The Neural Mechanism Underlying Ordinal Numerosity Processing

Titia Gebuis and Bert Reynvoet

Abstract

■ Changes in the sensory properties of numerosity stimuli have a direct effect on the outcomes of nonsymbolic number tasks. This suggests a prominent role of sensory properties in numerosity processing. However, the current consensus holds that numerosity is processed independent of its sensory properties. To investigate the role of sensory cues in ordinal number processes, we manipulated both dimensions orthogonally. Participants passively viewed the stimuli while their brain activity was measured using EEG. The results revealed an interaction between numerosity and its sensory properties in the absence of main effects. Different neural responses were present for trials where numerosity and sensory cues changed in the same direction compared with trials where they changed in opposite directions. These results show that the sensory cues are expected to change in concert with numerosity and support the notion that the visual cues are taken into account when judging numerosity. ■

INTRODUCTION

The development of mathematical abilities starts with the understanding of numerosity and the relations between different numbers. Infants acquire understanding of these principles that underlie the number system via nonsymbolic number stimuli (e.g., sets of dots; Feigenson, Dehaene, & Spelke, 2004). At 6 months, infants can dissociate different sets of items, and at 9 months, they can differentiate between sequences of increasing and decreasing numerosity (Brannon, 2002; Xu & Spelke, 2000). This understanding of ordinal relations but also the ability to approximate and manipulate nonsymbolic number is called number sense (Dehaene, 1997). A large number of studies investigated the neural mechanisms that support our number sense whereas the sensory properties (e.g., diameter and surface) of the nonsymbolic number stimuli were controlled for (e.g., Hyde & Spelke, 2009; Libertus, Woldorff, & Brannon, 2007; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). This resulted in the current hypothesis stating that we are equipped with an approximate number system that extracts numerosity from the visual scene independent of its sensory properties (e.g., surface, convex hull). However, an increasing number of studies show that the sensory properties of numerosity stimuli influence our ability to estimate or compare different sets of items (e.g., Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2012; Gebuis & Reynvoet, 2012b; Mix, Huttenlocher, & Levine, 2002) and that the sensory controls often do not suffice (Gebuis & Reynvoet, 2011, 2012a, 2013). These findings render the theory of the approximate number system incomplete.

The contribution of sensory properties in numerosity processing is clearly visible in behavioral studies. A set of items is estimated more or less numerously, depending on its different visual properties (e.g., Gebuis & Reynvoet, 2012c; Sophian & Chu, 2008; Miller & Baker, 1968). Similarly, across age groups performance on numerosity comparison or numerosity judgment tasks significantly differs between the trials where the larger numerosity consists of larger sensory cues than the trials where the larger numerosity consists of smaller sensory cues (e.g., Gebuis & Van der Smagt, 2011; Soltesz, Szucs, & Szucs, 2010; Rousselle & Noel, 2008; Rousselle, Palmers, & Noel, 2004). This difference in performance suggests an inability to reconcile inconsistent changes between numerosity and its sensory properties throughout the experiment (e.g., numerosity increases but the sensory properties decrease) and sometimes results in the removal of 30% or more of the participants (Gilmore, Attridge, & Inglis, 2011; Inglis, Attridge, Batchelor, & Gilmore, 2011). Although adults (Gilmore et al., 2011) and children above 8 years old (Inglis et al., 2011) have the necessary knowledge of ordinal relations to solve tasks on the basis of numerosity, they continue to respond based on sensory cues instead. The only plausible explanation for this unexpected behavior is that they were unable to judge numerosity because of the visual cues that changed inconsistently with numerosity across trials. Given the age of the children and adults as well as their knowledge about elementary mathematics (see mathematical tests administered in both studies), the ability to judge numerosity seems unrelated to basic number knowledge but instead resides in the interaction

University of Leuven

Journal of Cognitive Neuroscience 26:5, pp. 1013–1020
doi:10.1162/jocn_a_00541

between the continuous visual properties present in the stimuli and numerosity itself.

Similar conclusions could be drawn from an infant habituation study (Suanda, Tompson, & Brannon, 2008). Suanda et al. (2008) presented infants with stimuli that increased in numerosity while the size of the individual items remained constant. In this case, the infants could dissociate numerosity increasing trials from numerosity decreasing trials. However, when item size varied inconsistently with numerosity, the infants did not respond differently anymore to numerosity increasing and decreasing trials. These results implicate that infants have knowledge about ordinal relations but fail to respond to ordinal changes of numerosity when the continuous visual properties are manipulated inconsistently with numerosity. It appears that the infants expect numerosity and its sensory cues to change in concurrence. This is not surprising, as numerosity and its sensory cues always change together in everyday life (e.g., when more apples are added to a pile of apples, the size of the pile will increase but not decrease).

In the current study, we investigated this intricate relationship between numerosity and its continuous visual properties. To this end, we adapted the ordinality task employed by Suanda et al. (2008). We created sets of five numerosity stimuli of which the first four stimuli increased in numerosity and its visual properties. For the fifth image, these two variables were manipulated orthogonally (increase in both, decrease in both, increase in numerosity but a decrease in visual cues, and a decrease in numerosity but an increase in visual cues). Adult participants, naive to the subject under study, passively viewed the stimuli while their brain activity was measured using EEG. We used a passive viewing task to exclude a possible confound of decision or response processes (Van Opstal, Moors, Fias, & Verguts, 2008; Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Gobel, Johansen-Berg, Behrens, & Rushworth, 2004; Piazza et al., 2004) and to allow a direct comparison with the passive viewing studies of infants. Furthermore, this task allowed for the dissociation of the different viewpoints in numerical cognition. The role of sensory cues in numerosity processing is heavily debated in the numerical cognition literature. According to the approximate number system theory, numerosity should be processed independent of its sensory cues. Whether this is also the case for ordinal processes remains an open question. The passive viewing task employed in this study can dissociate the sensory from numerosity hypothesis based on differential responses in the brain. A difference in neural response between numerosity increase and decrease trials would indicate that ordinal processes occur independent of the continuous visual variables (e.g., Piazza et al., 2010; Halberda, Mazzocco, & Feigenson, 2008). In contrast, an interaction between numerosity and its continuous visual properties would indicate that ordinal processes do not occur independently of the visual properties. Such a result would support recent observations that changes in the sensory properties of numerosity stimuli directly influence numerosity perception (e.g., Gebuis & Reynvoet, 2012a, 2012b, 2013; Sophian & Chu, 2008).

METHODS

Participants

Twenty-four participants participated in the study. Of these, 22 were included in the experiment (aged 17–24 years). Two participants were excluded because they had more than 25% artifacts in the EEG data. All participants were native Dutch speakers and had normal or corrected-to-normal vision. Written informed consent was obtained according to the Declaration of Helsinki.

Apparatus, Stimuli, and Procedure

The stimuli were displayed on a 23-in. CRT monitor using Matlab 7.5 (MathWorks, Inc., Natick, MA). The viewing distance was approximately 57 cm. Stimuli were gray dots presented on a black background.

Each trial consisted of five dot arrays that were presented consecutively. Numerosity and visual cues (convex hull, aggregate surface, density, diameter, and contour length) increased in the first four dot arrays, whereas the visual cues of the fifth dot array increased in numerosity and visual cues (Condition 1), increased in numerosity but decreased in visual cues (Condition 2), decreased in numerosity and increased in visual cues (Condition 3), or decreased in numerosity and visual cues (Condition 4) with respect to the fourth dot array. Thus numerosity and visual cues were manipulated orthogonally for the fifth dot array (see Figure 1).

The fifth dot array was our stimulus of interest. We kept its visual and numerical properties constant across the four conditions. Consequently, differences in results cannot be attributed to differences in low-level sensory properties. To achieve this goal, Dot Arrays 1–4 had to differ across conditions in its numerical and visual properties. To keep numerosity constant for the fifth dot array, we used the following numerosity sequences: 6, 9, 14, 20, and 30 dots (Condition 1 and Condition 2) or 14, 20, 30, 46, and 30 dots (Condition 3 and Condition 4). In both cases, numerosity changed with a ratio of 1.5. To keep the visual cues constant for the fifth dot array, we used smaller dots for the first four dot arrays when visual cues had to increase (Condition 1 and Condition 3) and larger dots when visual cues had to decrease (Condition 2 and Condition 4; see Figure 1). Within each condition, we used the same range of dot sizes for the first four different dot arrays. Consequently, the average dot size was the same across the first four dot arrays, whereas aggregate surface, convex hull, and density increased with increasing numerosity. We chose this method because it resembles everyday situations. When for instance students enter a lecture

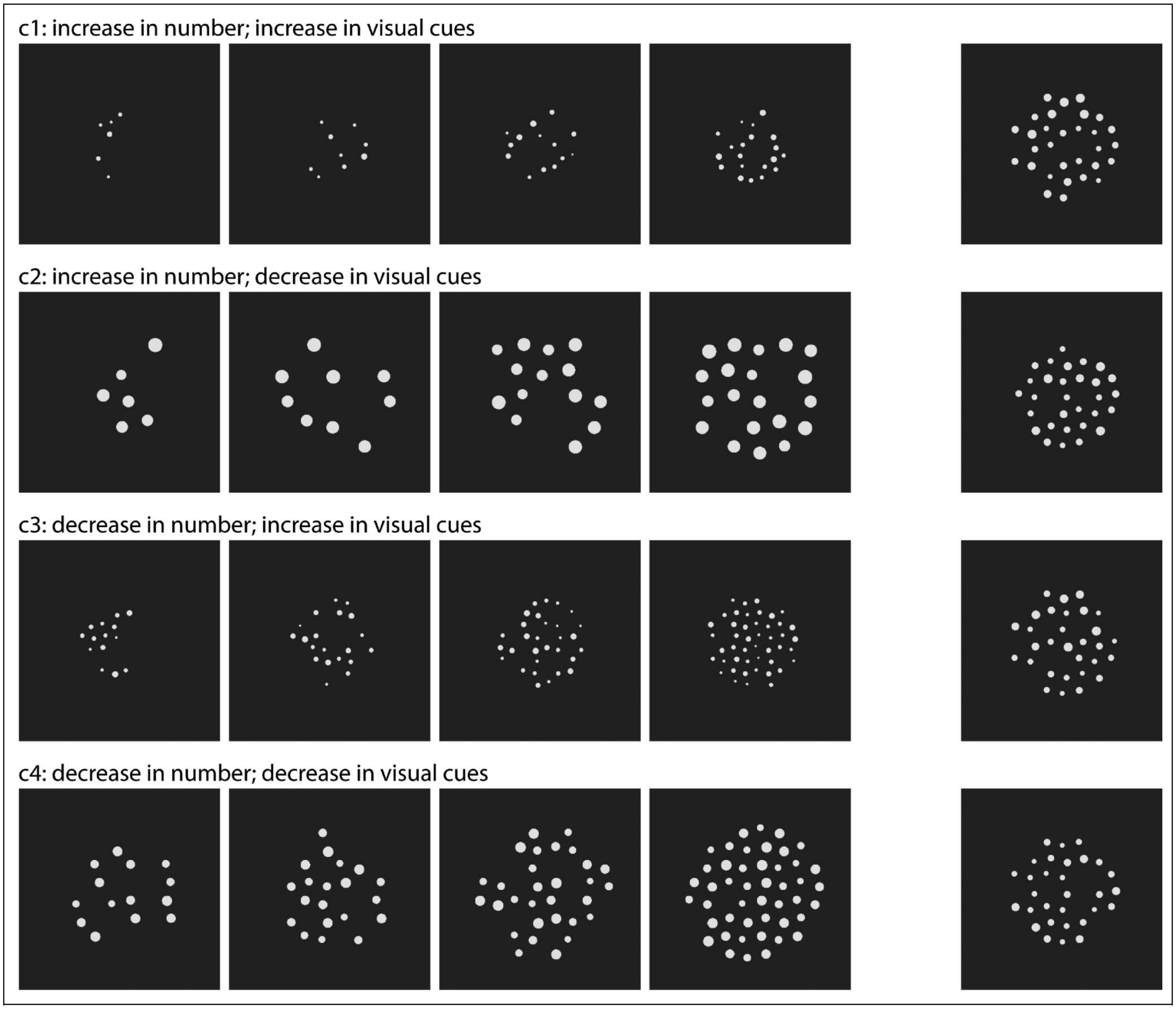

Figure 1. The four different conditions included in the ordinality task. In the different conditions, numerosity and its sensory properties increased with increasing number for the first four images. For the fifth image, numerosity and the sensory cues increased (c1), numerosity and the sensory cues decreased (c2), numerosity decreased but the sensory cues increased (c3), or numerosity increased while the sensory cues decreased (c4).

room, the aggregate surface, the density, and the convex hull (of the students) increase while, at the same time, the average size of the students remains relatively constant (but differences in size exist between students).

The numerosity increase conditions consisted of smaller numerosities than the numerosity decrease conditions (6–20 vs. 14–46). To prevent participants from noticing this manipulation, we included filler trials. In these filler trials, the numerosity increase conditions consisted of larger numerosities (14, 20, 30, 46, 68) than the numerosity decrease conditions (6, 9, 14, 20, 14). The visual cues of these sequences were manipulated in a similar manner as the experimental trials to create the same orthogonal design. These filler trials were not included in the analyses, as the fifth dot array was not controlled in numerosity and visual cue size.

In total, the experiment consisted of 240 trials (1200 dot arrays), of which 160 trials were experimental trials (40 trials per condition) and 80 were filler trials. Each trial started with a fixation cross for 500 msec; next the five dot arrays were presented consecutively (each dot array for 500 msec with an ISI of 500 msec). In between trials, a random interval between 1250 and 1500 msec was used. The trials were presented fully randomized. The participants were not informed about the numerosity or visual manipulation and were instructed to passively view the stimuli. To keep attention directed toward the screen, participants had to press the space bar whenever a stimulus consisting of green instead of gray dots appeared. To keep the maximum numerosity of experimental trials in the analyses, only filler trials could consist of green dots (approximately 10% of the filler trials).

Electrophysiological Recordings and Preprocessing

The EEG was recorded from 64 scalp electrodes according to the International 10/20 EEG system (sampling rate of 2048 Hz) using the Active Two system (BioSemi, Amsterdam, The Netherlands) relative to the common mode sense (CMS). The vertical EOG was recorded from electrodes attached above and below the left eye and the horizontal EOG from the outer canthi of both eyes.

EEG and EOG data were analyzed using EEGlab. The data were down-sampled to 250 Hz. EEG signals were filtered using a low-pass filter of 40 Hz and corrected for

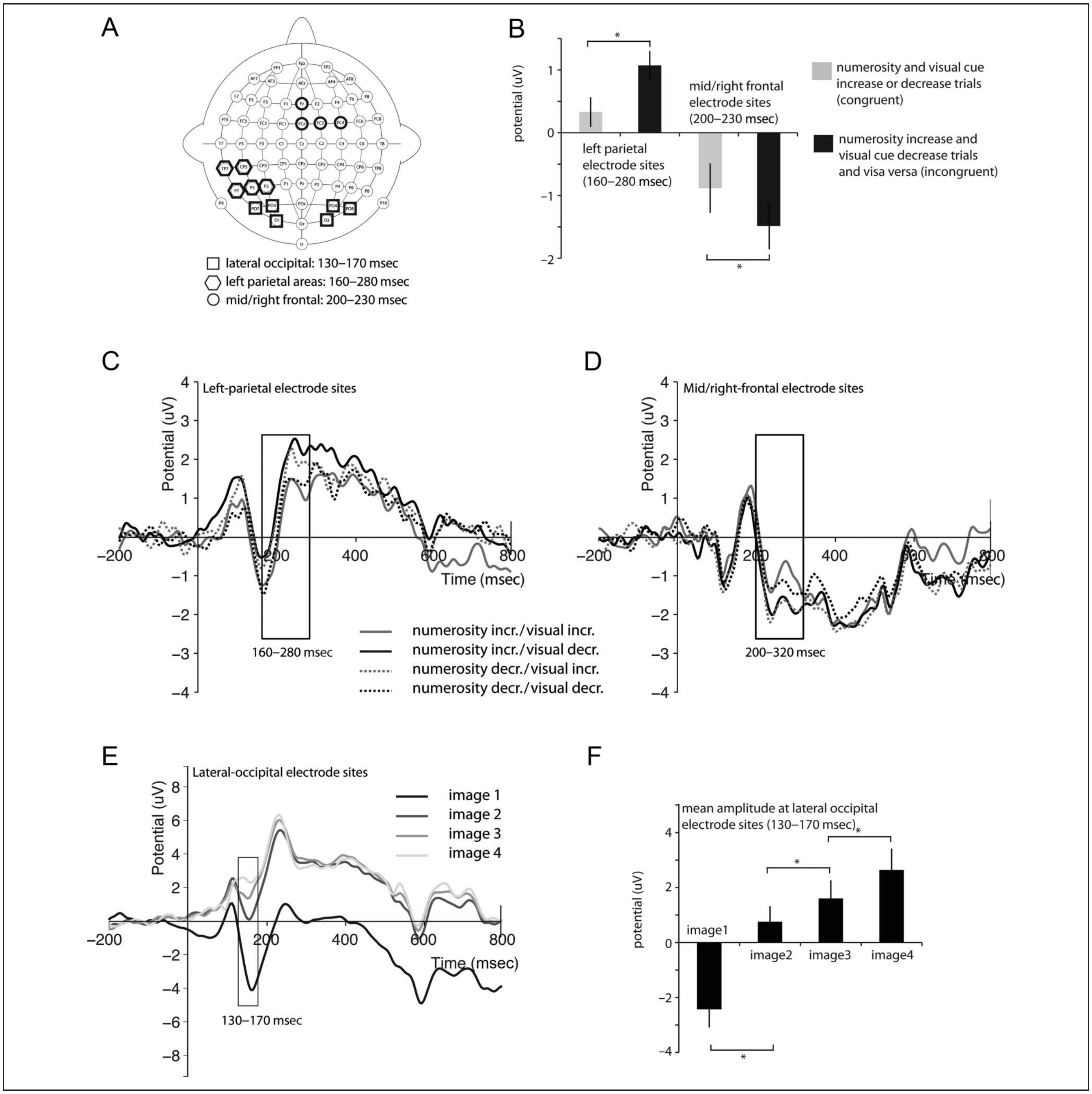

Figure 2. The ERP components involved in ordinal numerosity processing. The electrode sites reflecting the early sensory effects and the interaction (A). At the left parietal and mid/right frontal electrode sites, an interaction was observed between the sensory and the numerosity conditions. These results revealed a difference between the conditions where both the sensory properties and numerosity increased and the conditions where one of the two increased while the other decreased (B, C, and D). The neural responses to the sensory properties of the first four dot arrays show a more positive amplitude when the size of the sensory properties increases (E and F). Only a tentative explanation can be given about the large difference between the first dot array and the second to fourth dot arrays. The second to fourth dot arrays, in contrast to the first dot array, are preceded by another dot array. Fast presentation of one dot array after the other is likely to affect the data in a different manner than a dot array presented after a relatively long period of a black screen (i.e., the interstimulus interval).

eye movements using independent component analyses. The EEG was segmented into epochs from 200 msec before 800 msec after the presentation of the fifth dot array. The 200 msec prestimulus interval was used for the baseline correction. Trials with artifacts (amplitudes larger than ±100 μV), trials during which a response was given, and the "filler trials" were rejected from further analyses. Noisy electrodes were excluded from the analyses. A noisy electrode was defined as a single electrode that resulted in the rejection of more than 25% of all epochs recorded. Bad electrodes were interpolated using spherical splines. Two participants were not included in the analyses because more than 25% of the trials contained artifacts. For each of the four conditions, average ERPs per participant were derived.

To identify the electrodes and time windows of interest, a 2 (Numerosity: increase, decrease) × 2 (Visual Cue: increase, decrease) ANOVA was conducted for each data point between 0 and 600 msec after stimulus presentation. A conservative measure was used to identify electrodes and time windows showing significant results: $\alpha = 0.025$ and at least seven consecutive data points have to be significant in four neighboring electrodes (see for a similar approach Szucs & Soltesz, 2008; Szucs, Soltesz, Jarmi, & Csepe, 2007). Seven time points corresponds to a time window of 28 msec.

RESULTS

The point-by-point analyses revealed no main effects that met our criteria (at least seven significant consecutive data points at four neighboring electrodes when α is 0.025). A significant interaction between Numerosity and Visual Cues was present at left parietal electrode sides (TP7, CP5, P7, P5, P3; 160–280 msec) and at mid/right frontal electrodes sites (Fz, FCz, FC2, FC4; 200–320 msec; see Figure 2A). We created averages for the two electrode clusters obtained. Next, for the left parietal and right frontal area separately, the average amplitude of the time windows obtained in the point-by-point analyses were subjected to a 2 Numerosity (increase, decrease) × 2 Visual Cue (increase, decrease) repeated-measures ANOVA.

The left parietal area did not reveal a significant main effect for Numerosity, $F(1, 21) = 0.15$, $p = .69$, $\eta_p^2 = 0.007$, or Visual Cue, $F(1, 21) = 0.85$, $p = .37$, $\eta_p^2 = 0.04$, but the interaction between Numerosity and Visual Cues reached significance, $F(1, 21) = 18.06$, $p < .001$, $\eta_p^2 = 0.46$. More positive amplitudes were present for Conditions 2 (1.19 μV) and 3 (0.8 μV) than Conditions 1 (0.13 μV) and 4 (0.33 μV; see Figure 2B and 2C). Thus, larger amplitudes were present when numerosity increased and visual cues decreased or the reverse compared with trials where both numerosity and visual cues increased or decreased. Indeed, paired samples t test showed a significant difference between the average of Conditions 2 and 3 and the average of Conditions 1 and 4, $t(21) = -4.25$, $p < .001$.

Similar results were present for the mid/right frontal area: No significant main effect was present for Numerosity, $F(1, 21) = 0.15$, $p = .7$, $\eta_p^2 = 0.007$, or Visual Cue, $F(1, 21) = 0.24$, $p = .63$, $\eta_p^2 = 0.011$, but the interaction between the two was significant, $F(1, 21) = 13.24$, $p = .002$, $\eta_p^2 < 0.39$. More negative amplitudes were present for Conditions 2 (−1.7 μV) and 3 (−1.67 μV) than Conditions 1 (−1.05 μV) and 4 (−1.13 μV; see Figure 2B and D). Post hoc t tests showed that incongruent trials significantly differed between Conditions 2 and 3 versus Conditions 1 and 4, $t(21) = 3.64$, $p < .002$. Together, these results show different neural responses to violations of the relationship between visual cues and numerosity.

These results suggest that numerosity is not processed independent of its sensory cues. Instead, they support the idea that different sensory cues form the basis of our numerosity percept and influence our estimate of numerosity (e.g., estimating a relatively large number when the sensory cues are relatively large). However, according to this theory, the different sensory properties should be processed before the occurrence of the interaction. Previous studies showed that the N1 and P2 component at lateral occipital electrode sites are sensitive to the sensory properties of numerosity stimuli but not to numerosity itself (Gebuis & Reynvoet, 2012a, 2013). The visual properties of the fifth dot array were controlled and could therefore not give insight in the timing of visual processing of the stimulus. In contrast, the visual properties of the first to the fourth dot array were not controlled. Indeed, consistent with previous studies, the increase in visual properties for the first to the fourth dot array was visible in the EEG data at the lateral occipital electrode sites (O1, O2, PO3, PO4, PO7, PO8; see Figure 2A) around 130–170 msec. Paired samples t tests showed a significant difference between the first and second dot array, $t(21) = -6.1$, $p < .001$, between the second and third dot array, $t(21) = -3.4$, $p = .003$, and between the third and fourth dot array, $t(21) = -4.7$, $p < .001$ (see Figure 2E and F). Thus, the sensory processes at 130–170 msec preceded the interaction at 160–280 msec.

DISCUSSION

Infants, young children, and even adults show difficulties in judging numerosity when the sensory properties of the numerosity stimuli are manipulated inconsistently with numerosity (Gebuis & Van der Smagt, 2011; Suanda et al., 2008; Cantlon, Fink, Safford, & Brannon, 2007). To clarify the interaction between numerosity and its sensory properties, we conducted an EEG study where both were manipulated orthogonally. In our experiment, numerosity and its sensory properties increased in four consecutively presented dot arrays but changed for the fifth dot array. For this fifth dot array, both numerosity and its sensory properties increased or decreased, or one dimension increased while the other decreased.

The results revealed an interaction between the neural response for numerosity and its sensory properties in the absence of main effects. The absence of a main effect for numerosity and sensory cues in the presence of an interaction suggests that the participants did not blindly respond to the ordinal changes of sensory properties without making inferences about the numerosity they stand for and vice versa. For example, in the case of sensory properties, a single tiger is not estimated as more numerous than five mosquitoes just because the tiger is larger in size. Note that the absence of both main effects cannot be attributed to the size of the numerosity or sensory changes. Namely, the interaction between numerosity and its sensory properties indicates that both dimensions were manipulated above threshold.

This interaction between numerosity and its sensory properties shows different neural responses for trials where numerosity and sensory cues were manipulated in different directions (one dimension increased while the other decreased) compared with trials where both were manipulated in the same direction (both increased or decreased). These effects were visible at 160–280 msec at left parietal and at 200–230 msec at mid/right frontal electrode sites. Participants passively viewed the stimuli; therefore, differences in task difficulty, response, and decision processes cannot explain these effects. Furthermore, these results cannot be attributed to numerosity or sensory differences of the fifth dot array, as these were similar across conditions. This is also confirmed by the absence of an N1 or P2 amplitude effect at lateral occipital electrode sites. These ERP components process differences in low-level sensory properties of numerosity stimuli (Gebuis & Reynvoet, 2012a, 2013).

The fact that the sensory properties (e.g., contour, surface) of the fifth image were comparable between the different conditions does not allow investigating the timing of these low-level sensory properties of the stimuli. The sensory properties of the numerosity stimuli, however, did differ for the first four images but so did numerosity. Although the sensory cues were confounded with numerosity, previous studies showed that the N1 and P2 components are only sensitive to changes in low-level sensory cues and not numerosity (Gebuis & Reynvoet, 2012a, 2013; Turconi, Jemel, Rossion, & Seron, 2004; Handy & Mangun, 2000; Johannes, Munte, Heinze, & Mangun, 1995). In line with these previous studies, neural responses to low-level sensory processes were observed at the lateral occipital electrode sites. The processing of the visual properties of the numerosity stimuli occurred at 130–170 msec and thus preceded the interaction at 160–280 msec. This suggests that the numerosity judgments could be based on and influenced by the sensory properties. However, it should be noted that these results are only indirect evidence as sensory and numerosity could not be disentangled. Still, the idea that numerosity is not processed independent of its sensory properties has also been proposed in recent studies showing that the sensory properties of the dot arrays influence numerosity judgments (e.g., Harvey, Klein, Petridou, & Dumoulin, 2013; Dakin et al., 2012; Soltesz et al., 2010; Sophian & Chu, 2008; Ginsburg & Nicholls, 1988) and fits well with the notion that we integrate different sensory properties to judge numerosity (Gebuis & Reynvoet, 2012b).

The interaction between numerosity and its sensory cues reflects a violation of expectation. In infant habituation studies on numerosity processing, violation of expectation is considered a measure of numerosity processing (Suanda et al., 2008; Xu, Spelke, & Goddard, 2005; Brannon, Abbott, & Lutz, 2004; Brannon, 2002; Xu & Spelke, 2000). Infants respond differently to stimulus outcomes that are not in agreement with their expectations. Of course, this only occurs when the infant has knowledge about the topic under study. Without the necessary knowledge to solve the task, the infant would show the same response to trials where the outcome is correct and incorrect. Similar, in our study, the participant can only create expectations about the fifth image when the participant has knowledge about ordinal relations. Without having observed that sensory cues and numerosity increase across the first four images, no expectation can be created about the fifth image. Thus, the currently observed interaction is the result of a violation of the expectation that numerosity and its sensory cues should increase or decrease together in the fifth image.

For this reason, it can also be excluded that our results merely reflect a congruency effect (i.e., Conditions 1 and 4 being congruent and Conditions 2 and 3 being incongruent). Simply looking at the fifth image could not result in a congruency effect, as all these images were visually and numerically the same. Thus, a possible congruency effect could only occur when the fifth image is compared with the first four images. In this case, the fifth image of Condition 2 is incongruent for visual cues, and the fifth image of Condition 3 is incongruent for numerosity. If participants purely responded to the incongruence of either stimulus property, a similar or maybe even a stronger response can be expected for Condition 4 (here both number and visual cues are incongruent with respect to the preceding images). As this effect was not observed, an explanation on the basis of congruency appears incorrect. It should be noted that we do not claim that the ERP components showing the interaction reflect ordinal numerosity processes. These ERP components could also reflect more general cognitive abilities (e.g., attention). Nevertheless, they reflect the participant noticing that numerosity and its sensory cues do not change together in the same direction.

The understanding that the continuous visual properties can change inconsistently with numerosity is not yet present at infancy. Mix et al. (2002), for instance, showed that infants are prone to respond to a single sensory dimension when numerosity stimuli are presented, whereas Suanda et al. (2008) showed that infants fail to respond to ordinal relations in the absence of consistent sensory cues (but see for a different opinion Brannon et al., 2004; Xu & Spelke, 2000). Proficiency in judging numerosity when the sensory properties are inconsistently manipulated increases with increasing age. Four-year-olds perform below chance level (Soltesz et al., 2010), but a gradual increase in performance is visible in children from 5 years and older (Soltesz et al., 2010; Gebuis, Herfs, Kenemans, de Haan, & van der Smagt, 2009). Nevertheless, the ability to integrate the different sensory properties to judge numerosity remains visible in adults especially for the smaller ratio conditions (Gebuis & Van der Smagt, 2011). It is obvious that older children and adults do not lack the necessary number knowledge to solve the numerical tasks. It can therefore be questioned whether the numerosity tasks reflect our numerical abilities or just our ability to suppress or account for conflicting visual and numerical cues.

Together, our results give insight in the relationship between numerosity and its sensory properties. When visual processing of the stimuli finished, an interaction between numerosity and its sensory properties was visible. As visual processes preceded ordinal number processing, it appears likely that ordinal number processes are based on the integration of the different sensory properties that comprise the numerosity stimuli and are therefore influenced by the sensory properties.

Acknowledgments

This research was supported by the Marie Curie Intra European Fellowship (grant agreement no. 255140). We would like to thank Marleen Hinssen for her help with testing the participants and Caitlin Mullin for helpful comments.

Reprint requests should be sent to Titia Gebuis, Department of Experimental Psychology, KULeuven, Tiensestraat 102, 3000 Leuven, Belgium, or via e-mail: Titia.Gebuis@psy.kuleuven.be.

REFERENCES

Brannon, E. M. (2002). The development of ordinal numerical knowledge in infancy. *Cognition, 83,* 223–240.

Brannon, E. M., Abbott, S., & Lutz, D. J. (2004). Number bias for the discrimination of large visual sets in infancy. *Cognition, 93,* B59–B68.

Cantlon, J., Fink, R., Safford, K., & Brannon, E. M. (2007). Heterogeneity impairs numerical matching but not numerical ordering in preschool children. *Developmental Science, 10,* 431–440.

Cohen Kadosh, R., Cohen Kadosh, K., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-dependent and -independent representations of numbers in the parietal lobes. *Neuron, 53,* 307–314.

Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A., & Morgan, M. J. (2012). A common visual metric for approximate number and density. *Proceedings of the National Academy of Sciences, U.S.A., 108,* 19552–19557.

Dehaene, S. (1997). *The number sense: How the mind creates mathematics*. New York: Oxford University Press.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences, 8,* 307–314.

Gebuis, T., Herfs, I. K., Kenemans, J. L., de Haan, E. H., & van der Smagt, M. J. (2009). The development of automated access to symbolic and non-symbolic number knowledge in children: An ERP study. *European Journal of Neuroscience, 48,* 394–401.

Gebuis, T., & Reynvoet, B. (2011). Generating non-symbolic number stimuli. *Behavior Research Methods, 43,* 981–986.

Gebuis, T., & Reynvoet, B. (2012a). Continuous visual properties explain neural responses to nonsymbolic number. *Psychophysiology, 49,* 1649–1659.

Gebuis, T., & Reynvoet, B. (2012b). The interplay between nonsymbolic number and its continuous visual properties. *Journal of Experimental Psychology: General, 141,* 642–648.

Gebuis, T., & Reynvoet, B. (2012c). The role of visual information in numerosity estimation. *PLoS One, 7,* e37426.

Gebuis, T., & Reynvoet, B. (2013). The neural mechanisms underlying passive and active processing of numerosity. *Neuroimage, 70C,* 301–307.

Gebuis, T., & Van der Smagt, M. J. (2011). False approximations of the approximate number system? *PLoS One, 6,* e25405.

Gilmore, C., Attridge, N., & Inglis, M. (2011). Measuring the approximate number system. *Quarterly Journal of Experimental Psychology: (Colchester), 64,* 2099–2109.

Ginsburg, N., & Nicholls, A. (1988). Perceived numerosity as a function of item size. *Perceptual and Motor Skills, 67,* 656–658.

Gobel, S. M., Johansen-Berg, H., Behrens, T., & Rushworth, M. F. (2004). Response-selection-related parietal activation during number comparison. *Journal of Cognitive Neuroscience, 16,* 1536–1551.

Halberda, J., Mazzocco, M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature, 455,* 665–668.

Handy, T. C., & Mangun, G. R. (2000). Attention and spatial selection: Electrophysiological evidence for modulation by perceptual load. *Perception and Psychophysics, 62,* 175–186.

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex. *Science, 341,* 1123–1126.

Hyde, D. C., & Spelke, E. S. (2009). All numbers are not equal: An electrophysiological investigation of small and large number representations. *Journal of Cognitive Neuroscience, 21,* 1039–1053.

Inglis, M., Attridge, N., Batchelor, S., & Gilmore, C. (2011). Non-verbal number acuity correlates with symbolic mathematics achievement: But only in children. *Psychonomic Bulletin & Review, 18,* 1222–1229.

Johannes, S., Munte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Brain Research, Cognitive Brain Research, 2,* 189–205.

Libertus, M. E., Woldorff, M. G., & Brannon, E. M. (2007). Electrophysiological evidence for notation independence in numerical processing. *Behavioral and Brain Functions, 3,* 1.

Miller, A. L., & Baker, R. A. (1968). The effects of shape, size, heterogeneity, and instructional set on the judgment of visual number. *American Journal of Psychology, 81,* 83–91.

Mix, K. S., Huttenlocher, J., & Levine, S. C. (2002). Multiple cues for quantification in infancy: Is number one of them? *Psychological Bulletin, 128,* 278–294.

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., & Lucangeli, D. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition, 116,* 33–41.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron, 44,* 547–555.

Rousselle, L., & Noel, M. P. (2008). The development of automatic numerosity processing in preschoolers: Evidence

for numerosity-perceptual interference. *Developmental Psychology, 44,* 544–560.
Rousselle, L., Palmers, E., & Noel, M. P. (2004). Magnitude comparison in preschoolers: What counts? Influence of perceptual variables. *Journal of Experimental Child Psychology, 87,* 57–84.
Soltesz, F., Szucs, D., & Szucs, L. (2010). Relationships between magnitude representation, counting and memory in 4- to 7-year-old children: A developmental study. *Behavioral and Brain Functions, 6,* 13.
Sophian, C., & Chu, Y. (2008). How do people apprehend large numerosities? *Cognition, 107,* 460–478.
Suanda, S. H., Tompson, W., & Brannon, E. M. (2008). Changes in the ability to detect ordinal numerical relationships between 9 and 11 months of age. *Infancy, 13,* 308–337.
Szucs, D., & Soltesz, F. (2008). The interaction of task-relevant and task-irrelevant stimulus features in the number/size congruency paradigm: An ERP study. *Brain Research, 1190,* 143–158.
Szucs, D., Soltesz, F., Jarmi, E., & Csepe, V. (2007). The speed of magnitude processing and executive functions in controlled and automatic number comparison in children: An electro-encephalography study. *Behavioral and Brain Functions, 3,* 23.
Turconi, E., Jemel, B., Rossion, B., & Seron, X. (2004). Electrophysiological evidence for differential processing of numerical quantity and order in humans. *Brain Research, Cognitive Brain Research, 21,* 22–38.
Van Opstal, F., Moors, A., Fias, W., & Verguts, T. (2008). Off-line and online automatic number comparison. *Psychological Research, 72,* 347–352.
Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74,* B1–B11.
Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Developmental Science, 8,* 88–101.