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N2pc reflects two modes for coding the number of visual targets

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Abstract

Humans share with a variety of animal species the spontaneous ability to detect the numerical correspondence between limited quantities of visual objects and discrete auditory events. Here, we explored how such mental representation is generated in the visual modality by monitoring a parieto-occipital ERP component, N2pc, whose amplitude covaries with the number of visual targets in explicit enumeration. Participants listened to an auditory sequence of one to three tones followed by a visual search display containing one to three targets. In Experiment 1, participants were asked to respond based on the numerical correspondence between tones and visual targets. In Experiment 2, participants were asked to ignore the tones and detect a target presence in the search display. The results of Experiment 1 showed an N2pc amplitude increase determined by the number of visual targets followed by a centro-parietal ERP component modulated by the numerical correspondence between tones and visual targets. The results of Experiment 2 did not show an N2pc amplitude increase as a function of the number of visual targets. However, the numerical correspondence between tones and visual targets influenced N2pc amplitude. By comparing a subset of amplitude/latency parameters between Experiment 1 and 2, the present results suggest N2pc reflects two modes for representing the number of visual targets. One mode, susceptible to subjective control, relies on visual target segregation for exact target individuation, whereas a different mode, likely enabling spontaneous cross-modal matching, relies on the extraction of rough information about number of targets from visual input.

KEYWORDS

attention, N2pc, numerical correspondence, target individuation

1 | INTRODUCTION

Like several animal species, human infants a few months after birth possess some elementary abilities for numerical processing. These include the abilities to recognize that a given numerosity is being presented visually or auditorily, and to spontaneously match numerical information presented in various modalities (e.g., Barth, Kanwisher, & Spelke, 2003; Barth et al., 1999; Izard, Sann, Spelke, & Streri, 2006). When the number of discrete events falls in the so-called subitizing range (i.e., two or three objects), infants between 6 and 8 months are able to match visual displays that are numerically equivalent to auditory sequences, independently of whether such stimuli are presented concomitantly (Jordan & Brannon, 2010; Starkey, Spelke, & Gelman, 1983) or sequentially (Feigenson, 2011; Kobayashi, Hiraki, & Hasegawa, 2005). Similarly, adult participants compare quantities across different modalities (i.e., comparing tone sequences with white dot flashes) with the same ease and speed as they compare numerosities within modalities (i.e., comparing either tone sequences for the auditory modality or white dot flashes for the visual modality; Barth et al., 2003). These results suggest that cross-modal numerical associations are carried out using abstract numerical representations that do not depend on the acquisition of linguistic abilities or on fully developed processes subtending voluntary control (Barth et al., 2003).

In the visual domain, critical indications of the involvement of attention mechanisms in selecting discrete objects from multielement visual arrays have recently been provided using the ERP approach to the analysis of EEG data (Ester, Drew, Klee, Vogel, & Awh, 2012; Gebuis & Reynvoet, 2012; Hyde & Spelke, 2009, 2012 ; Hyde & Wood, 2011; Libertus, Woldorff, & Brannon, 2007; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013; Pagano & Mazza, 2012; Pagano, Lombardi, & Mazza, 2014). More specifically, these ERP studies have investigated the causal role of object numerosity in the modulation of a parieto-occipital ERP component, dubbed N2pc, using variants of the search task (e.g., Drew & Vogel, 2008; Eimer, 1996; Eimer & Grubert, 2014; Ester et al., 2012; Jolicœur et al., 2006; Luck & Hillyard, 1994; Mazza & Caramazza, 2011). The N2pc component is characterized by a larger negativity at parieto-occipital sites (e.g., PO7/8) contralateral to the visual hemifield occupied by the searched target usually unfolding between 200–300 ms (Luck & Hillyard, 1994) poststimulus. Though originally interpreted as indexing distractor suppression (Luck, Girelli, McDermott, & Ford, 1997), subsequent studies have shown results more compatible with the view that N2pc is related to target selection and consolidation (e.g., Corriveau et al., 2012; Eimer, 1996; Pomerleau et al., 2014).

A model postulating an explicit link between numerosity of targets and N2pc amplitude has been proposed by Mazza and colleagues (Mazza & Caramazza, 2015; Mazza, Turatto, & Caramazza, 2009; Mazza et al., 2013; see also, e.g., Ester et al., 2012), who have conceptualized N2pc as reflecting the activity of an attention-based individuation mechanism that provides an exact numerical representation of a limited set—three to four—of relevant objects. According to Mazza's model, the exact representation mechanism captured by the N2pc implies a high level of precision required for an object individuation system. The empirical evidence in support of this model (e.g., Mazza & Caramazza, 2011; Mazza et al., 2013; Pagano & Mazza, 2012; Pagano et al., 2014) is the demonstration of a progressive N2pc amplitude increase when the number of targets is increased in search tasks requiring explicit targets' enumeration, for example, when participants are asked to report the number of targets or to indicate a match/mismatch of target numerosity relative to a precued number (Mazza & Caramazza, 2011). Of interest in the present context, when participants are asked to simply report the presence—not numerosity—of at least one target in a search display, the N2pc is still elicited, showing, however, no amplitude modulation as the number of targets is varied (Mazza & Caramazza, 2011). This pattern of results is compatible with a corollary of Mazza''s model referring to the flexibility of the attention-based object's individuation system, which generates some form of numerical representation of target objects only when task relevant. Symptomatic of the generation of a numerical representation from visual input in this framework is the covariation of N2pc amplitude and the number of target objects.

Albeit less explicit in its current formulation, a second corollary of Mazza's model is that, when task irrelevant, a numerical representation of target objects is not generated, a process flagged by an N2pc that ostensibly does not vary in amplitude as the number of target objects is varied. Though conceivable, one issue that warrants further investigation is, however, the apparent incompatibility between this latter assumption—that is, no N2pc amplitude modulation, thus no targets' numerical representation—and the foregoing overview of work pointing to the involuntary and pervasive tendency of humans to encode discrete sensorial events taking into consideration their numerosity. In fact, the possibility that the N2pc may also capture different types of numerosity representation has not been explored so far, and this is surprising given the established evidence that partly intermingled neuronal networks in the parietal lobe can code various forms of abstract quantity representations (Tudusciuc & Nieder, 2013). As long as it can be shown that N2pc index various forms of quantity representation, which is the scope of the present investigation, the question that still awaits an answer is not just if target numerosity is extracted from multitarget visual arrays, but rather which type of numerosity.

Two experiments were designed to answer this question. In both experiments, participants were presented with a variable number of tones followed by a visual display containing a variable number of lateralized visual targets among homogenous distractors. In Experiment 1, in order to replicate the findings of Mazza and Caramazza (2011) using the present cross-modal design variant, participants were asked to respond based on the numerical correspondence between tones and visual targets. In Experiment 2, participants were explicitly dispensed from processing the auditory stimuli, and instructed to focus on the visual display to report a target presence in the search display.

Based on the results of Mazza and Caramazza (2011), we expected a top-down modulation over the mechanisms of coding the number of to-be-enumerated targets in Experiment 1. More specifically, we expected an N2pc amplitude modulation as a function of the number of visual targets in Experiment 1. In Experiment 2, in which participants were dispensed from processing both the auditory stimuli and the number of targets, we anticipated three possible outcomes: (a) A modulation of the N2pc as a function of numerosity driven by a spontaneous mechanism of cross-modal matching that operates much in the same way as in Experiment 1, despite task instructions; (b) a modulation of the N2pc as a function of cross-modal numerical correspondence relying on the extraction of a different type of numerical representation of targets' quantity; or (c) no modulation of the N2pc by either the number of targets or cross-modal numerical correspondence, converging with Mazza's view that the generation of numerical representations from visual input is generated only when task relevant. We anticipate that a more detailed connotation of the types of numerical representations that the present investigation will shed light on is provided in Discussion.

2 | MATERIALS AND METHOD

2.1 | Participants

Thirty-six healthy volunteers participated in the study after providing written informed consent: 19 (11 female, mean age 23.8 ± 2.7 years; 17 right-handed) were included in Experiment 1 and 17 (11 female, mean age 22.2 ± 2.5 years; 16 right-handed) in Experiment 2. Additional participants ($N = 2$ in Experiment 1, $N = 3$ in Experiment 2) were tested but excluded from the final analysis because they did not reach the minimum number of trials per condition (see Section). Moreover, one subject in Experiment 2 was excluded because of technical failure in data collection. All participants had normal or corrected-to-normal vision, and none reported a prior history of neurological disorders and/or was under medication at the time of testing. The experiments were conducted in accordance with the Helsinki Declaration II and were approved by the local ethics committee (Protocol 1661; *Comitato Etico della Ricerca Psicologica*, University of Padua).

2.2 | Stimuli

The auditory stimuli were 450 Hz, 500-ms long tones (44.1 kHz sample rate, 16-bit, monaural) presented at 90 dB via two loud speakers (one on the left and one on the right) placed behind the participants. If two or three tones were presented, they were separated by 50-ms silent intervals.

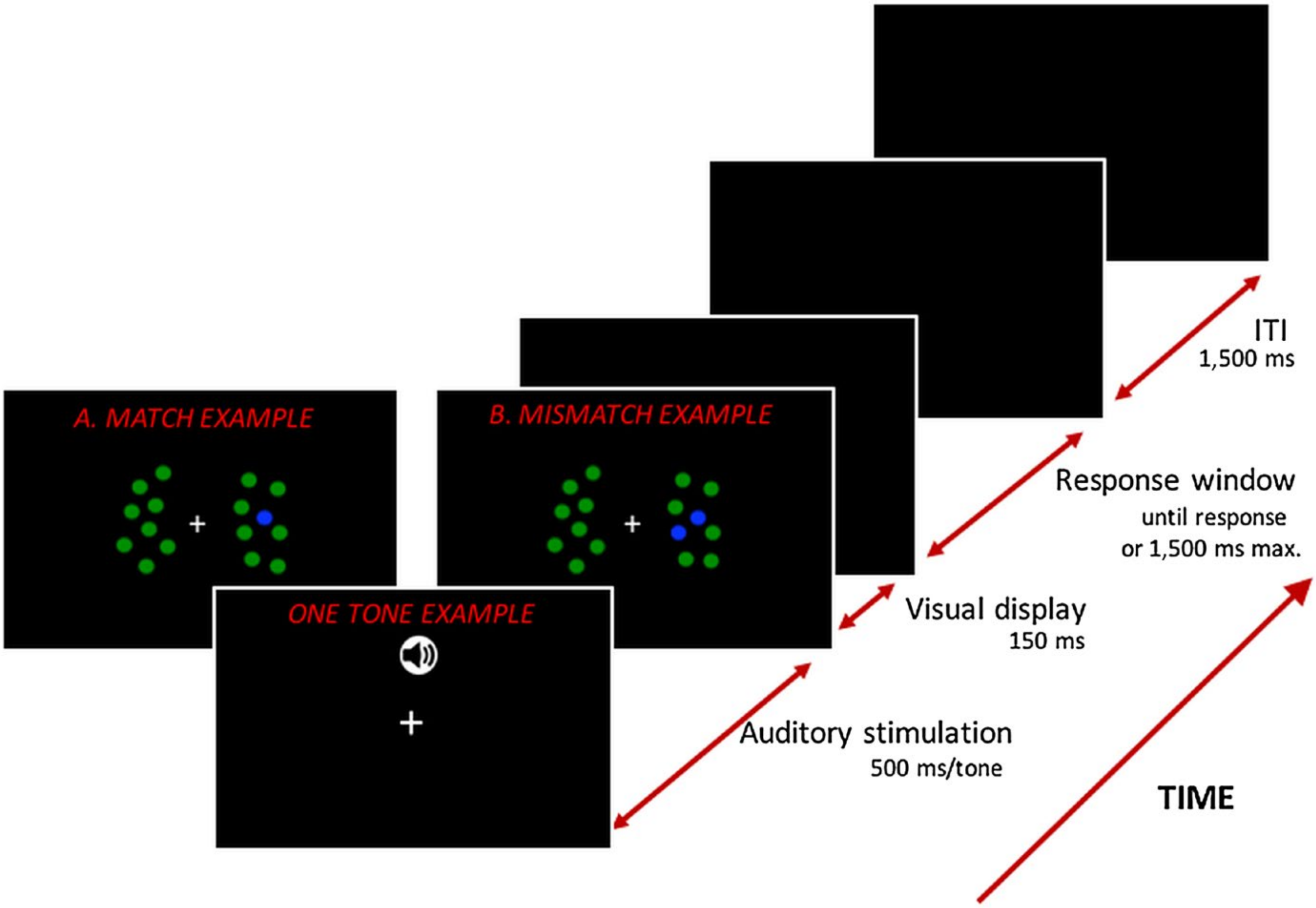

FIGURE 1 Experimental paradigm. On each trial, either 1, 2, or 3 dots (targets) followed the presentation of either 1, 2, or 3 tones. In the depicted examples, the number of visual targets matches the number of tones (1 in this example) in (a) the match condition, or not (b) the mismatch condition

The visual stimuli were blue and green dots located on an invisible 10 (columns, 11.4°) × 7 (rows, 8.6°) grid. The dots were presented on a black background on a 24" screen with 120 Hz refresh rate using E-Prime software (Psychology Software Tools Inc.). All the participants visualized the screen at a distance of 60 cm from which the diameter of each circle was 0.6° of visual angle. A white cross 0.2° wide and 0.2° high was used as fixation point.

2.3 | Procedure

The sequence of events on each trial of the present experiments is illustrated in Figure 1. Each trial began with the presentation of the auditory stimuli (either 1, 2, or 3 tones) accompanied by a continuously displayed fixation cross positioned at the center of the screen. This was immediately followed by the presentation of an array of 16 dots, half on the left and half on the right side of the white fixation cross. On each trial, either 1, 2, or 3 dots (targets) had a different color (either blue or green) from the other (either green or blue), and appeared with equal probability and in random locations either to the left or right of fixation, but never in the two columns closest to fixation within the invisible grid. When more than one dot, targets always appeared in spatially contiguous locations, with no separating distractors. Each visual display was presented for 150 ms.

Participants were seated in front of the computer monitor, and were instructed to maintain fixation at the center of the screen throughout the experiment and to avoid eyeblinks and movements during stimulus presentation. In Experiment 1, they were required to make a speeded yes/no response to indicate whether there was a numerical correspondence between number of tones and visual targets (henceforth, audio/visual numerical correspondence: match vs. mismatch). In Experiment 2, participants were required to make a speeded yes/no response to indicate the presence of at least one target element in the search display, while ignoring the tones. Responses were given by pressing one of two keys placed one on top of the other using the index finger of each hand. Response mapping was counterbalanced across participants. Maximum time for responding was 1,500 ms. The intertrial interval was 1,500 ms.

The location of the targets (left or right visual hemifield) was balanced across trials, and the color of the target was counterbalanced across participants. Participants first received one practice block of 10 trials and subsequently completed three experimental blocks. In Experiment 1, the experimental blocks consisted of 120 trials each, comprising 20 repetitions of each combination of number of targets (1, 2, or 3) and audio/visual correspondence (match or mismatch; see Figure 1). In Experiment 2, the three experimental blocks consisted of 200 trials each, comprising 20 repetitions of each combination of number of targets (1, 2, or 3) and audio/visual correspondence (match or mismatch) plus 80 additional trials in which no target was displayed. Only target-present trials were analyzed (see Section), thus leading to 60 trials per relevant cell (collapsed across right and left target locations) in both Experiment 1 and 2. Accuracy feedback was provided only during initial practice.

2.4 | Electrophysiological recording

The EEG was recorded using a Geodesic EEG amplifier (EGI GES-300) and a precabled 128-channel HydroCel Geodesic Sensor Net (HCGSN-128). Impedances for each channel were measured and adjusted until they were kept below 50 kΩ before testing, as recommended by the manufacturer guidelines. All electrodes were referenced to the vertex during the recording and were rereferenced offline to the average of all electrodes (see Dowdall, Luczak, & Tata, 2012; Shin, Wan, Fabiani, Gratton, & Lleras, 2008; Weymar et al., 2013, for similar referencing implemented in N2pc paradigms). Raw data were digitized at a sampling rate of 500 Hz.

2.5 | Data analysis

2.5.1 | Behavioral analysis

Data from practice trials and trials with incorrect or no responses were discarded from analysis. The mean response times (RTs) for correct responses were analyzed using a 3 × 2 repeated measures analysis of variance (ANOVA) considering number of targets (1 vs. 2 vs. 3) and audio/visual correspondence (match vs. mismatch) as within-participant factors. Greenhouse-Geisser adjustments were applied on the p values when pertinent. The same analysis as that performed on RTs was performed on the percentage of correct responses.

2.5.2 | Electrophysiological analysis

Signal preprocessing was performed using MATLAB 7.9.0 (MathWorks, Natick, MA) and EEGLAB 13.4.4 (Delorme & Makeig, 2004). Raw data were band-pass filtered offline (0.3–40 Hz) and downsampled to 250 Hz to reduce computational time and memory demands. EEG was segmented into 700-ms intervals, from 100 ms before to 600 ms after visual stimulus onset. The period of 100 ms preceding the visual display was used to calculate the baseline. A four-step procedure was performed to remove artifacts. Firstly, epochs containing nonstereotyped artifacts (e.g., movement, swallowing) were manually removed. Then, independent component analysis (ICA) was applied to identify and correct for eyeblinks and eye movements (see Aubin, Drisdelle, Corneyllie, & Jolicœur, 2013, showing no distortion of the N2pc component after ICA correction). Thirdly, data were examined combining joint probability and kurtosis automatic methods for rejection. Lastly, data were visually inspected, and epochs containing any residual artifact were manually removed. Electrodes that were consistently noisy during the entire recording were replaced through spherical spline interpolation. A minimum of 30 trials per condition/participant was chosen as criterion to ensure adequate signal-to-noise ratio. However, the application of the entire procedure ensured that 83.5% of all recorded trials (range: 78.9 to 85.8% across participants) could be retained. Only target-present trials with correct behavioral responses were analyzed.

One set of statistical analyses focused over the lateral parieto-occipital electrodes PO7 and PO8 (corresponding to channels 65 and 90 on the HCGSN-128; Luu & Ferree, 2005), where the N2pc component is maximal. Specifically, we calculated the mean difference amplitudes obtained by subtracting ERP waveforms at ipsilateral parieto-occipital electrodes (PO7 for left target location, PO8 for right target location, respectively) from those recorded at contralateral sites (PO8 for left targets, PO7 for right targets) within the 200–300 ms poststimulus interval—corresponding to the most typical time range of the N2pc (Luck & Hillyard, 1994) and about the one described in previous studies using paradigm similar to that used here (Mazza & Caramazza, 2011). Data were then analyzed using a 3 × 2 repeated measures ANOVA including number of targets (1 vs. 2 vs. 3) and audio/visual correspondence (match vs. mismatch) as within-participant factors.

Two separate grand-averaged waveforms were then constructed for the match/mismatch audio/visual correspondence conditions for an explorative second ERP analysis. Differences between these conditions were tested for statistical significance with the Mass Univariate ERP toolbox (Groppe, Urbach, & Kutas, 2011) through a two-tailed cluster-based permutation test based on the cluster mass statistic (Bullmore et al., 1999) and using a familywise alpha level of 0.05. The advantage of this statistical approach is that it avoids the a priori definition of time windows and/or scalp regions of interest, since the relevant univariate test comparing the conditions is performed for each (electrode, time) pair. In our case, 19,200 total comparisons were performed, corresponding to the combination of the 128 channels used for the EEG recording and the 150 time points included between 0 and 600 ms poststimulus (i.e., the length of our segment). Moreover, each comparison was repeated 2,500 times. For each permutation, all *t* scores corresponding to uncorrected *p* values of 0.05 or less were formed into clusters with any neighboring such *t* scores. The sum of the *t* scores in each cluster is the "mass" of that cluster, and the most extreme cluster mass in each set of tests was used to estimate the distribution of the null hypothesis.

2.5.3 | Regression analysis

We performed a stepwise regression in order to investigate whether measures of visual attentional individuation (i.e., the N2pc component) predicted neural correlates of judgment of audio/visual correspondence. The amplitude of the N2pc (i.e., difference between ERP waveforms at ipsilateral and contralateral occipitoparietal electrodes) in match/mismatch trials and the latency of the N2pc peak were included as predictors of the results obtained in the mass univariate analysis (i.e., the mean amplitude waveform difference between match and mismatch trials over the time points and across the channels showing the highest *t* values). In this sense, the correlational analyses were independent of our selection criteria, allowing us to avoid the circularity error (Kriegeskorte et al., 2010). Moreover, a Ljung-Box Q test for residual autocorrelation and an Engle test for residual heteroscedasticity were used to exclude serial physiological correlation between the predicted measure and the predictors.

3 | RESULTS

3.1 | Experiment 1: Explicit audio/visual matching

3.1.1 | Behavioral results

A graphical summary of the behavioral results of Experiment 1 is reported in Figure 2. The ANOVA carried out on manual

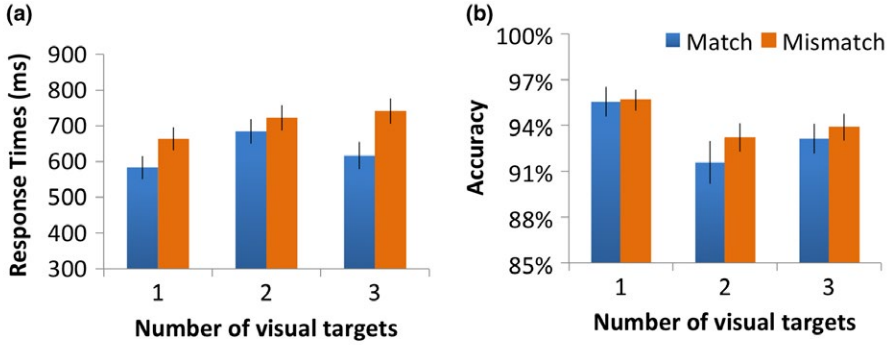

FIGURE 2 Behavioral responses obtained in Experiment 1. (a) Mean response times (RT) in milliseconds (ms). (b) Accuracy (percentage of correct responses) as a function of number of targets and audio/visual correspondence. Bars indicate ±1 standard error of the mean

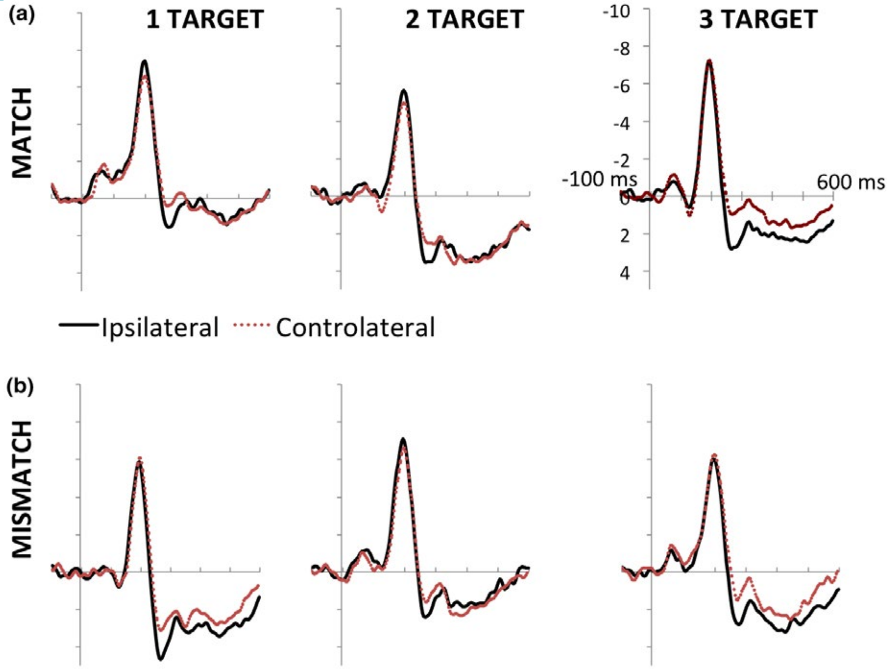

FIGURE 3 Grand-averaged ERP waveforms in the (a) match, and (b) mismatch conditions for the three visual target numerosities in Experiment 1

RTs (Figure 2a) showed a significant main effect of number of targets, $F(2, 36) = 46.6$, $p < 0.0001$; $\eta_p^2 = 0.72$. Follow-up analyses, using the Bonferroni method for multiple comparisons of estimated marginal means, revealed that participants were faster on trials displaying 1 target ($M = 623$ ms) than on those displaying 2 ($M = 703$ ms; $p < 0.0001$) or 3 targets ($M = 678$ ms; $p < 0.0001$). Participants' responses were longer for mismatch trials ($M = 709$ ms) compared to match trials ($M = 628$ ms), a finding substantiated by a significant main effect of audio/visual correspondence, $F(1, 18) = 54.8$, $p < 0.0001$; $\eta_p^2 = 0.75$. There was a significant interaction between the two factors, $F(2, 36) = 8.0$, $p < 0.005$; $\eta_p^2 = 0.31$, due to significant differences across all trials displaying 1, 2, and 3 visual targets in the two conditions (all ps < 0.01) but between 1 and 3 targets in the match condition ($p = 0.49$).

For the analysis of accuracy, the results of the ANOVA showed a significant main effect of number of targets, $F(2, 36) = 8.7$, $p < 0.005$; $\eta_p^2 = 0.33$. Follow-up analyses using the Bonferroni method for multiple comparisons of estimated marginal means revealed that participants were more accurate

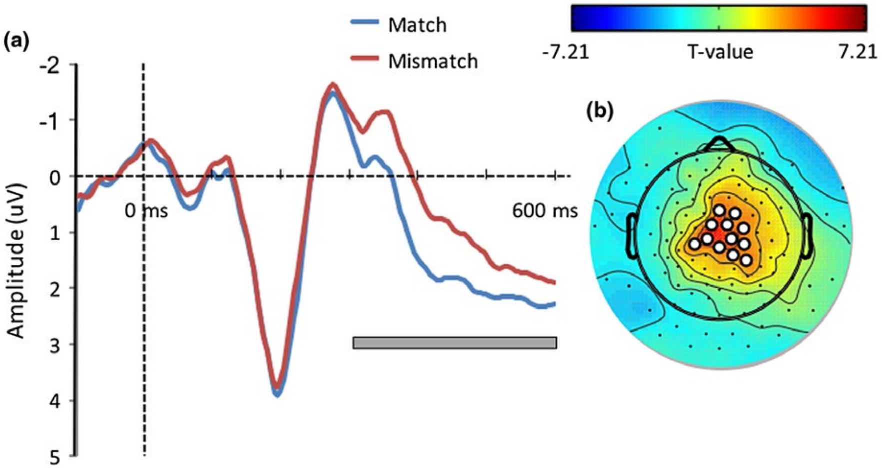

FIGURE 4 (a) Trace plot depicting the grand-averaged ERPs pooled over the electrodes showing the audio/visual matching effect. These electrodes are indicated as black circles in the topographical map on the right. Gray rectangle on the bottom indicates the time window in which the audio/visual matching effect was significant according to the cluster-based permutation test. (b) Topographical map shows the *t* values for the ERP audio/visual matching effect at the time point at which the effect was maximal. Color bar on the top indicates *t* values

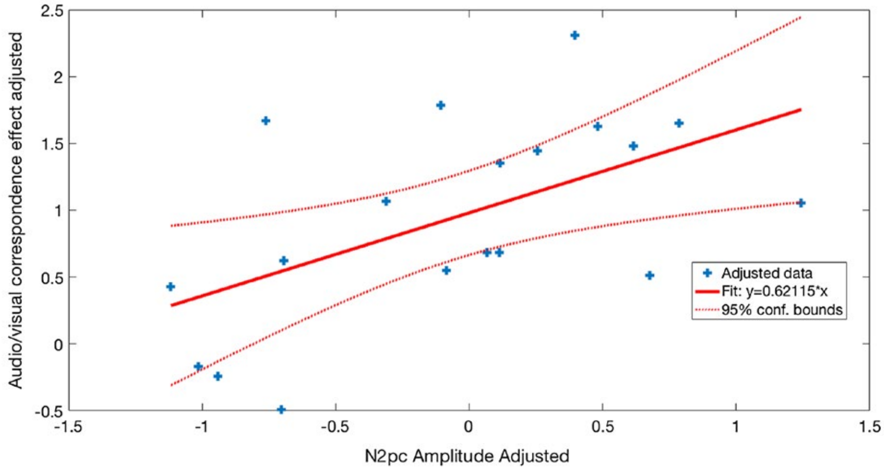

FIGURE 5 Partial regression leverage plot illustrating the unique effect and added value of the variable N2pc difference amplitude to the regression model. In addition to the scatter of residuals, the plot shows 95% confidence intervals (dotted red lines) on predictions from the fitted line (continuous red line)

on trials displaying 1 target ($M = 96\%$) than 2 ($M = 92\%$; $p < 0.01$) or three targets ($M = 93\%$; $p < 0.01$). No significant difference emerged between trials with 2 and 3 targets (Figure 2b). There was no significant effect of audio/visual correspondence, $F(1, 18) = 1.19$, $p = 0.28$; $\eta_p^2 = 0.06$, and no significant factor interactions.

3.1.2 | Electrophysiological results

A graphical summary of the electrophysiological results of Experiment 1 is reported in Figure 3. The ANOVA in the N2pc time range showed significant effects of number of targets, $F(2, 36) = 6.7$, $p < 0.01$; $\eta_p^2 = 0.27$. Neither the effect of audio/visual matching, $F(1, 18) = 0.23$, $p = 0.63$; $\eta_p^2 = 0.01$, nor the interaction among factors was significant. Follow-up comparisons revealed that the N2pc amplitude was larger for 3 targets than for both 1 ($p < 0.05$) and 2 targets ($p < 0.05$). N2pc grand-averaged mean amplitudes were −0.82, −0.45 and −1.38 μV for 1, 2, and 3 targets, respectively. There was no correlation between the behavioral measures on match and mismatch trials or trials with 1, 2, and 3 targets and the corresponding N2pc measures.

We, therefore, tested the statistical significance of the audio/visual correspondence effect by performing cluster-based permutation tests contrasting the ERPs for the match and mismatch conditions averaged across the three target numerosities. As graphically reported in Figure 4, the mass univariate analysis revealed significantly more negative ERP amplitudes for the mismatch condition than the match condition in a 300–600 ms time window over 12 centroparietal electrodes (critical t value = 2.13, $df = 18$, testwise $\alpha < 0.04$). Figure 4a shows the grand-averaged ERP and Figure 4b the corresponding topographic map for this result.

The results of the regression analysis are graphically illustrated in Figure 5. A regression analysis revealed that this ERP audio/visual correspondence effect (i.e., amplitude difference between match and mismatch conditions obtained in the mass univariate analysis) was predicted by the N2pc amplitude difference between match and mismatch conditions ($\beta = 0.62$; $p = 0.013$; $R^2 = 0.31$, $F(2, 17) = 7.57$; $p = 0.01$).

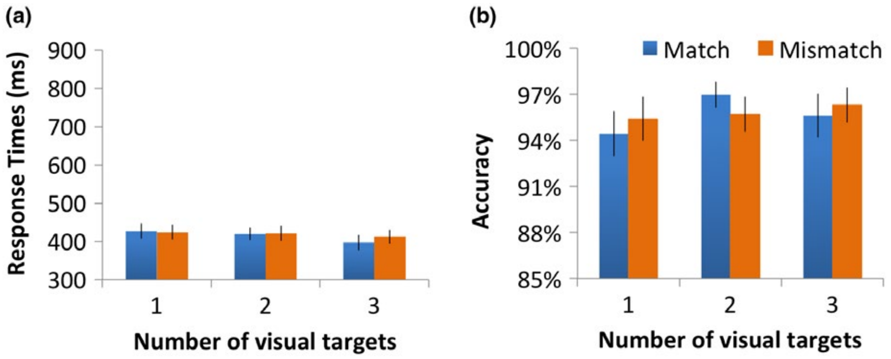

FIGURE 6 Behavioral responses obtained in Experiment 2. (a) Mean response times (RT) in milliseconds (ms). (b) Accuracy (percentage of correct responses) as a function of number of targets and audio/visual correspondence. Bars indicate ± 1 standard error of the mean

Importantly, the results of the Ljung-Box Q test showed that the N2pc component and the central ERP measures did not exhibit serial physiological correlation ($Q = 13.73$; $p = 0.60$). Moreover, no ARCH (autoregressive conditional heteroscedasticity) models could fit the residuals as showed by the Engle test ($T'R^2 = 0.90$; $p = 0.28$). The latency of the N2pc did not predict the audio/visual numerical correspondence effect in the regression model ($p > 0.05$).

3.2 | Experiment 2: Spontaneous audio/visual matching

3.2.1 | Behavioral results

A graphical summary of the behavioral results of Experiment 2 is reported in Figure 6. The analysis on RTs showed a significant effect of number of targets, $F(2, 32) = 14.12$, $p < 0.001$; $\eta_p^2 = 0.47$, because participants were faster on trials displaying three targets ($M = 405$ ms) than on those displaying two targets ($M = 420$ ms; $p < 0.001$) or 1 target ($M = 426$ ms; $p < 0.005$). There was no significant effect of audio/visual correspondence, $F(1, 16) = 1.15$, $p = 0.30$; $\eta_p^2 = 0.07$, and no significant interaction between factors (Figure 6a). The accuracy results showed no significant effect of number of targets, $F(2, 32) = 2.37$, $p = 0.11$; $\eta_p^2 = 0.13$, or audio/visual correspondence, $F(1, 16) = 0.09$, $p = 0.76$; $\eta_p^2 = 0.01$, and no interaction between factors (Figure 6b).

3.2.2 | Electrophysiological results

A graphical summary of the electrophysiological results of Experiment 2 is reported in Figure 7. The ANOVA showed a significant effect of audio/visual correspondence, $F(1, 16) = 5.64$, $p = 0.03$; $\eta_p^2 = 0.26$, due to a larger N2pc amplitude in mismatch (mean amplitude = −0.95 μV) than in match trials (mean amplitude = −0.33 μV). Neither the effect of number of targets, $F(2, 32) = 2.06$, $p = 0.16$; $\eta_p^2 = 0.11$, nor the interaction between factors, $F(2, 32) = 0.18$, $p = 0.82$; $\eta_p^2 = 0.01$, was significant. N2pc grand-averaged mean amplitudes were −0.34, −0.73, and −0.84 μV for 1, 2, and 3 targets, respectively. There was no correlation between the behavioral measures on match and mismatch trials or trials with 1, 2, and 3 targets and the corresponding N2pc measures.

Consistent with the results obtained for the N2pc component, in the mass univariate analysis we also found a significant effect of audio/visual correspondence in the time range between 150 and 200 ms. The results are graphically summarized in Figure 8.

As for Experiment 1, the mismatch condition showed larger negative amplitudes compared to the match condition. The effect was observed over seven centroparietal electrodes (critical t value = 4.84, $df = 16$, testwise $\alpha < 0.05$). There were no significant effects of audio/visual correspondence in different time windows. Figure 8a shows the grand-averaged ERP waveform and Figure 8b the topographic map of the audio/visual correspondence effect. Moreover, the regression analysis revealed that both latency and amplitude difference of the N2pc between match and mismatch conditions in the above mentioned

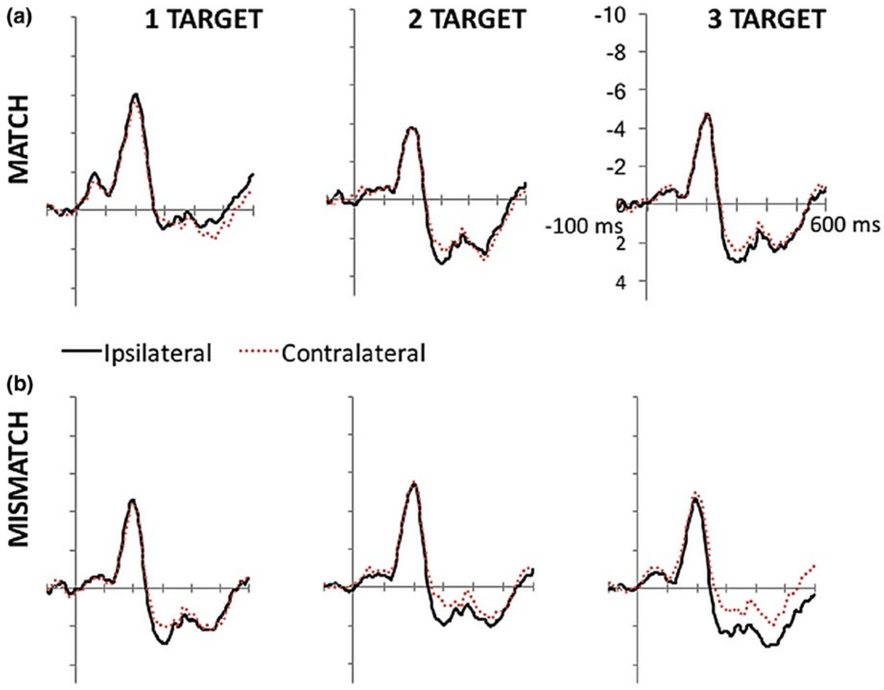

FIGURE 7 Modulation of the N2pc in Experiment 2. The figure shows grand-averaged ERP waveforms in the audio/visual (a) match, and (b) mismatch conditions

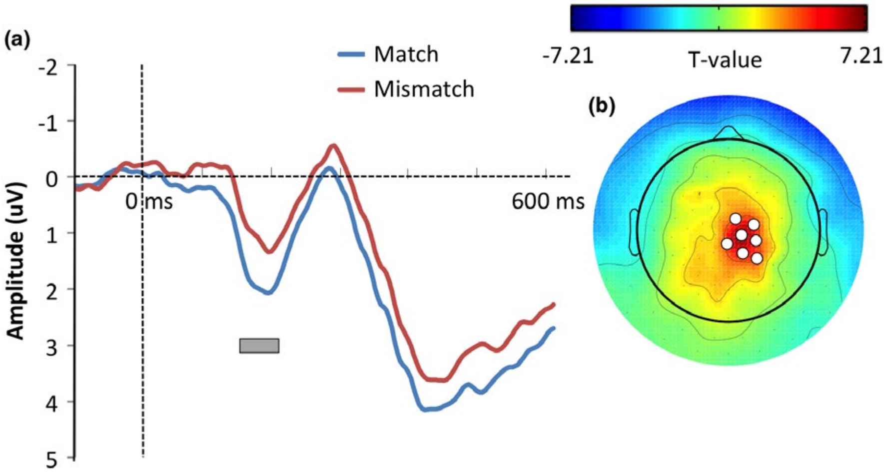

FIGURE 8 (a) Trace plot depicting the grand-averaged ERPs pooled over the electrodes showing the audio/visual matching effect. These electrodes are indicated as black circles in the topographical map on the right. Gray rectangle on the bottom indicates the time window in which the audio/visual matching effect was significant according to the cluster-based permutation test. (b) Topographical map shows the *t* values for the ERP audio/visual matching effect at the time point at which the effect was maximal. Color bar on the top indicates the *t* values

150–200 ms time window predicted the audio/visual numerical correspondence ERP effect ($R^2 = 0.35$, $F(2, 15) = 3.84$; $p = 0.04$). The results of the Ljung-Box Q test indicated no residual autocorrelation between the N2pc and the central ERP measures ($Q = 13.21$; $p = 0.66$). Moreover, no ARCH models could fit the residuals ($T'R^2 = 0.02$; $p = 0.90$). The contra-minus-ipsilateral ERP waveforms in the most informative conditions of Experiment 1 and 2 are displayed in Figure 9.

4 | DISCUSSION

Previous studies have shown that the enumeration of target elements embedded in multielement visual arrays is a mechanism that operates under top-down control, namely, only under conditions in which exact enumeration is necessary for task completion (Mazza & Caramazza, 2011). In the present study, we evaluated the effect of task demands

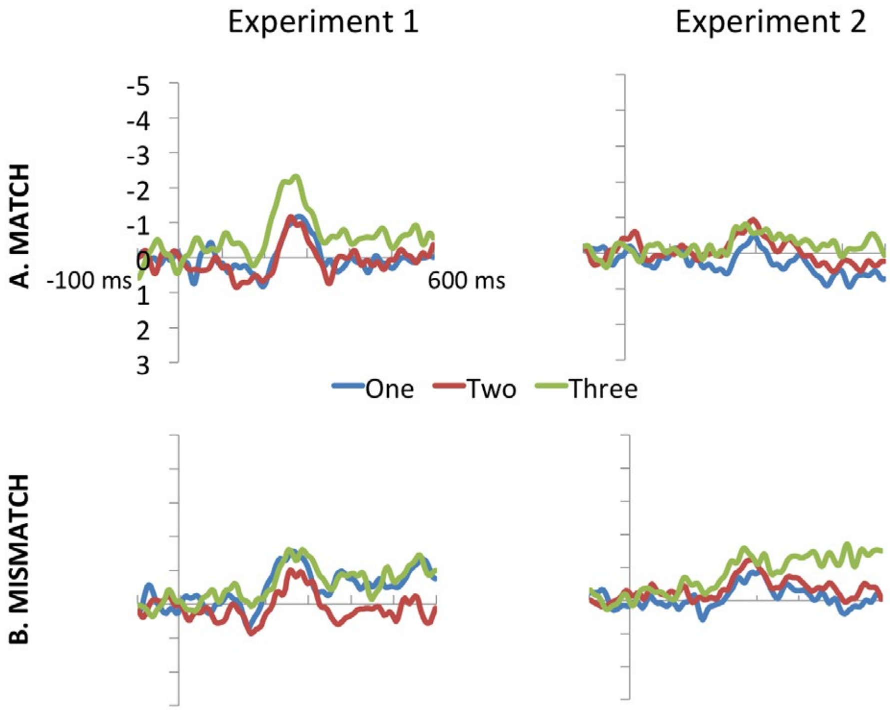

FIGURE 9 Grand-averaged difference waveforms obtained by subtracting ipsilateral from contralateral ERPs recorded at posterior sites PO7 and PO8

over cross-modal matching of numerosities. Specifically, we explored to what extent the explicit processing of the numerosity of auditory stimuli presented before a visual display influenced the visuospatial attentional mechanisms employed to enumerate and/or locate visual targets indexed by N2pc. In Experiment 1, participants were explicitly asked to process and compare the numerosity of both auditory and visual targets. In Experiment 2, they were instructed to report the presence/absence of any visual target in the visual display while ignoring the sounds. The results showed that the N2pc component increased as a function of the number of targets in Experiment 1, but not in Experiment 2. In Experiment 2, however, there was a modulation of the N2pc component as a function of the audio/visual numerical correspondence, such that N2pc amplitude was larger in mismatch trials relative to match trials. This suggests that, though task irrelevant, participants processed the quantity of both sounds and visual targets (Walsh, 2003) and detected the numerical correspondence of stimuli across modalities. In this perspective, the present results dovetail nicely with the account of Mazza and Caramazza (2011) that different mechanisms for object enumeration operate as a function of task demands. In addition, our findings point to a more precise definition of these top-down effects in cross-modal tasks. While exact enumeration was likely engaged in Experiment 1, the spontaneous recovery of some form of numerical representation must have taken place also in Experiment 2, despite the fact that the numerical information was task irrelevant.

Note that the detection of cross-modal numerical correspondence was evident in both experiments, yet at different stages of processing. In Experiment 1, when the instructions explicitly asked participants to indicate a cross-modal matching, the detection of numerical correspondence was evident in the ERP response at about 100–400 ms post-N2pc, whereas the congruency effect appeared at about the same time range of the N2pc component at around 150–200 ms in Experiment 2. The fact that the audio/visual correspondence effect in Experiment 2 arose prior to, or while, visuospatial attention was being allocated to visual targets might be taken as a further indication of the early processing of cross-modal numerical information (e.g., Egeth, Leonard, & Palomares, 2008; Olivers & Watson, 2008; Pinchamn & Szűcs, 2012; Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008, 2011), which likely operates involuntarily and independently of task demands.

The audio/visual correspondence effect observed in Experiment 1, on the other hand, may be indicative of the activation of higher order evaluation processes. In fact, latency, polarity, and scalp distribution of this effect resemble those typically observed in ERPs elicited during the evaluation of semantically inconsistent words embedded in sentences (Kutas & Federmeier, 2011) and arithmetically incorrect results in single-digit operations (Galfano, Mazza, Angrilli, & Umiltà, 2004; Galfano, Penolazzi, Vervaeck, Angrilli, & Umiltà, 2009; Niedeggen & Rösler, 1999; Niedeggen, Rösler, & Jost, 1999). These ERPs emerge when participants are presented, for instance, with a numerical problem (e.g., $3 \times 1 = ?$) and are then requested to detect whether a proposed result does match (e.g., 3) or not (e.g., 2) their numerical expectations (Avancini, Soltész, & Szűcs, 2015; Hsu & Szűcs, 2011; Szűcs & Csépe, 2005). It is thus plausible that similar mechanisms were elicited in our study when participants compared the numerosity of sounds (e.g., 3) with the incoming numerosity input (e.g., 2), giving rise to the “semantic like” numerical correspondence ERP effect peaking around 400 ms.

The nature of the cross-modal verification mechanism engaged in Experiment 1 was further qualified by the correlation analysis showing that, across participants, the greater the difference between mismatch and match trials in the N2pc time range, the larger the temporally trailing audio/visual correspondence effect. These results were additionally corroborated by the regression analysis showing that differences in the amplitude of the N2pc component were predictive of the subsequent audio/visual correspondence effect on the ERP response. Both the modulation of the N2pc component as a function of numerosity and the strong correlation between the N2pc and the subsequent audio/visual correspondence effect suggest altogether that the type of verification elicited in the explicit matching task involved a feed-forward process. After participants heard the sounds, visuospatial attention was deployed for targets' individuation. In doing so, crucially, the visual attentional system already conveyed information useful for predicting the final matching outcome, as hinted at by the results of the regression analysis. A conjectural hypothesis that follows from this pattern of results is that an early mechanism of cross-modal matching of numerosities, akin to the one observed in Experiment 2, was also active in Experiment 1, though perhaps subsiding to top-down control mechanisms that prevailed in the explicit task by postponing with the physiological response to audio/visual numerical correspondence.

An intriguing possibility to account for the different time course of the audio/visual numerical correspondence effects in Experiment 1 and 2 might reside in the different type of processing of the visual stimuli involved in the different tasks. In Experiment 2, numerosity was not task relevant, making it conceivable to hypothesize that subjects spontaneously processed generic spatial features of the set of elements (e.g., their global surface). In Experiment 1, the task assignment forced subjects to process the numerosity by going beyond it, and without limiting themselves to consider the extension of the area occupied by the contiguous targets. According to this view, the audio/visual correspondence effect in the two experiments might originate from two different sources. While the nature of the effect found in Experiment 1 might be caused by the match/mismatch between the semantic representation of numerosity of both acoustic and visual stimuli, the effect found in Experiment 2 might be driven by the match/mismatch between the perceptual features of auditory and visual stimuli or, in other words, their magnitudes. This hypothesis might explain the different time courses of the audio/visual correspondence effect on ERPs in the two experiments. We could speculate that in Experiment 1 visual features are ignored to facilitate numerical processing, consistent with recent theories regarding the cognitive basis of enumeration (Avancini et al., 2015; Semenza & Benavides-Varela, 2018).

The functioning of these mechanisms might be also affected by the number of elements whose quantity needs to be determined. Given that we focused on the enumeration of small quantities, it is presently premature to draw firm conclusions regarding the influence of auditory stimuli over visual-spatial attentional processes using greater numerosities (i.e., above the subitizing range). Based on previous N2pc studies using unimodal visual presentations (Mazza et al., 2013), we should expect a limited ability of the visuospatial system to simultaneously process a large subset of elements (above 3–4 items), yet this might not necessarily imply a limitation of cross-modal numerosity detection, which has been verified well above the subitizing range (e.g., for 4–18 objects) and even in very small infants (Izard et al., 2006). What seems clear from the present study is that both a rough and an exact cross-modal mechanism of quantity detection can operate within the subitizing range and that the selection of one or the other can be determined by task demands.

We cannot rule out the possibility that the early mechanism of cross-modal matching observed in Experiment 2 reflected an automatic evaluation of magnitudes rather than numerosities. Indeed, in our experiments, the time required to listen to the sounds increased as the number of sounds increased. Furthermore, the amount of area occupied by the target visual items increased as the number of relevant items increased. Although feasible, it must be noted that N2pc amplitude increments can hardly be functionally mapped onto increments of the area occupied by to-be-attended objects. Drew and Vogel (2008) tested this possibility by displaying sequentially a varying number of targets in successive frames, such that, across frames, the area occupied by the targets remained constant while the number of (summed) targets increased. The amplitude of N2pc and later components varied as a function of targets' number, not as a function of the visual area they occupied. We can think of no reason N2pc may have reacted to the spatial extent of the target area here, and not in the highly similar condition of Drew and Vogel (2008).

In the present experiments, we did not find any correlation between RTs and N2pc parameters. Such dissociations are common to cognitive ERP measures in general (Kutas & Federmeier, 2011), and to the N2pc in particular (e.g., Drew & Vogel, 2008; Kiss, Van Velzen, & Eimer, 2008; Robitaille & Jolicœur, 2006; Woodman & Luck, 2003), suggesting that the electrophysiological components reflect only a subset of the processes that contribute to RTs. ERPs are considered, in fact, informative specifically for this reason (Kutas & Federmeier, 2011).

The issue concerning the number-driven N2pc amplitude increase found in Experiment 1 vis-à-vis the constant N2pc amplitude found in Experiment 2 deserves a final comment. Although the present data do not allow us to put forth a parametrically supported model of the source of this effect, at least two classes of hypotheses can be entertained to provide an account encompassing previous findings as well as the present proposal related to N2pc different sensitivity to numerical processing. One class of hypotheses may explain the amplitude increase by appealing to the classical distinction between serial and parallel search scanning modes. Serial scanning would be engaged in tasks requiring explicit counting/enumeration, ensuing in a progressively greater N2pc amplitude as the number of to-be-scanned targets increases. Parallel scanning—perhaps associated with an expanded attention focus (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Jefferies & Di Lollo, 2009; Pashler, 1987)—would suffice to gather coarser information about targets' numerosity enabling spontaneous cross-modal matching. This class of hypotheses would incur in two problematic aspects described in prior work. One aspect is that serial scanning is more likely to bring about a progressive latency shift of N2pc owing to deploying serially a narrow focus of attention to close-to-contiguous targets in a visual search display (e.g., Woodman & Luck, 2003). A second aspect is that more than a single N2pc can be active in parallel when participants scan attentively multitarget arrays (Eimer & Grubert, 2014; see also Grubert, Fahrenfort, Olivers, & Eimer, 2017). This latter set of findings, however, raises a second, in our view more viable, explanation of the N2pc amplitude variations observed here and by Mazza and Caramazza (2011). Specifically, Eimer and Grubert (2014) showed that two lateralized targets displayed in the same visual hemifield tend to elicit an N2pc whose amplitude is double in size relative to either single N2pc elicited by two targets displayed in opposite visual hemifields. Perhaps, this is just what happens when exact targets' enumeration is task demanded: N2pc amplitude increases because each target elicits an N2pc at a specific spatial location when the targets, as in the present and Mazza and Caramazza's cases, are displayed in spatially distinct locations within the same visual hemifield. This would be instrumental in generating a high-resolution estimate of the number of targets to be passed on to response selection mechanisms. An attention focus zeroing in on every single target may not be necessary for simple target detection, where, however, a broader attention focus covering the area occupied by spatially contiguous targets may still be sufficient for the spontaneous encoding of rough estimates of the number of targets.

In conclusion, our findings show that the N2pc component captures the functioning of two different mechanisms of matching numerosities in audio/visual serial presentations, which are modulated by task demands: (a) A precise enumeration of the targets in the visual domain, which feeds forward information for a late congruency judgment; and (b) a spontaneous identification of cross-modal congruency possibly involving a shallow selection of the visual targets. While the first mechanism is activated when participants must explicitly evaluate numerical congruencies in both modalities, the second mechanism operates spontaneously and involuntarily.

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