fig. 1a).

Equivalence relations are relevant for the study of categorization because they do not rely on physical or perceptual similarities, and cannot be readily explained by traditional discrimination and generalization principles (Keller and Schoenfeld, 1950, Hall, 1996). Furthermore, it has been shown that additional learning involving one stimulus of an equivalence relation is transferred to the rest of the equivalence class without further training (Barnes et al., 1996; Roche and Barnes, 1997), providing a basis for generalization that is not constrained by stimulus perceptual similarities. In human research, transference of previous knowledge to the task is controlled by using novel abstract stimuli (Fields and Moss, 2007; Sidman, 1994), like abstract shapes or pictures (Haimson et al., 2009; Wang and Dymond, 2013) or pseudowords (Wang and Dymond, 2013), like trigrams (Barnes-Holmes et al., 2005). In this way, stimulus equivalence provides a controlled setting to study the emergence of stimulus-stimulus relations derived from associative learning, in the absence of semantic content or meaningful context.

Priming effects at both behavioral and neurophysiological levels have been observed within the context of equivalence relations in a study by Barnes-Holmes et al. (2005), in which a lexical decision task was adapted to compare stimulus pairs that were: related by direct training (baseline relations), related through equivalence (either by

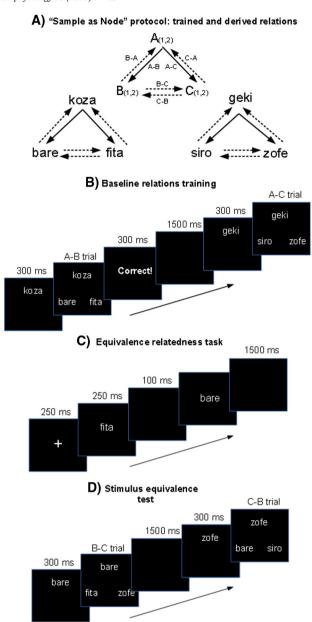


Fig. 1. A. Description of directly trained (solid lines) and derived (dotted lines) stimulus relations in the "Sample as Node" training protocol (up). Baseline relations A–B and A–C are established through MTS, while relations of symmetry (B–A and C–A) and equivalence (B–C and C–B) are derived from them. The relational structure of baseline and derived relations for the two three-member equivalence classes of the experiment is shown below (left and right). B. Examples of A–B and A–C trials from MTS training stage. C. Example of a related trial from the equivalence relatedness task, showing prime-target C1–B1 stimulus pair. The same trial structure and presentation format were used in the language priming task. D. Examples of B–C and C–B trials from Stimulus Equivalence Test. No feedback was provided during this stage.

symmetry, transitivity or both combined) or nonequivalent (either belonging to different equivalence classes or including a novel stimulus in the pair). Faster responses were observed when comparing both directly trained and equivalent stimulus pairs with nonequivalent ones. More crucially, a graded negativity was observed within the time window of N400, which was the largest for nonequivalent, intermediate for equivalent and the smallest for directly trained stimuli. This effect was interpreted as an analog of the N400 found in indirect semantic priming experiments. However, this N400-like component was not directly compared with the ERP elicited by semantically related words,

which would be necessary to determine the degree of overlap between both processes. A more recent study (Bortoloti et al., 2014) also observed larger N400-like ERPs to non-equivalent prime-target pairs, but did not include a semantic priming task. Another study (Haimson et al., 2009) aimed to compare electrophysiological correlates of equivalence and semantic relations, and found larger N400 effects for unrelated stimuli in both language and equivalence class contexts. Nevertheless, their results are limited by the following facts: 1) different subject samples were used in the language and equivalence tasks, which increases between-subject variability, 2) a statistic analysis for the comparison of the N400 effects found in each task was lacking. Therefore, the potential overlap between electrophysiological correlates of priming in language and equivalence relations has not been properly examined yet.

The main goal of the current study was to compare ERP correlates of priming in equivalence and semantic relations employing a within-subject design, in order to further analyze if similar N400 effects can be observed between words and meaningless pseudowords related through associative learning. We predict that related targets will elicit more positive ERPs, while unrelated targets will generate N400 potentials, within both language and stimulus equivalence contexts, despite the absence of semantic content.

2. Materials and methods

2.1. Participants

Sixteen healthy right-handed students (10 women), raging in age from 22 to 30 years (Mean: 25.19 ± 2.50) took part in the study. The subjects spoke Spanish as first language, had normal or corrected-to-normal vision and had no history of psychiatric or neurological disorders, neither were they under any medication at the time of the experiment.

2.2. Procedure

2.2.1. Stage 1: baseline relations training

In this stage, six stimulus-stimulus relations were trained by MTS procedures. Participants were instructed to decide which of the two comparison stimuli presented at the bottom of the computer screen corresponded to the sample stimuli presented at the top, informing their choice by pressing the right or left Ctrl key. They were also instructed to respond as fast and accurately as possible. They were told that they would receive corrective feedback (which consisted in the words "Correct" or "Error") after they made their choice. They were also informed that the stimuli would be meaningless artificial words and that their relation would be arbitrary. The following artificial words were used in the study: A1: koza, A2: geki; B1: bare, B2: siro; C1: fita; C2: zofe.

We chose a "Sample as Node" (also known as "One to many") training protocol because it has been shown to give better outcomes in stimulus equivalence tests (Arntzen et al., 2010; Arntzen and Holth, 1997, 2000). It consists in training a series of conditional discriminations using the same stimuli as sample in all trials (see Fig. 1a). Therefore, this stage consisted on three training blocks: AB, AC (presented in a counter-balanced order to all subjects) and a final mixed AB-AC baseline relations block. The first AB and AC training blocks had a duration of 16 trials, and the relations A1-B1, A2-B2; A1-C1, A2-C2 were trained on each one, respectively. The final mixed block had a duration of 64 trials, and all previously trained relations were presented again, in a pseudo-randomized order. Each training block was preceded by a computer screen summarizing the instructions. Each trial (see Fig. 1b) was initiated by the presentation of the sample stimuli at the center of the upper half of the screen, followed after 300 ms by the simultaneous presentation of both comparison stimuli at the left and right halves of the lower portion of the screen. Subjects could make their choice at any time after the presentation of the comparison stimuli, and it was immediately followed by the words "Correct" or "Error" as feedback. The inter-trial interval was 1500 ms. After completion of the three training stages, participants moved on to the priming tasks.

2.2.2. Stage 2: relatedness and semantic priming tasks

2.2.2.1. Equivalence relatedness task. In this stage, participants were informed that they would see a pair of successive stimuli appear at the center of the screen, and would have to decide if they were related or not. They were told that they would not receive feedback this time but it was still possible to get every answer right based on what was previously learned. Finally, they were told to make their responses after the presentation of the second stimulus in the pair, using the right and left Ctrl keys.

A total of 80 trials were presented, divided in two 40-trial blocks with a short break between them. Half of the stimulus pairs were related through combined symmetry-transitivity (B1-C1; B2-C2; C1-B1; C2-B2) and the other half unrelated (B1-C2; B2-C1; C1-B2; C2-B1). The trials were presented in a pseudo-randomized order (in order to prevent the same trial from appearing two times in a row). The position of the correct comparison stimuli was randomized across trials, such that it would appear with equal probability at each side of the screen. Each trial (see Fig. 1c) was initiated by the presentation of a fixation cross at the center of the screen, for 250 ms. It was followed by the first stimuli of the pair (prime), which disappeared after 250 ms and was followed by a 100 ms blank screen. After that, the target stimuli appeared, and subjects were able to make their response. In this way, stimulus onset asynchrony (SOA) was 350 ms, the same that was used in Kreher et al. (2006) semantic priming study. The inter-trial interval was 1500 ms.

During this stage, EEG activity was recorded and synchronized with the onset of target stimuli. Subject's accuracy was calculated as the percentage of correct responses and response times were measured from the onset of target stimuli in each trial. Means and standard deviations for both measures are shown in the results section.

2.2.2.2. Language priming task. The stimulus equivalence relatedness task was followed by a semantic priming task. Subjects were informed that they would have to repeat the previous task, but this time, the stimuli shown would be real words. The stage consisted on a single 50-trial block (see Fig. 1), where half of the word pairs were related (e.g.: bull-cow) and the other half were not (e.g.: couch-fruit). Word pairs were selected from a semantic priming study in Spanish (Girbau and Schwartz, 2011). A complete list of the word pairs can be found in the Appendix. There were no significant differences in lexical frequency (*Related*: 25.79 \pm 28.21; *Unrelated*: 26 \pm 36.16) (T(48) = 0.071, p > 0.9 – calculated using log-transformed values) or length (Related: 4.48 \pm 0.5; Unrelated: 4.8 ± 0.64) (T(48) = -1.945 p > 0.05) between related and unrelated prime words. Target words had a mean lexical frequency of 81.25 ± 121.43 and a mean length of 4.8 ± 0.57 . Spanish lexical frequencies were obtained from BuscaPalabras software (Davis and Perea, 2005).

Trial structure and SOA where the same as in the equivalence relatedness task, and EEG activity was recorded during this stage as well, synchronized to the onset of the target word. Percentage of correct responses and response times were measured in the same way too.

2.2.3. Stimulus equivalence test

After the priming tasks, the formation of two three-stimulus equivalence classes (A1–B1–C1: *koza-bare-fita*; A2–B2–C2: *geki-siro-zofe*) was assessed by MTS-tests of the combined symmetry-transitivity ("equivalence") relation. This stage consisted on a single block of 32 trials where derived relations BC (B1–C1; B2–C2) and CB (C1–B1; C2–B2) were tested without further reinforcement (see Fig. 1). Subject's

instructions and stimulus presentation format (see Fig. 1d) were the same as in the training stage, although this time they were informed they would not receive further feedback.

2.2.4. EEG recording and analysis

EEG Activity was recorded from 30 cap-mounted tin electrodes (extended international 10/20 system, Electro-Cap International Inc.) with a biauricular reference using an AKONIC BIOPC system. Electrode impedances were kept under 10 k Ω . EEG signal was sampled at 256 Hz and filtered offline at 0.5–30 Hz (this range was chosen in order to optimize later ICA decomposition, following Groppe et al., 2009; Mognon et al., 2011). EEG preprocessing and ERP analysis were analyzed using EEGLAB software v11.0.3.1. ERPs epoch length was 2000 ms, and a 200 ms pre-stimulus baseline correction was applied. Ocular artifacts were removed from the data by means of the ADJUST ICA-based correction algorithm (Mognon et al., 2011). Epochs containing other kinds of artifacts were detected by visual inspection and excluded from the analysis (resulting in a trial loss lesser than 5%).

Time-windows of interest for ERP analysis were determined by visual inspection of grand-average waveforms and previous literature, following standard procedure in language priming (Batterink et al., 2010; Justus et al., 2009; Radeau et al., 1998; Kreher et al., 2006; Misra and Holcomb, 2003; Ortu et al., 2013) and previous stimulus equivalence studies (Barnes-Holmes et al., 2005; Yorio et al., 2008).

ERPs mean voltage was calculated within time-windows and analyzed by means of two separate ANOVAs: one performed on the midline electrodes and the other on six regions of interest, each containing the average value of a group of four electrodes (Leone-Fernández et al., 2012). The six regions were grouped between the two hemispheres (left and right) as following: left anterior (LA: average between F7, F3, FC5, Fp1), left central (LC: FC1, C3, CP5, T7), left posterior (LP: CP1, P7, P3, O1), right anterior (RA: F4, F8, FC6, Fp2), right central (RC: FC2, C4, CP6, T8), and right posterior (RP: CP2, P4, P8, O2). Therefore, a $6 \times 2 \times 2$ repeated measures ANOVA was performed on the midline electrodes with Electrode (Fpz, Afz, Fz, Cz, Pz, POz), Task (equivalence relatedness, semantic priming) and Condition (related, unrelated) as within-subject factors, and a $3 \times 2 \times 2 \times 2$ repeated measures ANOVA was conducted on the regions of interest, with Region (anterior, central, posterior), Hemisphere (left, right), Task and Condition as within-subject factors. Effect sizes were estimated by the partial eta-squared coefficient η_p^2 (Cohen, 1973; Haase, 1983). Greenhouse-Geisser correction was applied in cases of sphericity violations, and Bonferroni adjustment was used for post hoc pairwise comparisons.

In order to compare the time-course of the original ERPs between tasks, latencies were estimated using the fractional area latency measure (Hansen and Hillyard, 1980; Kiesel et al., 2008; Luck, 2005). Fractional area latency was defined as the point within the time-window of interest that divided the area under the ERP waveform in half, for each experimental condition, in each participant; and calculated using the ERPLAB Toolbox (Lopez-Calderon and Luck, 2014). ERP latencies were analyzed in the same way as mean voltages.

3. Results

3.1. Behavioral data

3.1.1. Baseline relations training

Participants were successful at learning the baseline stimulus relations (AB and AC), as was reflected in their performance during training. Mean percentage of correct responses was 85.63 \pm 14.14% in the AB block, 91.88 \pm 13.51% in the AC block and 93.28 \pm 8.84% in the mixed AB–AC block.

3.1.2. Equivalence relatedness and language priming tasks

Participants also performed well in the equivalence relatedness and semantic priming tasks. Their accuracy was lower in the equivalence relatedness (87.11 \pm 11.47%) compared to semantic priming (98 \pm 1.63%) (T(15) = -3.877, p = 0.001), which was expected since their previous exposure to language was much more extensive.

Priming effects in accuracy and mean response times were analyzed by means of a 2×2 repeated measures ANOVA, with Task (equivalence, language) and Condition (related, unrelated) as within-subject factors. No significant priming effects were observed over accuracy (p's > 0.121). Individual response times of correct responses were logtransformed for statistic analysis (latencies outside the range of twostandard deviations, as well as those responses faster than 200 ms were excluded as suggested in Ratcliff, 1993, resulting in a trial loss no greater than 3%). Main effects of Task (F(1,15) = 69.546, p < 0.001, η^2_p = 0.823) and Condition (F(1,15) = 30.011, p < 0.001, η^2_p = 0.667), but no Task \times Condition interaction (p = 0.328) were observed. While responses were generally faster in the semantic priming task, priming effects were significant both in the equivalence relatedness (Related: 1291.76 ± 334.15 ms, *Unrelated*: 1424.44 ± 273.40 ms) and semantic priming (*Related*: 832.70 \pm 156.53 ms, *Unrelated*: 882.37 \pm 170.19 ms) tasks.

3.1.3. Stimulus equivalence test

In accordance with their performance in the equivalence relatedness task, participants completed the stimulus equivalence test (CA block) successfully (87.15 \pm 10.13%), thus verifying the formation of two 3-stimulus equivalence classes.

3.2. ERP analysis

Visual inspection of grand average waveforms in the equivalence relatedness task indicated a posteriorly distributed negativity for unrelated stimulus pairs within the range of 300–500 ms. The latency and topography of the effect were congruent with previous descriptions of N400 in sentence and priming contexts (see Kutas and Federmeier, 2011, for a review). Furthermore, similar effects were previously reported within the same time range in stimulus equivalence studies (Barnes-Holmes et al., 2005; Haimson et al., 2009). In the semantic priming test, unrelated stimuli elicited a larger N400 effect in the same time window. Furthermore, an additional effect was identified for unrelated words in this task: a posterior positivity between 500 and 660 ms. Its time range and topography were similar to those of a late positivity observed in semantic priming tasks (Holcomb, 1988; Kreher et al., 2006; Rugg, 1987; Ruz et al., 2003).

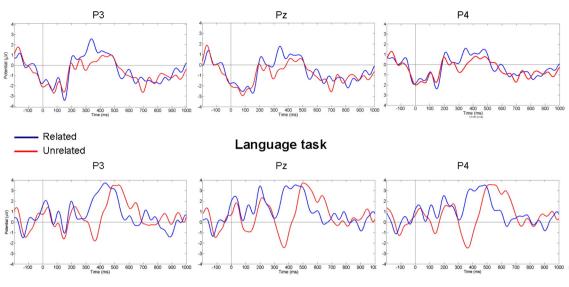
Two time windows of interest were defined based on visual inspection and previous literature: 1) N400 (300–500 ms) and 2) late positivity (560–660 ms). Fig. 2 displays grand average ERP waveforms at three representative sites (upper panel) and difference wave topographies in the time windows of interest (lower panel) for both tasks.

3.2.1. N400 (300-500 ms)

A significant Condition main effect (F(1,15) = 26.869, p < 0.001, $\eta^2_p = 0.642)$ and a Hemisphere \times Task \times Condition interaction (F(1,15) = 11.276, p = 0.004, $\eta^2_p = 0.429$) were found in the regions of interest ANOVA. Unrelated stimuli elicited larger negativities at both left (p = 0.002) and right (p = 0.001) sites in the semantic priming task, while this effect was significant at left (p = 0.028) and marginally significant at right (p = 0.068) sites in the equivalence relatedness task. Additionally, ERPs for unrelated targets were more negative in the semantic priming than in the equivalence relatedness task at right sites (p = 0.029), while this difference did not reach significance at left sites (p = 0.084).

In the midline electrodes ANOVA, a Condition main effect (F(1,15) = 16.992, p = 0.001, η^2_p = 0.531) and an Electrode × Task × Condition interaction (F(5, 75) = 2.706, p = 0.019, η^2_p = 0.216) were observed. The N400 was larger for unrelated targets at all sites in the semantic priming task (p's < 0.004), but this difference was only significant at





Difference wave topographies (Unrelated - Related)

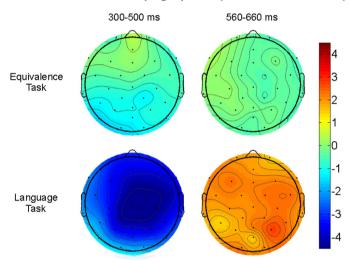


Fig. 2. Grand-average ERP waveforms (upper panel) at sites P3, Pz and P4 by task (stimulus equivalence up, language down) and experimental condition (blue for related and red for unrelated stimuli) (up). Difference wave (unrelated minus related condition) topographies (lower panel) within the three time-windows of interest, by task (down). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

POz (p = 0.044) and marginally significant at Pz (p = 0.082) in the equivalence relatedness task. In addition, negativities for unrelated targets were larger in the semantic priming tasks when compared with the equivalence relatedness task at frontocentral sites (AFz, Fz, Cz) (p's < 0.021).

Regions of interest ANOVA of fractional area latencies indicated a marginally significant Region \times Task \times Condition interaction $(F(2,30)=3.449,p=0.065,\eta^2_p=0.187).$ No significant differences in latencies of related or unrelated targets were found between tasks, in any of the regions $(p\mbox{'s}>0.229).$ On the other hand, latencies were shorter for related targets at anterior (p=0.013) and central (p=0.046) sites in the semantic priming task only. Midline electrodes ANOVA showed a significant Electrode \times Task \times Condition $(F(5,75)=4.624,p=0.011,\eta^2_p=0.236).$ No significant differences were found for any experimental condition at any electrode site between tasks $(p\mbox{'s}>0.173),$ but latencies were significantly shorter for related targets at Afz (p=0.038) and Cz (p=0.022) in the semantic priming task only. Mean fractional area latencies and standard

deviations combining all electrode sites were as following: Equivalence, related: 399.73 \pm 27.06; Equivalence, unrelated: 411.615 \pm 35.53; Language, related: 402.96 \pm 24.41; Language, unrelated: 418.78 \pm 34.08.

3.2.2. Late positivity (560–660 ms)

A significant Task \times Condition (F(1,9) = 6.110, p = 0.009, $\eta^2_p = 0.375$) interaction was found in the regions of interest ANOVA. The positivity was larger for unrelated targets in the semantic priming task (p < 0.001), but the difference was non-significant in the equivalence relatedness task (p = 0.686).

The midline electrodes ANOVA indicated a Task × Condition interaction (F(1,15) = 9.364, p = 0.008, $\eta^2_{\,p}$ = 0.384) and an Electrode × Task interaction (F(5,75) = 11.186, p = 0.002, $\eta^2_{\,p}$ = 0.427). The difference between unrelated and related targets was significant in the semantic priming task (p = 0.002), but not in the equivalence relatedness task (p = 0.593). In addition, the semantic priming task elicited more

positive brain potentials for both conditions than the equivalence relatedness task at sites Cz, Pz and POz (p's < 0.001).

No latency analysis was carried out because this ERP was absent in the stimulus equivalence task.

4. Discussion

Participants were able to learn the baseline stimulus relations and form two three-member equivalence classes. Priming effects were observed at behavioral level as significantly faster responses to related targets, both in the semantic priming and the equivalence relatedness tasks. This result was consistent with previous studies that showed facilitation priming for prime-target pairs from the same equivalence class, related through nodal stimuli (Barnes-Holmes et al., 2005). At the electrophysiological level, priming effects were observed as a reduction in N400 potentials for related targets that was significant in both tasks, but larger and more broadly distributed in semantic priming. An additional late positivity following the N400 was identified in this particular task only. These findings are discussed in detail below.

4.1. N400

The presence of an N400 potential after a pair of stimuli that did not belong to the same equivalence class is congruent with the findings of Barnes-Holmes et al. (2005), Bortoloti et al. (2014) and Haimson et al. (2009). A recent study failed to find consistent evidence of N400 effects while comparing related vs unrelated stimulus pairs (Wang and Dymond, 2013). However, the authors reckoned that "the absence of N400 may have resulted from the combinations of trial types presented, but also from the different experimental manipulations employed." While the closest antecedent of a comparison between equivalence and semantic relations is Haimson et al. (2009), it was mainly a descriptive study, used different groups of subjects for each task and did not provide a statistic analysis of the ERPs. Therefore, our experiment is the first to directly compare electrophysiological correlates of semantic associations and derived stimulus relations within the same subjects. While our results suggest a certain degree of functional overlap between them, the magnitude and the topography of the effects were not

The main difference between the N400 priming effects (the difference between ERP's evoked by related and unrelated stimuli within the N400 range) elicited by semantic and equivalence relations was that the size was larger in the former, which could be attributed to the subject's higher proficiency and larger experience with language. Similar effects on N400 priming were observed in a variety of studies that compared brain responses to semantic anomalies between native speakers and late learners of English (Hahne et al., 2006; Moreno and Kutas, 2005; Ojima et al., 2005; Weber-Fox and Neville, 1996). Furthermore, a recent study (Newman et al., 2012) concluded that the N400 effect amplitude was directly proportional to proficiency in both L1 and L2 learners. Therefore, larger priming modulations might be observed within equivalence classes after subjects underwent more extensive training, and reached higher performance levels. The fact that stimulus pairs were indirectly related in the equivalence task (because they were linked through a nodal stimulus), but directly related in the semantic priming task, may have also contributed to smaller priming effects in the former. N400 priming decreases for indirectly related stimuli have been previously observed both in language (Kiefer et al, 1998; Kreher et al., 2006; Weisbrod et al., 1999) and equivalence classes (Barnes-Holmes et al., 2005).

An additional difference was that ERPs evoked by semantically unrelated words were significantly more negative than those found after non-equivalent stimuli. This might seem counterintuitive, as N400 potentials are usually larger after pseudowords than real words (Rugg and Nagy, 1989). However, this result might be explained as a consequence of our experimental design. Considering that the number of stimuli was

significantly smaller in the equivalence task, and that prime-target pairs were repeated through it, it is possible that non-equivalent pseudoword targets had become more predictable and expected than unrelated words. It has been shown that N400 is reduced for high frequency words presented in isolation (Smith and Halgren, 1987), highly expected words within sentence contexts (Kutas and Hillyard, 1984; see Kutas and Federmeier, 2011 for a review) and more predictable targets in priming tasks (Lau, Holcomb and Kuperberg, 2013). Furthermore, N400 repetition effects have been observed for pseudowords (Deacon et al., 2004) and illegal strings (Laszlo et al., 2012). Therefore, the smaller N400 amplitude of nonequivalent stimuli might be attributed to predictability modulations. This explanation would be compatible with a connectionist network study that showed how the N400 could be interpreted as an index of implicit prediction errors within semantic memory (Rabovsky and McRae, 2014).

We also observed a slight left lateralization of the N400 in the equivalence relatedness task (where the difference between unrelated and related targets was more significant at left sites), a fact that had been previously reported (Barnes-Holmes et al., 2005). This hemispheric asymmetry was absent in the language task. While this difference would suggest that both tasks did not rely on completely overlapping neural mechanisms, it should be noted that N400 topography has proven difficult to define, as scalp distributions tend to vary according to the task, stimulus modality and stimulus type (Kutas and Federmeier, 2011). Beyond the divergences in scalp topography, converging evidence from intracanial recordings, magnetoencephalography and event-related optic signals (Tse et al., 2007) suggests that the N400 is not the product of a single, static neural source, but it would rather reflect a stream of activity starting at the left superior temporal gyrus, and spreading through the temporal and frontal lobes. Despite hemispheric lateralization, the similarities between priming effects indicate that intra-experimentally defined associations between pseudowords engage similar neural mechanisms than semantic relations within the N400 time range. This finding is compatible with the claim that the N400 arises from a time period in which stimulus-driven activity enters into temporal synchrony with a broad multimodal neural network, whose current states have been shaped by recent and long-term experience of a wide range of types (Kutas and Federmeier, 2011), including world experience and recent linguistic and non-linguistic input.

An additional factor that might have contributed to ERP differences between tasks is the lack of a counterbalanced presentation among subjects. The main reason for having presented the tasks in a fixed order to all participants was to prevent that the linguistic nature of the semantic priming task induced the subjects to look for (or arbitrarily assign) meanings in the pseudowords of the equivalence task. Our concern was to keep the equivalence experiment as least semantically biased as possible. On the other hand, we considered that the semantic priming task should be easier and less demanding for the subjects (because of their previous knowledge of word meanings and relations) and therefore, less susceptible to fatigue effects. Furthermore, we believed it was more likely that previous word processing (far more established and familiar to the subjects) would bias equivalence relations processing than the other way around. We acknowledge that this precludes us from discarding potential task order effects in our experiment. It should be noted, however, that confound factors like habituation or fatigue are more likely to decrease the size of the effect in the second task, while our results showed precisely the opposite (larger N400 priming in the semantic task).

ERP latency analysis showed no significant differences between tasks in the time-course of brain potentials elicited by related and unrelated targets, which further suggests a functional similarity of priming effects based on semantic relations and associative learning. We did find some evidence of shorter ERP latencies to semantically related stimuli at frontocentral sites (although the interaction was only significant in the midline electrodes ANOVA). While this effect did not reach significance in the ROI ANOVA, similar priming effects over N400

latencies have been previously reported (Deacon, Mehta, Tinsley and Nousak, 1995). The absence of such differences on ERP latencies between equivalent and non-equivalent stimuli might also be explained by the relatively smaller number of stimuli in this task, which may have affected N400 amplitudes as well.

While previous studies showed how the N400 is modulated by the acquisition of meaning in semantic contexts (Borovsky et al., 2012, 2013; Mestres-Missé et al., 2007), the present work shows how combined associations of meaningless pseudowords can also modulate this ERP. Crucially to our hypothesis, priming effects over N400 within equivalence classes occurred in the absence of any semantic context, since the stimuli consisted of pseudowords without referent or meaning, and the associations between them were completely arbitrary. Furthermore, when debriefed, our participants claimed that they found no resemblance between the pseudowords and actual words, nor did they apply any previous (extra-experimental) knowledge while solving the task (although it is unlikely that it might have influenced significantly the obtained results, we acknowledge that "bare" is meaningful in English, and should not be used in future studies with Spanish-English bilingual subjects). Baseline trained relations arose from operant conditioning, and equivalence relations (the ones that were assessed in the relatedness task) derived from the combination of symmetry and transitivity on the set of directly trained stimuli. The significance of this fact becomes clear when we consider that previous studies found N400 effects using non-linguistic, but meaningful stimuli, like pictures (Barrett and Rugg, 1990; Holcomb and McPherson, 1994; Ganis et al., 1996), faces (Barrett et al., 1988; Barrett and Rugg, 1989; Olivares et al., 1999) and environmental sounds (Van Petten and Rheinfelder, 1995). On the other hand, stimulus equivalence studies have found priming effects over an N400-like potential using equivalent pseudoword trigrams (Barnes-Holmes et al., 2005) and abstract pictures (Haimson et al., 2009) as stimuli. In these studies, as well as in ours, the links between stimuli were indirect, and derived from baseline relations priorly established by associative learning. The fact that N400 modulations could still be observed within this context could be interpreted as convergent evidence with recent studies that aimed to dissociate associative and semantic priming effects over this potential. Associative relationships in language depend on the co-occurrence of two words in a specific order, regardless of their meaning or semantic properties (Anderson and Charles, 1977). Therefore, any two words can be associated as long as one tends to follow the other in a common usage, even without sharing any physical or conceptual properties (for instance, the word pairs: "traffic-jam", "nursery-rhyme" or "atombomb") (Kiss et al., 1973). Semantic relations, on the other hand, rely on the overlapping features of the word referents, be it physical (Kawamoto, 1993; Masson, 1995; Moss et al., 1994); or conceptual (Huettig and Altmann, 2005), and can be defined independently of their contiguity in everyday language (for instance, the word pairs: "pig-chicken", "violin-guitar" or "cereal-bread"). However, there are many cases where featural overlap is the reason why the words tend to co-occur in language (as in the case of the word pairs: "brother-sister", "gold-silver" or "lion-tiger"), and so they are related both semantically and associatively. Priming effects over response times have been observed for word pairs that were either semantically (McRae and Boisvert, 1998; Perea and Rosa, 2002) or associatively (Ferrand and New, 2003; Perea et al., 1997; Williams, 1996) related, and it has been shown that associative priming has a larger effect size, although the effect is enhanced for words that share both types of relations (Lucas, 2000). Despite this distinction, most ERP priming studies have failed to discriminate between associative and semantic relations until recently (Rhodes and Donaldson, 2007; Ortu et al., 2013). Rhodes and Donaldson (2007) found N400 modulations in word pairs that were either associatively related or both semantically and associatively related, but not in word pairs that were semantically related only. Moreover, Ortu et al. (2013) compared processing of word pairs with varying degrees of associative relationship, while holding constant their semantic congruency. They found larger N400 effects when comparing unrelated vs highly associated pairs ("cherry-tree") with unrelated vs moderately associated pairs ("camera-lens"). The authors concluded that N400 could be modulated by associative relations independently of semantics. They also suggested that: a) their results were congruent with N400 effects observed in stimulus equivalence studies (where the stimuli were non-linguistic and their associations were defined intraexperimentally) and b) these findings indicated the generality of the associative mechanism underlying the N400. Finally, they proposed that the N400 "does not reflect the transient activation of semantic knowledge. Rather the N400 effect appears to reflect the acquisition of meaning via associations formed by the contiguity of distinct elements within one's experience" (Ortu et al., 2013). The similarity of N400 effects in language and stimulus equivalence observed in our experiment would further support this view, showing that stimulus associations learned in operant conditioning contexts can facilitate processing in a similar way than word associations acquired by language exposure. In addition, we showed that this facilitation can occur between stimuli that were not directly associated during training, but are linked through a commonly related stimulus, in the same way that indirect priming takes place between indirectly related words. While this interpretation is attractive, we reckon that we did not distinguish semantic and associative relations within our priming task, and that we should try to replicate our current findings while systematically varying the degree of semantic and associative relationship of the words. In addition, both direct and indirect priming effects should be compared.

Regarding the nature of equivalence stimulus relations, it has been suggested that the associative structure of equivalence classes resembles that of several memory network models (Fields et al., 1990; Fields and Nevin, 1993; Fields and Verhave, 1987; Fields et al., 1984). In the case of language, words within memory are represented as nodes interconnected by conceptual relations (Anderson, 1983; Collins and Loftus, 1975; McClelland and Rumelhart, 1988). When a subject sees or hears a word, its node becomes active, and this activation spreads automatically to other related concepts (for instance, presentation of the word "tiger" should also activate "lion" and "stripes"). If a word from one of these preactivated (or "primed") nodes is perceived shortly after, its processing will be facilitated. This facilitation would be larger for directly related concepts, smaller for concepts related through additional nodes (for instance, "lion" and "stripes", which are connected by the word "tiger") and lowest or absent for unrelated words. Gradual reductions of priming effects in response times and N400 are compatible with these models (Kiefer, et al., 1998; Kreher et al., 2006; Weisbrod, et al., 1999), suggesting that facilitation is inversely related to the number of nodes linking prime and target. While controlled or strategic processes may also explain priming in certain contexts (Neely, 1977), automatic spread of activation accounts for most indirect priming effects under conditions that favor automatic processing, such as the short SOA (<400 ms) we employed in our experiment (Franklin et al., 2007; Deacon et al., 1999; Anderson and Holcomb, 1995; Kreher et al., 2006).

In equivalence classes, each stimulus can be considered as a node connected to the other members of the class by trained or emergent relations. Additionally, some of these relations are direct (baseline, symmetry) while others involve intervening nodal stimuli (transitivity, equivalence). A graded N400 effect was reported in Barnes-Holmes et al. (2005) study when comparing directly trained and derived equivalence relations resembling indirect semantic priming. In our study, all stimulus pairs were either related or unrelated through combined symmetry–transitivity, therefore, N400 priming effects could only be mediated by a common nodal stimulus. The relation between the magnitude of the priming effects over N400 and the number of nodes connecting the stimuli within an equivalence class could be further analyzed by future studies that compared stimulus pairs related by one, two and three-node transitivity (for instance: A–C, A–D and A–E) or equivalence

(C–A, D–A, E–A). So far, current and previous evidence suggests that indirect priming effects of equivalence and semantic relations can be observed over the N400 potential. While we cannot claim that this result is by itself evidence of automatic spread of activation through the nodes of different relational networks, it is certainly compatible with such an account. On the other hand, we consider that this interpretation is not necessarily at odds with an associative account of N400 priming effects (Rhodes and Donaldson, 2007; Ortu et al., 2013). If N400 is sensitive to associations established through subject's experience instead of semantic properties, as the aforementioned experiments suggest, this could be interpreted as automatic activation spread through associative (instead of semantic) links within language relational networks.

4.2. Late positivity

A posteriorly distributed late positivity was found for unrelated targets in the semantic priming task, while this effect was absent in the equivalence relatedness task. The same pattern of results was observed previously in Haimson et al.'s (2009) study, when comparing the groups of subjects exposed to unrelated words and non-equivalent stimulus pairs. This kind of positivities have been observed in word priming tasks that require explicit judgments about the stimuli (Kreher et al., 2006; Holcomb, 1988; Rugg, 1987; Ruz et al., 2003), and have been interpreted as an index of strategic or controlled information retrieval processes during semantic tasks (Olichney et al., 2000; Rugg and Curran, 2007; Van Petten et al., 1991), or potentially conscious recognition of prime-target relationships (Duzel et al., 1997). These accounts may explain why the positivity could not be found in the equivalence relatedness task: since the equivalence stimuli were meaningless and their associations were arbitrary, there was no semantic information to recognize or retrieve about them, and therefore no late posterior positivity could have been elicited. On the other hand, a different study (Bermúdez-Margaretto et al., 2014) found familiarity modulations in a similar late positive component (LPC) elicited by isolated meaningless pseudowords in a lexical decision task. In this study, pseudowords were repeated along six block of trials, and the amplitude of the LPC increased from being virtually absent to reaching the level of real words. Considering that the component has been related to the episodic memory retrieval (Rugg and Curran, 2007; Rugg and Yonelinas, 2003), the authors concluded that LPC repetition effects reflected a strengthening of pseudoword visual memory traces that was a consequence of repeated exposure. The discrepancy between Bermúdez et al. results and ours regarding the LPC might be related to the different experimental tasks employed. Bermúdez et al. gave their subjects a lexical decision task, which implied searching for the pseudowords in their mental lexicon. The access to the pseudowords would have been facilitated by repetition, and the improved recognition of the pseudowords would have been reflected by the increasing LPC. In this case, enhanced recognition of pseudowords would have helped the subjects to identify the items as non-lexical, contributing to their task performance (this was actually reflected in both the speed and accuracy of their responses). While the stimuli were also repeated several times during the test stage in our experiment, the identity of the target (whether it had been previously seen or not, whether it belonged to the mental lexicon or not) was not task-relevant by itself in our experiment. What was relevant was that whether the target was related to the prime or not. And since these relations were not further trained or reinforced after the training stage, no facilitated recognition should have been expected during test, even if the stimulus pairs were indeed repeated. Furthermore, the symmetry-transitivity combined relations (unlike semantic relations) could not be directly retrieved from memory, since they were not trained directly, but derived from baseline relations instead. Therefore, we would expect no LPC elicited by equivalence relations in our experiment. This interpretation would be consistent with Haimson et al. (2009) results, who did not found the LPC in a similar stimulus equivalence priming task.

4.3. Conclusion

In summary, we found significant behavioral and N400 priming effects for both semantically related words and indirectly related pseudowords within equivalence classes. This finding indicated a similar (while not identical) pattern of brain activity for the processing of word relations in language and indirect associations between non-lexical items derived from associative learning, in the absence of meaningful references or context. This result might be considered consistent with recent associative accounts of N400 effects (Rhodes and Donaldson, 2007), as has been suggested by Ortu et al. (2013). Further evidence for this interpretation could be obtained by systematically comparing associatively and semantically related word pairs (as in Rhodes and Donaldson, 2007) with priming effects in equivalence classes. In addition, future studies should analyze direct and indirect priming in stimulus equivalence and language in order to compare graded N400 effects in both contexts.

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