Multiple Object Individuation and Exact Enumeration

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Abstract

■ Exact computation of numerosity requires the selective individuation of the elements to be enumerated so that each element is counted once and only once. Such a mechanism should operate not only when the elements to be enumerated are presented in isolation but also when they are presented in cluttered scenes. To uncover the electrophysiological correlates of the level of object representation necessary for exact enumeration, we examined ERP measures during the execution of a target enumeration task. A variable number (1–4) of lateralized targets were presented with or without distracters on the target side. An early nonlateralized response (N1, 120–180 msec) was modulated by target numerosity only when presented without distracters. By contrast, the amplitudes of a lateralized and later response (N2pc, 180–300 msec) increased as a function of target numerosity both with and without distracters, reaching a plateau at three targets. We propose that the stage of processing reflected in the N2pc corresponds to the component of individuation that binds specific indexes to properties and locations and that this provides the representation type necessary for exact enumeration. ■

INTRODUCTION

Sensitivity to the numerosities of the objects present in the environment seems to be a universal trait of humans, including infants (e.g., Feigenson, Dehaene, & Spelke, 2004), and animals of several species (e.g., monkeys, chicks, fish; Haun, Jordan, Vallortigara, & Clayton, 2010; Cantlon & Brannon, 2006; Nieder, 2005). Accordingly, it has been proposed that apprehension of numerosities represents a basic ability of the brain, like the ones that process color, size, space, or motion (Burr & Ross, 2008; Walsh, 2003; Dehaene, 1997).

Several theories of number processing have drawn a distinction between approximate and exact computation of the number of objects presented in the visual field (e.g., Piazza, 2010; Feigenson et al., 2004; Mandler & Shebo, 1982). This distinction captures the contrasting subjective experiences we have in sensing the approximate number of fruits piled up in a stand at the market versus the sense of selecting the several fruits we have chosen to buy. According to these theories, approximate and exact enumeration rely on distinct perceptual processes.

Approximate enumeration is achieved through a system that computes magnitudes in an analog way, as for any other sensory stimulus dimension (Piazza, 2010). Although it is not clear yet what physical factors govern this type of computation, previous research (e.g., Dehaene & Changeux, 1993) has suggested that approximate enumeration can be seen as resting on a relatively early perceptual mechanism that appraises at a glance the entire configuration of elements in a display by relying on their status of "spatially" separable entities but with imprecise and coarse featural encoding.

In contrast, exact computation of numerosity requires the selective marking of each individual element of the set to be enumerated to ensure that each element is counted once and only once. In exact enumeration, a distinction has been drawn between the way small (i.e., up to about three-four elements) and large numerosities are processed (e.g., Ansari, Lyons, van Eimeren, & Xu, 2007; Trick & Pylyshyn, 1993). The distinction is thought to reflect the special status of small numerosities that accrues to them in virtue of the cognitive system's ability to exploit a basic property of the visual perceptual system: the ability to individuate simultaneously three to four objects in a scene (Pylyshyn, 2001). Individuation is the ability to process each element of a set as possessing specific features and as being separated from other elements. Although its processing structure remains to be fully determined, individuation can result in a set of more robust representations of the isolated objects (for instance, as a consequence of feature binding; e.g., Kahneman, Treisman, & Gibbs, 1992), making them ready for further processing (and eventually leading to full object identification). As such, it seems to be the logical prerequisite for exact enumeration, as well as for the execution of other tasks that require multiple object processing, such as multiple object tracking and memory tasks. Early proposals argued that visual object individuation operates separately from attention (Trick & Pylyshyn, 1993) but recent research has suggested that simultaneous indexing of relevant items in a scene is tightly related to attention (Vetter, Butterworth, & Bahrami, 2011; Xu & Chun, 2009; Ansari et al., 2007; Cavanagh & Alvarez, 2005). Indeed, it is widely assumed that individuation is a

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key function of attention (for a discussion, see Cavanagh, 2011). Because simultaneous object individuation is limited to three to four items, exact enumeration of larger numerosities must rely on the repeated and successive application of the individuation mechanism over the array of objects to be enumerated.

The distinction we have just described does not imply that the mechanisms underlying approximate and exact enumeration are incompatible with one another. For instance, both mechanisms may be at work during visual enumeration of small numbers of objects, as recent results on humans and monkeys seem to suggest (Burr, Anobile, & Turi, 2011; Nieder & Miller, 2004). However, we hypothesize that the representations over which exact and approximate computation take place are different, being more detailed in the former case, and that only those formed during individuation are a key factor in exact enumeration of objects.

Crucially, the individuation mechanism should operate not only when the elements to be enumerated are presented in isolation but also when they are presented in cluttered scenes (i.e., together with distracting objects, see Trick & Pylyshyn, 1993). The functioning of this mechanism should in turn be reflected in a neural response pattern with the following characteristics. First, it should be affected by the number of the specific elements whose quantity needs to be determined (i.e., the targets) and, second, because of its limited ability to process simultaneously only a small subset of target individuals, it should reach a plateau at three to four elements. The profile of this neural pattern of response should be present both when the targets are presented in isolation and when they are presented together with irrelevant elements (distracters). For these reasons, in the present ERP study, we focus specifically on the exact enumeration of small quantities by manipulating the presence of distracters presented together with the to-be-enumerated targets. On the assumption that the perceptual component (and associated attention processes) that underlies exact enumeration is modulated by the number of relevant elements (with a limit in simultaneous processing at approximately three to four elements), we would expect an effect of target numerosity both when the target elements are shown in relative isolation and when they are presented with distracters.

Previous studies on enumeration in humans have not given a definitive answer to the questions raised here. Most studies typically presented the target elements in isolation (i.e., without distracters) or did not manipulate the presence/absence of distractors within a single experiment (e.g., Trick & Pylyshyn, 1993). Furthermore, it has proven difficult to distinguish between the functioning of different perceptual subcomponents involved in computing object quantity on the basis of behavioral measures alone. Although fMRI studies have identified regions in frontal, parietal, and temporal cortical areas that seem to be associated with a neural distinction between exact and approximate enumeration (for reviews, see Hyde, 2011; Nieder & Dehaene, 2009), the brain circuitry involved in enumeration of targets among distracters has not been addressed. Here we adopted an ERP approach that, given its excellent temporal resolution, represents the best neuroimaging technique to isolate the effects taking place at different stages of analysis in terms of their underlying temporal brain dynamics. In the context of the present research question, this approach is well suited to help uncover the crucial perceptual stage that forms the basis for exact enumeration.

In our study, we specifically focused on two components of the ERP signal, the N1 and the N2pc. Both these components have been traditionally examined in a wide range of tasks for the study of attentional functions. For instance, several results obtained with spatial cueing paradigms show enhanced amplitudes on the N1 (a negative component peaking at approximately 150 msec) for attended versus unattended elements, inviting the inference that this ERP component reflects the spatial distribution of attention in the visual field (e.g., Mangun, Hillyard, & Luck, 1993). The N2pc is a lateralized posterior response occurring after the N1 (with an onset latency of approximately 180 msec) that typically occurs in visual search paradigms, whenever a relevant object is presented in one hemifield together with distracters (Eimer, 1996; Luck & Hillyard, 1994). The N2pc has typically been interpreted as the neural correlate of attention selection in the visual field, either through distracter suppression (see Luck, Girelli, McDermott, & Ford, 1997) or through target enhancement (see Mazza, Turatto, & Caramazza, 2009; Eimer, 1996). Given that N1 and N2pc have been associated with attentional functions (albeit in the context of different experimental paradigms) and on the assumption that attention is intrinsically related to individuation, both these components are ideal candidates for testing the neural underpinnings of exact enumeration. Indeed, recent studies have started to investigate the role of these ERP components in tasks related to object numerosity processing.

Previous ERP studies on number-related tasks (Hyde & Spelke, 2009, 2012; Libertus, Woldorff, & Brannon, 2007; Nan, Knösche, & Luo, 2006) have found modulations in the N1 as a function of item numerosity. In particular, Hyde and Spelke (2009, 2012) found that the N1 increases in amplitude as a function of item numerosity up to three elements and proposed that it reflects multiple object individuation. However, in these (as well as in the previous) studies no explicit enumeration task was required; in addition, only one type of elements were always presented (with the exception of Nan et al., 2006), thus leaving unexplored whether or not the observed electrophysiological pattern is related to a specific target-related individuation mechanism or to a more general encoding of the overall amount of items presented.

By contrast, other recent studies on multiple targets presented among distracters (during multiple object tracking, see Drew & Vogel, 2008; or during exact enumeration, see Ester, Drew, Klee, Vogel, & Awh, 2012; Pagano & Mazza, 2012; Mazza & Caramazza, 2011) show that the amplitude of the N2pc is sensitive to target numerosity (when these are presented in one hemifield only), increasing up to approximately three to four elements.[1] However, given that distracters were always presented on the target side, it is not clear whether this response is directly involved in the individuation of target elements per se or whether it simply reflects the effort of separating the targets from distracters (for instance, by suppressing the irrelevant objects presented on the target side). The only exception is represented by Experiment 2 in the Ester et al. (2012) study, in which targets were presented without distracters in the target field. This study differs substantially from Ester et al. as follows. First, the specific aim of our study was to examine the neural correlates underlying the perceptual stage that is crucial for exact enumeration. Specifically, on the assumption that the perceptual component that underlies exact enumeration is modulated by the number of relevant elements (reaching a plateau at approximately three to four elements), we would expect an effect of target numerosity both when the target elements are shown in relative isolation and when they are presented with distracters. For this reason and differently from Ester et al. (2012), we focused on small target quantities and crucially manipulated the presence of distracters in the target field within a single experiment. In doing this, we were also trying to reconcile the apparently contrasting results and interpretations from our group (i.e., Pagano & Mazza, 2012; Mazza & Caramazza, 2011) with those from Hyde and Spelke (2009, 2012). For this reason, we additionally focused on the N1 component.

METHODS

Participants

Twelve volunteers (six women, aged 20–31 years) with normal or corrected vision participated in the experiment, after providing written informed consent. The study was approved by the University of Trento Ethics Committee.

Stimuli and Procedure

Equiluminant red and green diamonds (17 cd/m^2) were presented on a black background (1 cd/m^2). Each diamond (0.6° × 0.8°) had a 0.4° corner trimmed on the left or right side (Figure 1). On each trial, the display (duration = 150 msec) contained a variable number of diamonds, distributed to the left and right side of the fixation circle (0.2°); one, two, three, or four diamonds (targets) had a unique color (either red or green) relative to distracters. On multiple target trials, all targets were presented on the same side (either left or right). The color of the target(s) and of the distracters was counterbalanced across participants. The crucial manipulation concerned the presence of distracters in the target field. On no-distracter trials, no distracters were presented on the target(s) side. On distracter-present trials, distracters were always intermingled with targets on the target side. To avoid sensory imbalance, which would make it difficult to disentangle the interpretation of any lateralized neural effect as being related to the processing of relevant elements from an interpretation in terms of asymmetries in the sensory responses, we always presented an equal number of items in each hemifield. For the no-distracter condition, this resulted in a variable number of overall elements as a function of target numerosity (e.g., two elements—one target and one distracter in opposite hemifields—were presented in the one-target trials; see Figure 1). In the distracter condition, a fixed number of 16 elements, 8 in each hemifield, were presented. Given that in the no-distracter condition distracter numerosity was the same as target numerosity, participants could have relied on either distracters or targets to respond correctly. To discourage the adoption of such a strategy, we introduced catch trials, in which there was a mismatch between the number of distracters and the number of targets. Given the low proportion of these catch trials in the experiment, they were not included in the ERP analyses. Participants reported as fast as possible the number of targets presented on each trial by pressing one of four keys on a computer keyboard with the index or middle fingers of their both hands. Response assignment was counterbalanced across participants. Maximum time for responding was 1500 msec. The intertrial interval was 1500 msec. Participants performed 1 training block of

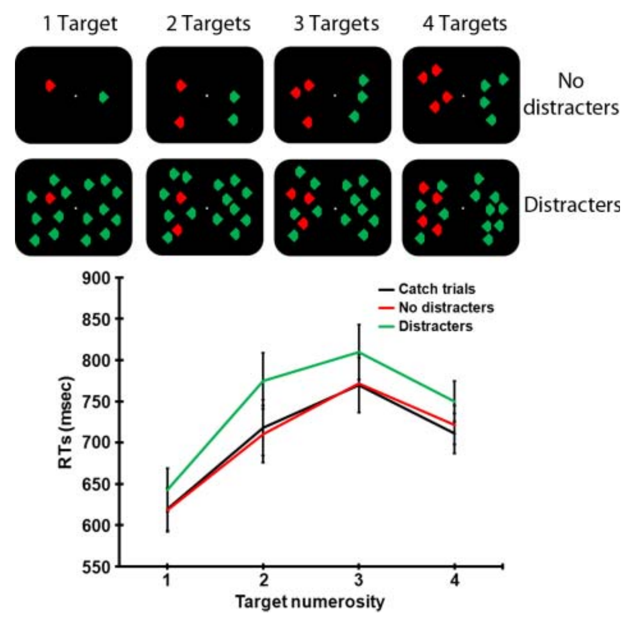

Figure 1. Top: Examples of stimulus displays with one, two, three, and four targets on both no-distracter (first row) and distracter (second row) trials. Bottom: Behavioral results indicate an increase in RTs as a function of target numerosity followed by an end effect in all three conditions (distracter, no-distracter, and catch trials).

40 trials and 10 experimental blocks with 144 trials per block (64 no-distracter trials; 64 distracter trials; 16 catch trials; an equal number of trials were delivered for each target numerosity).

EEG Recording and Data Analysis

EEG was recorded from 25 electrodes (including PO7, PO8, O1, and O2) and from a left earlobe electrode, with a right-earlobe reference, and then re-referenced off-line to the average of the left and right earlobe sites (bandpass filter = 0.01–40 Hz, A/D rate = 1000 Hz). Horizontal EOG was recorded from electrodes positioned on the outer canthi of both eyes. Impedance was kept below 6 kΩ for all electrodes. Trials with horizontal eye movements (horizontal EOG exceeding ±30 μV), eye blinks, and other artifacts (any electrode exceeding ±80 μV) were excluded.

Averages for correct responses were computed relative to the 100-msec interval preceding the display onset, separately for each condition and target side (left, right). Statistical analyses for the nonlateralized activation (N1, 120–180 msec; the time window was approximately centered around the N1 peak as visible from the grand-averaged waveform of all conditions) were conducted on mean amplitude and peak latency values at posterior electrode sites (PO7, PO8, O1, O2) collapsed across target side. The analysis of the mean amplitudes and peak latencies of the lateralized activity (N2pc, 180–300 msec; the time window was approximately centered around the N2pc peak of the grand-averaged waveform) was conducted on difference amplitudes, obtained by subtracting ERP waveforms at ipsilateral posterior electrodes (i.e., PO7 and O1 for left targets; PO8 and O2 for right targets) from those recorded at contralateral sites (i.e., PO8 and O2 for left targets; PO7 and O1 for right targets), collapsed across target side. These values (as well as behavioral data) were submitted to a repeated-measures ANOVA with Numerosity (one, two, three, four), Distracter Presence (distracter, no distracter, and catch trials—for behavioral data only) and ERP Component (N1, N2pc; for ERP data only) as factors. When appropriate, Greenhouse–Geisser corrections for sphericity violations were applied, and corrected p values are reported. Significant effects were further explored by means of contrast analysis.

RESULTS

Behavioral Performance

Two ANOVAs were conducted on RTs for correct responses between 200 and 1500 msec and on the percentage of correct responses.

Both ANOVAs on RTs and correct responses showed significant effects of Numerosity and Distracters, both Fs > 9.3, all ps < .001, whereas a significant interaction emerged for RTs only, $F(6, 66) = 5.6, p < .001$. Participants were overall faster and more accurate on no-distracter and catch trials, relative to distracter trials, all ps < .006, with no difference between catch and no-distracter trials (Figure 1). In all the conditions, Numerosity has the same quadratic pattern, all ps < .003, indicating that participants were increasingly slower and less accurate for numerosities up to three targets, whereas an end effect was visible for the largest target numerosity in the set (i.e., four elements).

ERP Results

ERP results point to two main modulations of electrophysiological activity. First, the early nonlateralized response (N1, 120–180 msec) was modulated by target numerosity but only when no distracters were presented on the target side (Figures 2 and 4). In contrast, the N2pc amplitudes (180–300 msec) increased as a function of target numerosities (up to three targets) in both conditions (Figures 3 and 4).

The two overall ANOVAs on mean amplitudes and peak latencies with Numerosity, Distracter, and ERP Components indicated a significant three-way interaction, both Fs > 8.6, both ps < .001. Therefore, we explored the effects of Numerosity and Distracter separately for each ERP response.

N1

The ANOVA on mean amplitudes indicated significant effects of Distracter, $F(1, 11) = 9.3, p = .01$, of Numerosity, $F(3, 33) = 14.2, p < .001$, and of their interaction, $F(3, 33) = 14.0, p < .001$. Separate ANOVAs showed no effect of Numerosity in the distracter condition, whereas a significant effect was found in the no-distracter condition, $F(3, 33) = 17.5, p < .001$, and with significant quadratic trend ($p < .005$), with increasing amplitudes as a function of numerosities up to three targets (i.e., six elements overall; see Figure 2).

The ANOVA on peak latencies showed the same significant effects, all Fs > 24.3, all ps < .001. Latencies were overall earlier in the distracter condition. No significant effect of numerosity emerged for the distracter condition, whereas this was significant, $F(3, 33) = 55.2, p < .001$, and with a significant quadratic trend ($p < .002$) in the no-distracter condition. The N1 occurred progressively earlier for increasing numerosities, reaching a plateau at three targets.[2]

N2pc

A different pattern emerged in the analysis of the N2pc data (Figures 3 and 4). As for the N1, there were significant effects of Distracter, $F(1, 11) = 52.7, p < .001$, of Numerosity, $F(3, 33) = 39.0, p < .001$, and of their interaction, $F(3, 33) = 6.7, p < .001$. Separate ANOVAs on both

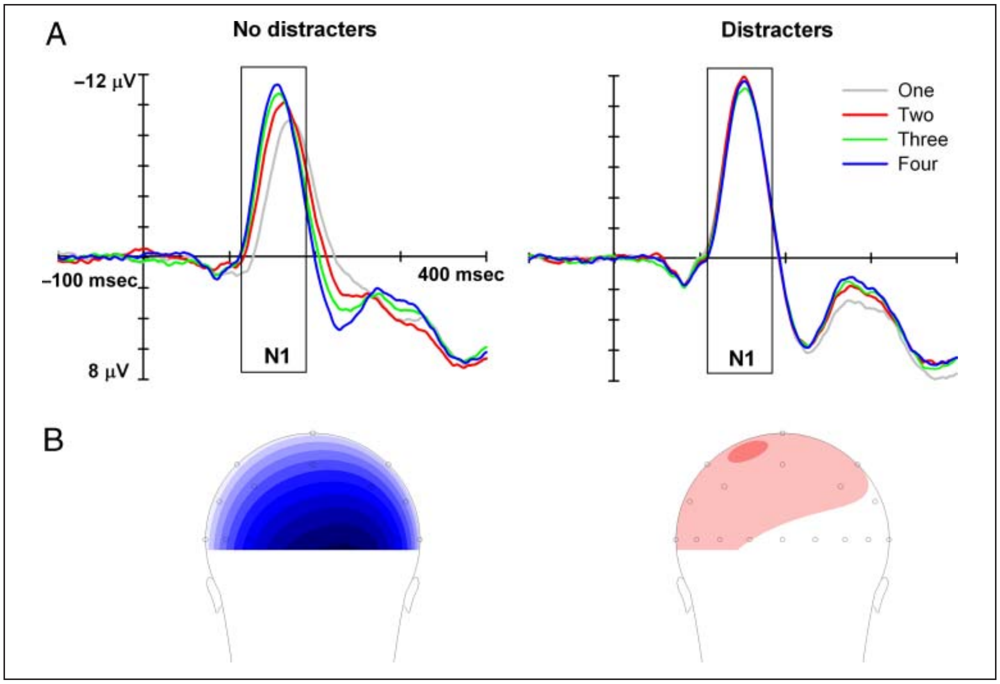

Figure 2. (A) N1 modulations. Grand-averaged nonlateralized ERP waveforms obtained in the 400 msec poststimulus interval at posterior electrode PO7/PO8 and O1/O2 in the no-distracter (left) and distracter (right) conditions. The N1 component was modulated in amplitude by target numerosity only on no-distracter trials. (B) Topographical ERP scalp distribution maps for the difference between four and one target of the N1 (150 msec) are shown for the no distracter and distracter conditions. The scale was optimized for each condition (No distracter: −7/+2 μV; Distracter: ±3 μV). Negative values are depicted in blue; positive values in red (white = zero).

distracter and no-distracter conditions showed a significant effect of Numerosity (both Fs > 5.4, both ps < .005), both with a significant quadratic trend ($p < .025$). The N2pc amplitudes increased as a function of target numerosities in both conditions, reaching an asymptote at three targets (see Figure 3).[3]

The ANOVA on the N2pc peak latencies revealed significant effects of Distracter, $F(1, 11) = 25.4$, $p < .001$, of Numerosity, $F(3, 33) = 7.6$, $p < .001$, and of their interaction, $F(3, 33) = 7.9$, $p < .001$. Separate ANOVAs revealed no significant effect of Numerosity in the distracter condition, whereas this was significant in the no-distracter condition, $F(3, 33) = 8.8$, $p < .001$, with later latencies for larger numerosities, as indicated by a significant linear trend ($p < .004$). Notably, this pattern was in the opposite direction compared with the N1 component, which showed earlier latencies for larger numerosities.

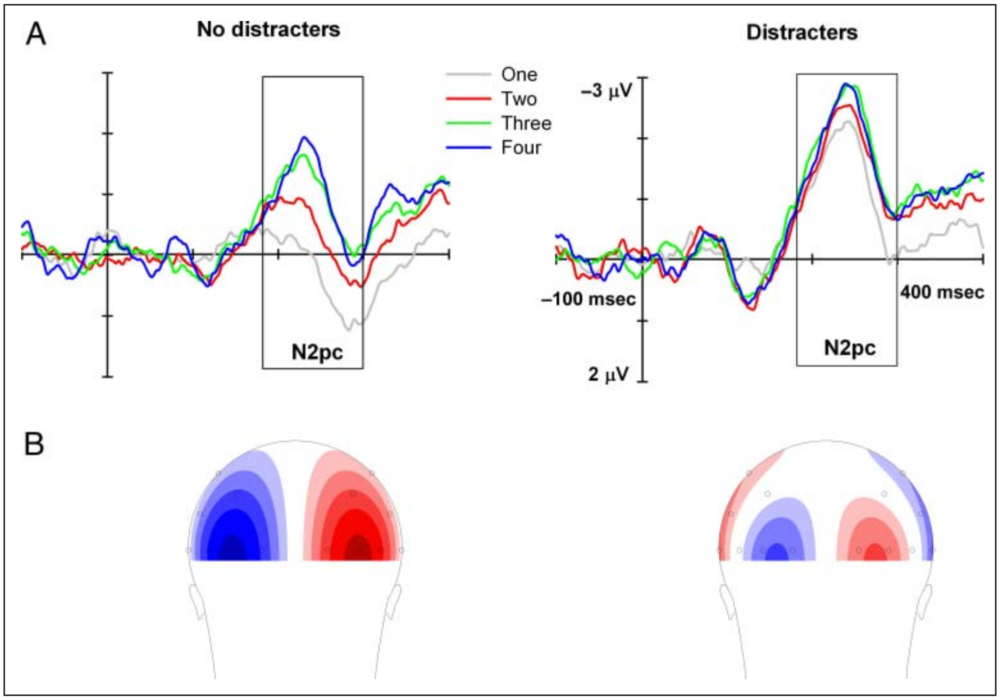

Figure 3. (A) N2pc modulations. The grand-averaged lateralized ERP difference waveforms, obtained by subtracting the ipsilateral activations from contralateral activations at posterior sites PO7 (and O1) and PO8 (and O2), show a modulation of the N2pc amplitudes as a function of target numerosity for both no-distracter (left) and distracter (right) trials. (B) Topographical ERP scalp distribution maps of the N2pc (240 msec) are shown for the no distracter and distracter conditions for the difference between four and one target. The maps were obtained by computing the contralateral minus ipsilateral difference activity and mirrored across the midline. The scale was optimized for each condition (No distracter: ±3 μV; Distracter: ±1.5 μV).

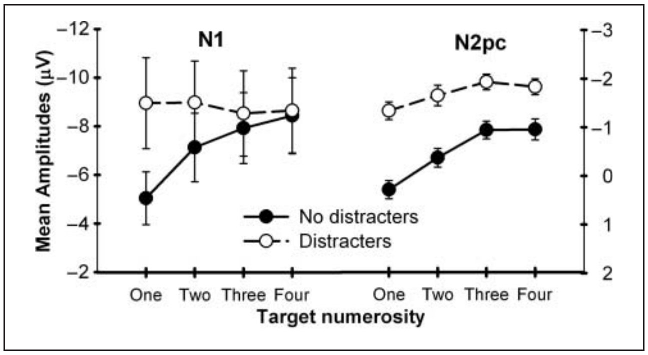

Figure 4. Mean amplitudes and standard errors of N1 (120–180 msec) and N2pc (180–300 msec) as a function of distracter presence and target numerosity.

Control Analysis

In our study, target numerosity was correlated with modulation in sensory parameters (such as luminance or area). Previous research (e.g., Johannes, Munte, Heinze, & Mangun, 1995) has shown that such modulation can have a direct effect on the N1, but it also has an effect on earlier components, such as the P1. Therefore, to assess whether the presence of sensory effects related to the increase in target numerosity, which should be maximally evident in the no-distracter condition, has a main and direct role in the generation of the effects visible in our ERP data, we conducted an additional ANOVA on the P1 mean amplitudes (60–100 msec poststimulus) with Numerosity and Distracter as factors. Neither the effect of Numerosity nor the interaction was significant, both *p*s > .78.

DISCUSSION

We used electrophysiological recordings during an exact enumeration task to address whether the specific computation of multiple relevant objects can be dissociated from mechanisms that may only be sensitive to the overall (target and distracter) quantity of objects in the visual field. The results suggest that this may in fact be the case.

Behavioral data showed an overall increase of RTs for the distracter condition, suggesting that distracters interfere with the process of individuating multiple targets for exact enumeration. Target numerosity led to the same pattern of results in all conditions (distracters, no distracters, catch trials), with larger RTs for larger target sets and an end effect for the largest numerosity. Importantly, the fact that no difference in RTs was visible between no-distracter and catch trials indicates that participants did not rely on specific strategies based on distracter numerosity to infer the correct answer.

ERP results indicated that target numerosity had similar effects on the N2pc both with and without distracters, providing novel information on the mechanism involved in computing exact object numerosity. Specifically, the N2pc amplitudes were modulated by target numerosity in both the target only and target plus distracter conditions. The fact that the N2pc modulation was visible even when no distracters were presented on the target side reasonably dismisses the possibility that this pattern is exclusively related to distracter suppression and, in line with very recent findings (Ester et al., 2012; Pagano & Mazza, 2012; Mazza & Caramazza, 2011), indicates that this electrophysiological response reflects the functioning of a processing stage that is tightly associated with the exact computation of the relevant quantities. In particular, we propose that it reflects the selective and simultaneous individuation of a subset of target elements in the visual field by means of a mechanism that binds featural properties and locations. This interpretation is substantiated by the lateralized nature of the N2pc (a proxy for location coding), by its asymptote at three targets (an index of capacity limit in simultaneous processing), and by the fact that it is found both when distracters are present and when they are absent (a proxy for selective individuation of the target elements). In line with this interpretation, the overall longer latencies observed in the N2pc for the distracter condition relative to the no-distracter condition indicate, as would be expected if this response, were sensitive to relevant rather than irrelevant numerosities, that extracting targets from a visual display may take longer when they are spatially intermingled with distracters.

In contrast, the N1 pattern was differentially modulated by target numerosity as a function of distracter presence. In line with previous findings (e.g., Hyde & Spelke, 2009, 2012), in the no-distracter condition the amplitude of the N1 was modulated by target numerosity, being progressively larger for the larger target sets up to a limit of three targets (six elements). N1 latencies in the no-distracter condition were also modulated by target numerosity, with progressively earlier latencies for the larger target sets. In the distracter condition, in which the total number of elements (always 16) was larger than in the no distracter condition, the N1 was overall larger and earlier. However, no differences in the N1 emerged among the target numerosities.

It is important to note that in our experiment (as well as in previous studies, e.g., Hyde & Spelke, 2009; Nan et al., 2006), the increase in item numerosity is confounded with increases in other continuous variables (e.g., total area and luminance). This leaves open the possibility that sensitivity to sensory properties, rather than to item numerosity per se, may account for the N1 pattern found for both conditions and especially for the no-distracter condition (see Gebuis & Reynvoet, 2012; Libertus et al., 2007, for such an account). For this reason and under the assumption that sensory properties should influence the earliest stages of stimulus processing, such as the one reflected by the P1 component (e.g., see Johannes et al., 1995, for the specific case of luminance), we conducted an additional analysis on this component. Unlike the N1 component, no numerosity-related effect was found for the P1 component. Therefore, it is difficult to explain the N1 pattern found in this study directly and exclusively in terms of sensory effects, although we acknowledge that future research will need to address this issue more deeply.

According to Hyde and Spelke (2012), the N1 numerosity modulation reflects "the distribution and maintenance of attention to particular locations in space evoked by particular items." Interestingly, they interpreted the occurrence of earlier N1 latencies for larger compared with smaller sets of elements by assuming that in the former case the group of elements is treated and selected as one item, whereas multiple items are selected in parallel for smaller numerosities. As a consequence, selection is slower in the case of multiple items (small numerosities) relative to the selection of the group of elements (large numerosities). Although the present results may be partially explained in these terms, they add novel information on the way numerosities are computed by indicating that these "locations" in space are selected with no reference to the relevance for the task at hand. In other terms, our findings indicate that, although the N1 may be sensitive, at least to some degree, to the number of elements presented in the visual field, it does not discriminate between relevant and irrelevant quantities. These results resonate with the idea that the N1 reflects the functioning of a perceptual mechanism that extracts the information of the overall amount of elements in a display by relying on their status of "spatially" separable entities but with imprecise and coarse featural encoding. The results also indicate that this mechanism alone does not provide sufficient information for exact enumeration.

The present results provide significant constraints on theories of numerosity representation and of multiple object processing in general.

First, given that the N2pc pattern shows the same inflection point in neural activation (at around three targets) as a function of target elements both with and without distracters and that this inflection point is not obtained because of a ceiling effect (as might otherwise be the case for the N1 component), we can infer that the representation generated by the neural structures underlying the N2pc contains the fine-grained information required for exact enumeration. This conclusion is in line with recent proposals (see Ester et al., 2012) arguing for a neural fixed-capacity model of enumeration, in which small target quantities are enumerated via a multiple object individuation mechanism. More generally, the present findings converge with previous studies (e.g., Drew & Vogel, 2008) in suggesting the existence of a perceptual mechanism that provides separate representations of a subset of the objects in the visual field that are then further elaborated and used for the execution of several tasks involving multiple objects, such as enumeration, multiple object tracking, and memory tasks. Importantly, our results provide evidence that only the representation generated at the stage of the N2pc is necessary for exact enumeration independently of whether target elements are presented alone or together with irrelevant objects.

Second, the N1 pattern found in our study suggests that the stage of processing reflected in this component does not distinguish between target versus nontarget quantities. On the basis of this result, we speculate that the representation captured in the neural structures generating N1 may provide the basic information required for approximate enumeration, as it reflects the overall number of items in the visual map. Whether this representation is exclusively related to numerosity or is the result of an interaction between numerosity and sensory cues (see Gebuis & Reynvoet, 2012) remains an open question. One could argue that, given that the maximum number of elements presented in our study was only 16 and that Hyde and Spelke (2009, 2012) did not find modulations for arrays larger than three (but see Libertus et al., 2007; Nan et al., 2006), our N1 data do not directly speak to the issue of approximate enumeration. However, because no target-related N1 modulations were found in the distracter condition, the modulations visible in the no-distracter condition cannot be directly related to the processing of the exact numerosities of the targets, but rather to a more approximate and relatively imprecise coding of quantities. Our results do not exclude the possibility that the representations formed at the N1 stage could be used for exact enumeration (as suggested by the object-individuation account of the N1 in Hyde & Spelke, 2009, 2012), but this would only be possible for the special case where the elements to be enumerated do not have to be distinguished from each other on the basis of some perceptual features (e.g., color). More generally, as hypothesized for the mechanism of individuation, these representations are not specifically related to enumeration/estimation tasks but are common to several tasks requiring multiple object processing. Indeed, the existence of early-level structural representations of the scene layout (proto-objects) can explain why, contrary to the sparse (fully) conscious representation indicated by phenomena like change blindness, we usually have the feeling of being able to see all the things out there (Rensink, 2004).

In conclusion, the results reported here show that the selection of multiple relevant elements can be dissociated from the processing of the general (target and distracter) quantity of objects in the visual field. Expanding upon previous interpretations (e.g., Ester et al., 2012; Pagano & Mazza, 2012; Mazza & Caramazza, 2011), we propose that the stage reflected in the N2pc may reflect the component of individuation that binds relevant properties and locations, as inferred from its lateralized nature and from its target numerosity-related modulations both with and without distracters. As a result of this operation, a more stable representation of the relevant objects becomes available, making them ready for further processing, including exact enumeration.

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Notes

1. Pagano and Mazza (2012) found an N2pc asymptote at five targets. However, in that study, we used a limited rather than a continuous range of numerosities, making it difficult to estimate the exact numerosity of the N2pc plateau. Moreover, the data in that study additionally suggested that, whereas good performers reached an N2pc asymptote at five elements, this asymptote was set at three elements for poor participants.

2. According to previous studies (e.g., Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998), a positive component occurring at approximately 200–250 msec (P2p) may correlate with approximate computation, being sensitive to the ratio difference between successive arrays. However, here we were interested in enumeration of items that are simultaneously presented. Moreover, the ANOVA on this component in our experiment showed a significant Distracter × Numerosity interaction, $F(3, 33) = 15.0$, $p < .001$, with the same pattern found for the N1. Therefore, similarly to the N1, the neural representations reflected by the P2p are not sufficient for exact enumeration.

3. One may wonder how the behavioral end effect is related to the ERP patterns found in the N2pc and N1. As far as the N2pc data are concerned, we have previously shown (Mazza & Caramazza, 2011, Experiment 1) that this component increases linearly for one to three targets both when an end effect was visible for three targets in the behavioral data and in the absence of an end effect (Experiment 3). Together with the results by Ester et al. (2012), showing a similar N2pc asymptote as in this study in the absence of an end effect, this renders a direct account of the N2pc target-related modulations in terms of a behavioral end effect unlikely to be successful. Similarly, if the behavioral end effect had affected the N1 component, we would have expected an effect on this component for both the distracter and no-distractor condition where behavioral end effects were obtained. However, this was not the case. Finally, to compare our results with those from previous studies (e.g., Hyde & Spelke, 2009), we additionally specifically tested for a significant linear trend only in the one to three numerosity range, thereby excluding behavioral end effects, for both the N1 and N2pc amplitudes. The results confirmed our main analyses showing the presence of a significant linear trend in the N2pc for both distracter and no distracter conditions (both ps $<$ .001) and a significant linear trend in the N1 for the no distracter condition only ($p < .001$). Thus, the behavioral end effects in exact enumeration tasks do not affect the numerosity-related ERP modulations considered here.

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