Asymmetric Processing of Numerical and Nonnumerical Magnitudes in the Brain: An fMRI Study

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Abstract

■ It is well established that, when comparing nonsymbolic magnitudes (e.g., dot arrays), adults can use both numerical (i.e., the number of items) and nonnumerical (density, total surface areas, etc.) magnitudes. It is less clear which of these magnitudes is more salient or processed more automatically. In this fMRI study, we used a nonsymbolic comparison task to ask if different brain areas are responsible for the automatic processing of numerical and nonnumerical magnitudes, when participants were instructed to attend to either the numerical or the nonnumerical magnitudes of the same stimuli. An interaction of task (numerical vs. nonnumerical) and congruity (congruent vs. incongruent) was found in the right TPJ. Specifically, this brain region was more strongly activated during numerical processing when the nonnumerical magnitudes were negatively correlated with numerosity (incongruent trials). In contrast, such an interference effect was not evident during nonnumerical processing when the task-irrelevant numerical magnitude was incongruent. In view of the role of the right TPJ in the control of stimulus-driven attention, we argue that these data demonstrate that the processing of nonnumerical magnitudes is more automatic than that of numerical magnitudes and that, therefore, the influence of numerical and nonnumerical variables on each other is asymmetrical. ■

INTRODUCTION

The last time you visited the supermarket, you probably looked for the shortest line to the cashier. What guides our size estimation in such situations? The most common theories in the numerical cognition literature suggest that we rely on numerical magnitude, namely, the numerosity of items in a set—in our example, the number of people standing in line (for a review, see Piazza, 2010; Feigenson, Dehaene, & Spelke, 2004; Dehaene, 1997). According to these theories, we are born with a system (often referred to as the approximate number system; Piazza, 2010) that enables the detection, estimation, and manipulation of numerical magnitudes. This ability is considered to be the building block of our numerical abilities.

The theories mentioned above are based, at least in part, on studies that employed nonsymbolic numerosities (such as arrays of dots or collections of objects) as stimuli. Such stimuli are useful because they do not require any language or formal knowledge to be processed and can be used to study numerical skills in different cultures, preverbal babies, and animals (e.g., Pisa & Agrillo, 2008; Pica, Lemer, Izard, & Dehaene, 2004; Mix, Huttenlocher, & Levine, 2002). However, it is very difficult to measure numerosity processing in isolation (from hereon, we refer to this as numerical magnitude) when using visual displays of nonsymbolic numerical magnitudes; many nonnumerical visual properties are either correlated or anticorrelated with the numerical magnitude of groups of objects in space. These visual properties are continuous, noncountable dimensions such as density, total surface area, and so forth (hereafter, we will refer to all continuous properties as "nonnumerical magnitudes"). Therefore, it is also possible that, when you are deciding which line to join in the supermarket, you are using nonnumerical magnitudes or a combination of numerical and nonnumerical magnitudes (Leibovich & Henik, 2013; Henik, Leibovich, Naparstek, Diesendruck, & Rubinsten, 2012; Mix et al., 2002).

Indeed, there is evidence that both numerical (Cantlon, Libertus, et al., 2009; Nieder & Dehaene, 2009) and nonnumerical (e.g., Leibovich & Henik, 2013, 2014; Gebuis & Reynvoet, 2011; Mix et al., 2002; Clearfield & Mix, 1999) magnitudes are being processed automatically when comparing numerical magnitudes. That is, for example, when deciding which of two dot arrays is numerically larger, the task-irrelevant nonnumerical magnitudes (e.g., array, density) influence response times and accuracy although they are not relevant to the task. It is less clear, however, if both numerical and nonnumerical magnitudes are processed automatically to the same degree (i.e., symmetrical automatic processing) or if one magnitude dimension is more automatic (i.e., asymmetrical automatic processing). Understanding the relationship between processing numerical and nonnumerical magnitudes has the potential to elucidate the primitive substrate underlying magnitude processing. More specifically, the more automatic representation dictates, in a sense, which core system(s) will be

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more readily activated during numerical magnitude processing, how the magnitudes will be processed, and by which strategy the comparison task (and any conflicting dimensions inherent in the task) will be resolved. Put differently, the more automatic magnitude dimension (either numerical or nonnumerical) might also be the more basic representation on which a more sophisticated magnitude representation can be built.

Behavioral studies have approached the question of automaticity by varying the degree to which numerical and nonnumerical magnitudes are correlated with one another. For example, Hurewitz, Gelman, and Schnitzer (2006) had participants compare two dot arrays, where the total surface area of the dots was congruent (i.e., the array that contained more dots also contained more surface area) or incongruent (i.e., the array with more dots contained smaller surface area), with respect to the numerosity of the dots. Participants were asked to decide either which dot array contained more dots or which array had the greater surface area. Both tasks produced a congruity effect; incongruent trials were slower than congruent trials, suggesting that both numerical and nonnumerical magnitudes were processed automatically. The congruity effect in the numerical task, however, was larger, suggesting that nonnumerical magnitudes were processed more automatically than numerical magnitudes. In a similar design, Nys and Content (2012) reached the opposite conclusion; they found larger congruity in the nonnumerical task, suggesting that numerical magnitudes are processed more automatically.

Although the most common view in numerical cognition is that numerosities might be processed by a separate and dedicated system, this is not the only possibility. There are, in fact, theories suggesting that, because of the natural correlation between numerical and nonnumerical magnitudes, the processing of these magnitudes is holistic, that is, different weights are given to different visual properties when one needs to make a numerical estimation (Cantrell & Smith, 2013; Leibovich & Henik, 2013; Gebuis & Reynvoet, 2012b; Stoianov & Zorzi, 2012; Mix et al., 2002).

To date, there has been no exploration of the asymmetry in processing numerical and nonnumerical magnitudes at the level of the brain. Although behavioral congruity effects indicate whether the task-irrelevant dimension was processed automatically, they tell us little about the specific origins and mechanisms underlying the congruity effect as well as potential differences between them. Investigating congruity effects at the brain level, however, can reveal the mechanisms that give rise to them. For example, in the study by Cohen Kadosh et al. (2007), participants were asked to compare two symbolic numbers in terms of their physical (i.e., which number is physically larger?) and numerical (i.e., which number is numerically larger?) sizes. The behavioral results revealed that both physical size and numerical value were processed automatically and to the same extent (i.e., there was no interaction of task and congruity). At the brain level, however, an interaction of task and congruity revealed that the left frontal operculum exhibited a significant effect of congruity in the numerical but not in the physical comparison task. Thus, if different mechanisms underlie the resolution of conflict depending on whether numerical or nonnumerical magnitude is the relevant dimension, different brain regions or networks should exhibit an interaction of task and congruity on the brain level.

Against this background, we ask if different brain areas are responsible for the automatic processing of numerical and nonnumerical magnitudes when deliberately attending to either the numerical or the nonnumerical properties of the same stimuli. To pursue this aim, we used one set of nonsymbolic numerical magnitude stimuli (a pair of gray dot arrays) and directed participants' attention either to the number of dots in the display (i.e., numerical task) or to the total surface area of all the dots in the array (i.e., nonnumerical task). The numerical and nonnumerical magnitudes were congruent in half of the trials, such that the array containing more dots also had greater total surface area, density, average dot size, and so forth for all the nonnumerical magnitudes. In the other half of the trials, numerical magnitudes were incongruent with all the nonnumerical magnitudes.

As is evident from the review above, it is not yet clear if asymmetry between the dimensions exists. Accordingly, it is possible that only the main effect of congruity will be evident at the brain level, revealing stronger activity during incongruent relative to congruent trials in areas related to cognitive control (e.g., ACC, dorsolateral pFC). However, if asymmetry in the relative congruity effect of numerical and nonnumerical magnitudes exists, it would be evident in an interaction of task and congruity. Areas that have different activities in this interaction could be magnitude specific—parietal areas that are specific to numerical or nonnumerical magnitude processing (e.g., Chassy & Grodd, 2012; Castelli, Glaser, & Butterworth, 2006; Cohen Kadosh et al., 2005; Pinel, Piazza, Le Bihan, & Dehaene, 2004). In addition, given that any asymmetry in congruity effects will reflect different levels of automatic processing, one might predict that areas commonly associated with bottom–up and top–down visual attention could be differentially modulated by congruity in the numerical and nonnumerical comparison tasks (e.g., He, Zuo, Chen, & Humphreys, 2013; Hyde & Spelke, 2012; Holloway & Ansari, 2010).

METHODS

Participants

Thirty-two students from the University of Western Ontario, Canada, were recruited to participate in the experiment. The experimental procedures were approved by Western University's medical research ethics board. All participants were right-handed and monolingual native English speakers, with intact or corrected vision and no reported learning disabilities or attention deficits. Participants were compensated for their participation in the experiment with a monetary reimbursement ($25). Thirteen participants were excluded from the analysis due to either (a) excessive motion during scanning (more than 3-mm deviation from the first image collected and/or more than 1-mm deviation between one functional image to the next functional image—four participants), (b) misunderstanding of the task instructions (e.g., responding to the numerical and not the nonnumerical magnitudes or vice versa—one participant), or (c) low accuracy rates in one condition or more (less than 50% accuracy—eight participants). This was due to participants misunderstanding task instructions; after the first 2 days of running the experiment, we noticed that some of the participants did not understand the instructions correctly. For example, some participants thought that "more gray" referred to the shade of gray and not the total area of gray. Because there was no feedback or practice, we only found out about this at the end of the scan. As a result, with all the other participants, we verified that they understood the results by asking them to explain the task in their own words.

For the remaining 19 participants, 9 (six women) started with the numerical task, and 10 (six women) started with the nonnumerical task. The average age of the participants was 22 years and 9 months (*SD* = 6 years and 8 months). There were no significant age differences between the two groups ($t < 1$, *ns*).

Stimuli

Pairs of dot arrays (light gray dots on black background, separated by a vertical gray line) were presented in the middle of a 1024 × 768 pixel screen in an area of 300 × 175 pixels. The dot arrays were created with a Matlab code detailed in Gebuis and Reynvoet (2011). This code records five different nonnumerical magnitudes: average diameter (because dots differed in size, the average diameter of the dots in an array is computed), total surface area (the sum of surface area for the dots in each array), area extended (the smallest contour that included all of the dots, as if an elastic band was wrapped around the dots), density (area extended divided by total surface), and total circumference (the sum of the circumferences of all dots in an array). Each array contained 20, 30, or 40 dots. The numerical ratio was either 0.5 (20 vs. 40) or 0.67 (20 vs. 30). Examples of the stimuli can be seen in Figure 1.

Congruity Manipulation

Numerical magnitude was either congruent or incongruent with all five nonnumerical properties. In congruent stimuli, the array containing more numerous dots also had larger average dot size, total circumference, total surface area, density, and area extended, compared with the array containing less dots. In incongruent stimuli in the array containing more dots, all five nonnumerical properties were smaller compared with the array that contained the more numerous dots (see Figure 1).

Controlling for Nonnumerical Properties

The current set of stimuli contained numerical ratios of either 0.5 (e.g., 20 vs. 40 dots) or 0.67 (e.g., 20 vs. 30 dots). To check if the ratio between the five nonnumerical magnitudes was different in the two numerical ratios, we treated numerical ratios of 0.5 and 0.67 as two groups and performed two-tailed t tests for independent samples separately for each of the five nonnumerical magnitude ratios. The ratio between the nonnumerical magnitudes was calculated similarly to the ratio between the numerical magnitudes (e.g., if the total surface area of array "a" was 3000 pixels and of array "b" was 9000 pixels, the density ratio was 0.33). None of the t tests resulted in a significant difference between the groups (in all cases, $p > .1$), suggesting similar averages of nonnumerical magnitude ratio for numerical ratios of 0.5 and 0.67.

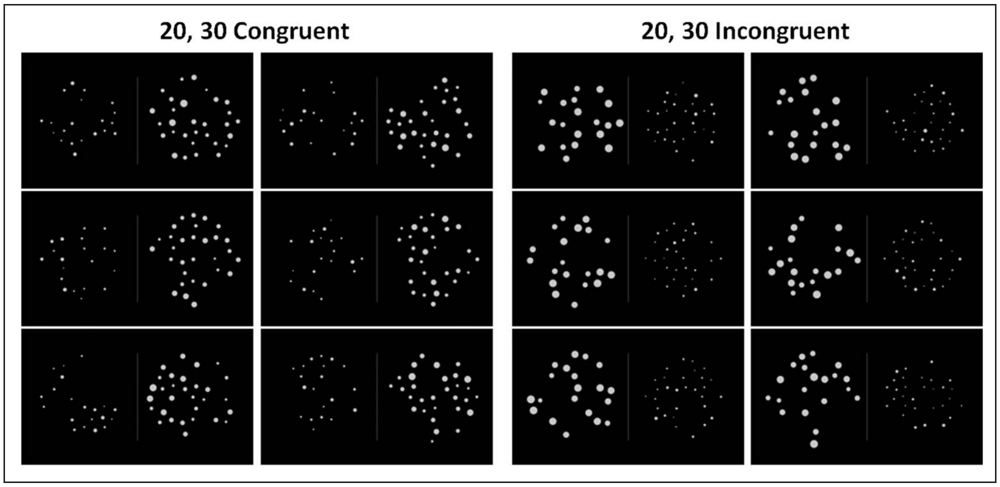

Figure 1. Example for congruent and incongruent trials.

Just like numerical ratio can affect performance (i.e., the larger the ratio, the more difficult it is to decide which array contains more dots—the ratio effect), so can the ratio between nonnumerical magnitudes. As indicated by Barth (2008), the ratio between the cumulative area in incongruent trials tends to be higher (i.e., the magnitudes are more similar and the ratio between them is closer to 1) than in congruent trials. In such cases, an alternative explanation to the RT differences between incongruent and congruent trials can be deduced, namely, that the ratio between total surface areas in incongruent trials was higher than in congruent trials and therefore significantly affected performance between congruent and incongruent trials. To avoid that confound in the current work, we kept the ratio between average nonnumerical magnitude in all our stimuli within a constant range. The average nonnumerical ratio was calculated by averaging the ratio of all five nonnumerical magnitudes for every pair of arrays. For example, for pair "x" where the ratio between the densities is 0.3, between the total surface areas is 0.5, between average dot sizes is 0.4, between total circumference is 0.6, and between the area occupied by the arrays is 0.5, the average nonnumerical ratio is 0.46. The range of average nonnumerical ratios for all our stimuli was between 0.37 and 0.45 (average = 0.42, *SD* = 0.04). This average range was the same for both congruent and incongruent stimuli.

Tasks

Participants performed two tasks in two separate runs. The order of the tasks was counterbalanced. The only difference between the two runs was the task instructions given at the beginning of each run. In the numerical task, participants were asked to choose the array containing more dots. In the nonnumerical task, participants were asked to choose the array containing more gray area. Each run contained 80 stimuli: 2 (congruity) × 4 (pairs) × 10 (different variations for each pair). The side of the larger dot array was counterbalanced. Each stimulus was repeated only once in each run. Thus, participants encountered the same stimuli twice: once in the numerical run and once in the nonnumerical run.

Procedure

Before starting the scan, participants signed a consent form and were given general instructions about the task. An event-related fMRI design was used to acquire functional imaging data. Each scan included an anatomical scan and two functional runs. Before each functional run, participants read instructions specific to the task. Each trial started with a black screen showing a vertical gray line in its center. In the middle of the gray line, a red fixation cross appeared. To achieve deconvolution of the BOLD response, a jitter interval between 4000 and 6000 msec (80 different intervals in total) was used before the fixation cross turned green (for 250 msec) to alert the participant that a dot stimulus was soon to appear, thereby allowing participants to get ready to respond. After the green fixation cross disappeared, a black screen with a vertical gray line was presented for 700 msec. Thereafter, two dot arrays were presented for 700 msec and finally replaced by a black screen with a gray vertical line for 1100 msec. Participants were able to respond to the stimulus from the time the dot arrays were displayed on the screen until a new trial with a red fixation cross started. The participants were instructed to respond with a button press with the hand corresponding to the side of the presentation of the array containing the larger area/numerosity. The procedure of the paradigm is depicted in Figure 2.

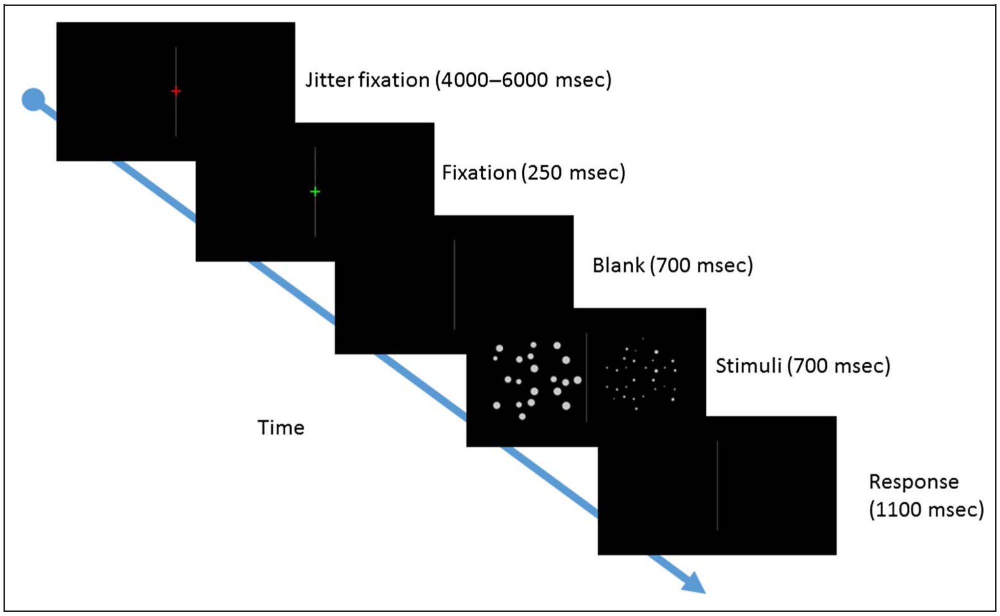

Figure 2. Procedure.

fMRI Data Acquisition

A 3-T Siemens (Berlin, Germany) Tim Trio whole-body MRI scanner was used to collect the functional and structural data of this study. The brain anatomy of each participant was collected with high-resolution T1-weighted images using a magnetization prepared rapid gradient echo sequence (1 mm^3, repetition time = 2300 msec, echo time = 4.25 msec, flip angle = 9°). An echo planar (EPI SE) sequence was used to measure BOLD brain signal of the functional run with a 32-channel Siemens head coil. The order of imaging acquisition was ascending—interleaved, covering the whole brain of participants. The acquisition resulted in 318 whole-brain images per functional run, with a total length of 10 min 30 sec per run. For each functional volume, 38 slices were collected, resulting in a 3-mm isovoxel resolution over a 64 × 64 voxel matrix. The repetition time was 2000 msec, the echo time was 52 msec, and the flip angle was 78°.

Imaging Analysis

Brain Voyager QX 2.4 (Brain Innovation, Maastricht, The Netherlands) was used to analyze the functional and structural data sets. Each individual data set was preprocessed according to the following steps: Functional imaging data were first corrected for slice scan time acquisition (ascending—interleaved, using a cubic-spline interpolation algorithm); a high-pass (general linear model—Fourier) frequency filter with a cutoff value of 2 sines/cosines cycles was applied to remove low-frequency signals; finally, a trilinear/sinc interpolation approach was used to remove and adjust head motion. To be included into the study, participants' movement parameters had to stay within 3 mm of overall movement (maximum deviation from the first volume) and within 1-mm volume-to-volume movement (maximum deviation from one collected functional image to the next collected functional image). Participants who were included in the study showed a maximum movement between 0.04 and 1.76 mm (mean = 0.37 mm, *SD* = 0.33 mm); volume-to-volume movement ranged from 0.006 to 0.31 mm (mean = 0.04 mm, *SD* = 0.042 mm).

An automatic alignment procedure (as implemented in Brain Voyager) was used to spatially align the functional runs of each participant onto the corresponding anatomical scan (gradient-based affine alignment). The quality of the alignment was checked visually, and the fine alignment was corrected manually if the automatic procedure did not reveal a sufficient alignment. Subsequently, the co-aligned images were transformed into Talairach space (Talairach & Tournoux, 1988). This was achieved in two consecutive steps: First, using the landmarks of the anterior commissure (AC) and the posterior commissure (PC), the anatomical image of each participant was transformed into AC–PC plane position; second, the boundaries of the brain tissue were manually selected and transformed into the Talairach grid using a trilinear interpolation algorithm (Talairach & Tournoux, 1988).

Individual data sets were entered into a general linear model for group-based analysis. All functional events of the two conditions (i.e., numerical and nonnumerical) were convolved with a two-gamma hemodynamic response function to predict the BOLD function (Friston, Josephs, Rees, & Turner, 1998). Congruent and incongruent trials across the two functional runs were modeled separately to investigate brain activation differences related to congruency. Incorrect responses were not included in the analysis. The statistical maps derived from brain activation contrasts were thresholded with an uncorrected p value of .005 and subsequently cluster corrected to correct for multiple comparisons and to adjust Type I error to a level of $p < .05$. This was achieved by an iterative "Monte Carlo Simulation" (1000 iterations), which estimates the minimum size of a functional cluster to be significant on the basis of functional data from this study (Forman et al., 1995).

RESULTS

Behavioral Analysis

Response-box data from one participant were not registered during the functional runs because of a technical malfunction. Hence, the results of 18 participants are reported. ANOVA with Task and Congruity as within-subject

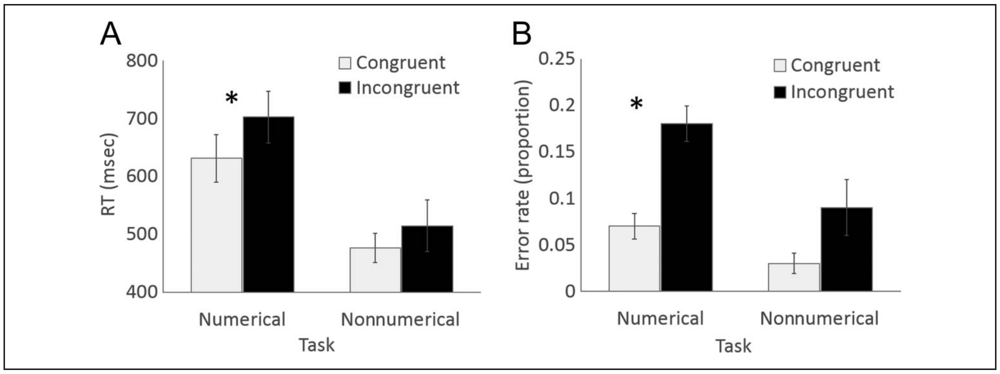

Figure 3. Behavioral results. (A) RT results. Although the congruity effect in the numerical task was significant, there was only a pattern of congruity effect in the nonnumerical task. (B) Accuracy results. For clarity, the results are reported as error rates but calculated using arcsin transformation of the proportion of accuracy. Here too, there is a significant congruity effect in the numerical task and a marginally significant congruity effect in the nonnumerical task. *$p < .05$.

variables and the order of task administration as between-subject variable was performed twice: once with RT and once with accuracy as dependent variables.

RTs below 150 msec and above 2000 msec were excluded from the analysis (less than 10% of the data). RT analysis revealed that performance in the nonnumerical task was faster than in the numerical task, $F(1, 16) = 36.45$, $p < .001$, $\eta^2_p = .69$. In addition, congruent trials were faster and more accurate than incongruent trials, $F(1, 16) = 8.08$, $p < .001$, $\eta^2_p = .33$ (see Figure 3A). The interaction between Task and Congruity was not significant ($F(1, 16) = 1.08$, $p = .31$, $\eta^2_p = .06$). Because of our specific question regarding possible asymmetry of the congruity effect, we performed separate analyses of the congruity effect for each task. These analyses revealed that response to congruent trials was significantly faster than that to incongruent trials, $F(1, 16) = 11.88$, $p < .05$, $\eta^2_p = .42$. In the numerical task, however, RT was only slightly faster for congruent trials than for incongruent trials, $F(1, 16) = 2.02$, $p = .17$, $\eta^2_p = .11$ (Figure 3A). There was no effect for Task order ($F < 1$, *ns*) and no interaction with Task and/or Congruity.

Because of the relatively high accuracy rates in the tasks (Table 1), accuracy data were transformed using arcsin, before performing a three-way ANOVA (as described for the RT data). This analysis revealed that accuracy was higher in the nonnumerical task than in the numerical task, $F(1, 16) = 40.05$, $p < .001$, $\eta^2_p = .71$, and that congruent trials were more accurate than incongruent trials, $F(1, 16) = 0.8$, $p = .38$, $\eta^2_p = .04$, for RT and accuracy, respectively. The interaction of Task and Congruity was not significant, $F < 1$, *ns*. Because of our question regarding asymmetry of the congruity effects in the two tasks, we tested the congruity effect for each task separately. Similar to the RT data, the congruity effect was significant in the numerical task. Namely, congruent trials were significantly more accurate than incongruent trials, $F(1, 16) = 20.8$, $p < .001$, $\eta^2_p = .56$. In the nonnumerical task, however, the congruity effect was marginally significant. Namely, congruent trials were only slightly more accurate than incongruent trials, $F(1, 16) = 3.58$, $p = .07$, $\eta^2_p = .18$. The results are depicted in Figure 3 and plotted as error rates to demonstrate that the same pattern of results occurred in both RT and accuracy data. Here too, there was no main effect of Order ($F < 1$, *ns*) and no interaction with Task and/or Congruity.

Table 1. Mean RT and Accuracy Rates

Task	*Congruity*	*RT (msec)*	*Accuracy (%)*
Nonnumerical	Congruent	476 (25)	97 (4.8)
Nonnumerical	Incongruent	514 (44)	91 (12.8)
Numerical	Congruent	631 (41)	93 (6.2)
Numerical	Incongruent	702 (44)	82 (8.2)

Standard deviations (*SD*s) are in parentheses.

fMRI Analysis

To investigate whether there was significant brain activation as a function of task administration order, we conducted a whole-brain between-group *t* test (numerical task first > nonnumerical task first). This analysis did not show any brain areas that were affected by task administration order at $p < .005$ (cluster corrected for multiple comparisons, $p = .05$). Therefore, all subsequent analyses were collapsed across groups.

Brain Activations Related to Congruency

To investigate the impact of congruency on brain activation, we performed a whole-brain *t* test statistic pitting the brain signal related to the incongruent condition against the brain signal associated with the congruent condition across both tasks (i.e., combined for the numerical and nonnumerical tasks). The results of this analysis (see Table 2 for all contrasts) revealed two regions—left posterior cingulate gyrus and left precentral gyrus—that were more strongly activated in the incongruent condition compared with the congruent condition. The left inferior parietal cortex, including the left angular gyrus and supramarginal gyrus (SMG), was more strongly activated in the congruent conditions than in the incongruent conditions.

Brain Activation Differences between the Numerical and Nonnumerical Tasks

To unravel the brain regions that showed significant brain activation differences between the two tasks, we calculated a whole-brain *t* test between the brain activation of the numerical task versus the brain activation of the nonnumerical task. Results of this analysis revealed greater activation in the numerical compared with nonnumerical condition in the left medial cingulate gyrus and left anterior insula. The reverse contrast revealed differences in the left superior frontal gyrus (SFG), posterior cingulate gyrus, left SMG (near the inferior parietal cortex area), right sub-OFC, left SMG, and regions in the left and right inferior parietal cortex. An inspection of the beta weights for the two conditions in these regions revealed significant differences in deactivation (compared with baseline) in the numerical condition relative to the nonnumerical condition. In other words, these areas exhibited greater deactivation in the numerical compared with the nonnumerical task.

Interaction of Task and Congruity

We conducted a voxelwise whole-brain analysis to evaluate potential differences between brain activation resulting from the congruity effect in the numerical task and the congruity effect in the nonnumerical task. In this whole-brain analysis, we contrasted the congruity effects in the different tasks, namely, (numerical task: IC > C) >

Table 2. Brain Regions by Contrast

Brain Region	*Coordinates: x, y, z*			*t*	*Cluster Size (Voxels)*
Congruity effect: incongruent > congruent					
Left SFG (cingulate gyrus)	−4	19	42	6.3	2835
MFG/left IFG	−40	−5	30	5.3	850
Congruity effect: congruent > incongruent					
Right middle temporal gyrus	41	−68	27	6.51	2232
Posterior cingulate gyrus	−16	−53	15	6.57	5480
Task effect: numerical > nonnumerical					
Left cingulate gyrus/SFG	−4	7	45	5.11	2612
Left insula	−37	19	12	4.03	948
Task effect: nonnumerical > numerical					
Right sub orbitofrontal gyrus	8	46	−12	5.85	3270
Left SFG	−7	55	21	5.01	1240
Posterior cingulate gyrus	−7	−50	27	4.03	1073
Left SFG	−16	40	42	4.43	1296
Left SMG/IPL	−43	−59	30	4.13	678
Task × Congruity					
rTPJ	56	−41	21	4.44	562

$p < .005$ (cluster corrected for multiple comparisons, $p = .05$). Coordinates are in Talairach space.

MFG = middle frontal gyrus; IFG = inferior frontal gyrus; IPL = inferior parietal lobe.

(nonnumerical task: IC > C). Arithmetically, this amounts to a +−−+ contrast (with the four conditions in order being numerical IC, numerical C, nonnumerical IC, and nonnumerical C). This analysis revealed voxels that were differently activated by the two congruity effects across the entire brain. The results of this analysis revealed one brain area—the right TPJ (rTPJ; see Figure 4A). As can be seen from the data plotted in Figure 4B, this

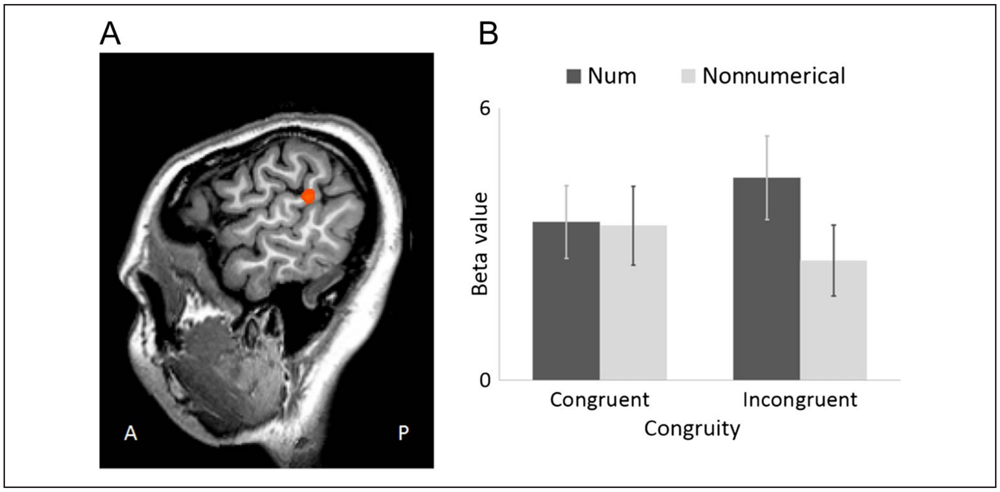

Figure 4. Task × Congruity interaction. (A) Sagittal view (56, −39, 24), showing the right TPJ area in orange. (B) Beta-value plot. A = anterior; P = posterior; Num = numerical task.

interaction was characterized by a difference in the amount of activation between the numerical and non-numerical condition for the incongruent but not the congruent condition. Specifically, in when participants' attention was directed towards the numerical magnitude of the dot arrays, there was more activation in the rTPJ when numerical and non-numerical variables were incongruent with one another compared, relative to when they were congruent. To test whether the different activation level in the rTPJ during incongruent trials for the numerical and nonnumerical conditions is related to differences in RTs, we extracted differences between beta values during incongruent trials of the numerical and nonnumerical tasks for each participant (i.e., β incongruent [numerical] $-$ β incongruent [nonnumerical]). These values were correlated with the RT differences between the incongruent trials of both tasks (i.e., RT incongruent [numerical] $-$ RT incongruent [nonnumerical]). This correlation was not significant, $r = .12$, *ns*. Thus, the differences in activation of the rTPJ during incongruent trials cannot be attributed to differences in RT.

DISCUSSION

Is there an asymmetry between automatic processing of numerical and nonnumerical magnitudes? Consistent with our hypothesis, the functional brain imaging data reported herein, specifically the activity of rTPJ in the interaction of task and congruity, suggest that nonnumerical magnitudes are being processed more automatically than numerical magnitudes.

In this study, we used neuroimaging to directly investigate asymmetries in processing nonsymbolic, numerical, and nonnumerical magnitudes. Such an asymmetry was found in the behavioral data because the congruity effect was stronger in the numerical task than in the nonnumerical task. Similar asymmetry was also reported in a similar design by Leibovich, Henik and Salti (2015). Importantly, this asymmetry was also found at the brain level in the rTPJ where a greater congruity effect on brain activation was found for the numerical condition compared with the nonnumerical condition. The rTPJ has been suggested to have the role of a "circuit breaker" during top–down attention (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002), biasing attention based on the relative saliency of the stimuli (Mevorach, Humphreys, & Shalev, 2009). For example, if a fire alarm were to sound while concentrating on a top–down, goal-directed task, like reading these lines, the rTPJ will be activated to redeploy the attention from the goal-directed task (i.e., reading) to stimulus-driven action (i.e., listening to the alarm).

In the numerical cognition literature, the rTPJ has previously been associated with stimulus-driven attention during numerosity processing. In an fMRI study by Ansari, Lyons, van Eimeren, and Xu (2007), brain activations during the processing of small nonsymbolic numerosities (i.e., 1–4) were compared with brain activations during the comparison of larger nonsymbolic numerosities. This study revealed that the rTPJ was active for small numerosity comparison and suppressed for large numerosity comparison. In view of these findings, the authors suggested that different attentional systems were used during small and large numerosity comparisons. Specifically, the authors argued that, during small number processing, stimulus-driven attention is engaged to a greater extent than is the case for larger numbers, where stimulus-driven information is suppressed. In general, activation of the rTPJ is thought to reflect the activation of a stimulus-driven (ventral) attentional network that reorients attention to salient, task-relevant stimuli. In contrast, suppression of the rTPJ activity suggests reliance on a goal-directed (dorsal) attentional network, where stimulus-driven information is suppressed rather than enhanced during processing. Similar results were found in an ERP study (Hyde & Spelke, 2012) and in additional functional imaging studies (e.g., He et al., 2013; Vetter, Butterworth, & Bahrami, 2011).

In line with the account for the rTPJ as a circuit breaker that redeploys attentional resources according to the relative saliency of the stimuli, we suggest that the interaction of task and congruity can be attributed to the different saliency of numerical and nonnumerical magnitudes. We submit that irrelevant nonnumerical magnitudes are more salient when processing numerical magnitudes than irrelevant numerical magnitudes are during the processing of nonnumerical magnitudes. Put differently, our data suggest that, when attention is directed toward the number of items in a display, the task-irrelevant nonnumerical dimensions of the stimuli interfere with the decision. Conversely, when attention is directed toward the nonnumerical dimensions, the numerosity of the display does not appear to exert the same magnitude of interference. Therefore, the rTPJ may reflect a pattern of asymmetric automatic processing of numerical and nonnumerical magnitudes. These results appear to contradict the findings of Park et al. (Park, DeWind, Woldorff, & Brannon, 2015). This study used the temporal resolution of an EEG and found that, during passive viewing of dot arrays, response to numerical magnitudes occurred earlier than response to nonnumerical magnitudes and that the brain was more sensitive to changes in numerical than in nonnumerical magnitudes. As a result, Park et al. suggested that numerosities are being processed by a separate system. Importantly, our data cannot answer the question of whether numerical and nonnumerical magnitudes are being processed by the same system. Our study investigated the relative use of numerical and nonnumerical magnitudes when top–down attention is being deployed differently. Ours and Park et al.'s study address two different questions and use different methodologies; whereas the study of Park et al. used EEG and based the hypothesis on the time of processing, in the current work, we used fMRI, and the hypothesis was focused on the neural regions that reveal different patterns of activity in the different conditions.

Against this background, it is reasonable to assume that, during the comparison of numerical magnitudes, relative to comparing nonnumerical magnitudes, there is a need for greater engagement of top–down attentional control mechanisms to inhibit the influence of task-irrelevant nonnumerical magnitudes. Consistent with this prediction, we found that, during the numerical task, areas associated with cognitive control (i.e., left cingulate gyrus and left insula) were more strongly activated than in the nonnumerical task. Areas associated with the default mode network (Gusnard & Raichle, 2001), namely, left SFG and left SMG, were more strongly deactivated compared with baseline during the numerical task relative to the nonnumerical task (see Table 2, "Task effect").

There is, however, another potential explanation to this pattern of results. The congruity effect has two components: facilitation and inhibition. Facilitation indicates the degree to which participants benefit from having more than one source of information that is congruent with the correct decision. In contrast, inhibition indicates the extent to which having conflicting sources of information negatively affects performance. To be able to distinguish between these two components, however, a neutral condition is needed. Unfortunately, it is physically impossible to create pairs of dot arrays that will differ in their numerical magnitude but will be identical in all the nonnumerical magnitudes (Leibovich & Henik, 2013). As a result, it is possible to explain our results as an outcome of integration rather than interference. Indeed, there is evidence suggesting that the rTPJ is involved in the integration of different features (Pollmann, Zinke, Baumgartner, Geringswald, & Hanke, 2014). It is possible that, when comparing nonnumerical magnitudes, one does not have to extract the numerical information from the stimulus because there are already multiple magnitudes that point to the same direction (at least in this set of stimuli). In numerical comparisons, however, it might be more efficient to integrate or to pay attention to nonnumerical information because these correlate with one another in the environment.

Critically, the same stimuli were used for both numerical and nonnumerical comparison tasks. Participants viewed the same stimuli in both tasks and, in congruent trials, made the same motor response; the only difference between the tasks was different deployment of top–down attention to the different magnitudes. As a result, the contrast of task and congruity is not affected by differences in the stimuli. However, using the same stimuli for both tasks made it impossible to match task difficulty. The behavioral and functional main effects of Task show that the numerical task was more difficult; responses were less accurate and slower, and there was more cognitive-control-related activity in the numerical task than in the nonnumerical task (e.g., insula, medial cingulate, precentral gyrus) and more default mode network activity in the nonnumerical task (e.g., SMG, angular gyrus, SFG). Nevertheless, there was no correlation between RT and rTPJ activity in the Task × Congruity interaction, suggesting that this critical interaction cannot be explained in terms of differential task difficulty between the numerical and non-numerical conditions.

As discussed in the Introduction, the relative saliency of numerical and nonnumerical magnitudes is a question of great importance in the quest to better understand the mechanisms by which nonsymbolic numerical magnitudes are processed. Most of the theories in the field of numerical cognition claim that the most basic building block of numerical abilities is numerical magnitude and that large numerosities, like the ones used in this study, are being processed independently of nonnumerical magnitudes (Odic, Libertus, Feigenson, & Halberda, 2013; Burr & Ross, 2008; Feigenson et al., 2004; Dehaene & Changeux, 1993). The findings reported herein suggest that it is faster and requires fewer top–down attentional control mechanisms to discriminate nonnumerical magnitudes. In addition, irrelevant nonnumerical magnitudes during numerical magnitude comparison are associated with the activation of a region that is thought to be the key to stimulus-driven attentional control. This association was not found for irrelevant numerical magnitudes during nonnumerical magnitude comparisons. These findings are in line with previously reported behavioral findings. For example, Leibovich and Henik (2014) found that participants were faster and better at discriminating between areas of squares than between numerical magnitudes and that, in numerical magnitude comparisons, reliance of irrelevant nonnumerical magnitudes that were not correlated with numerosity explained half of the explained variance in RT. Accordingly, we suggest that the current results support the claim that nonnumerical dimensions play a very basic and central role in comparative nonsymbolic number judgments (Leibovich & Henik, 2014; Gebuis & Reynvoet, 2012a; Henik et al., 2012).

Conclusions

This study represents, to the best of our knowledge, the first investigation into the neural correlates of the relationship between numerical and nonnumerical magnitudes during dot comparison. Consistent with the notion that numerical and nonnumerical magnitudes are processed during dot comparison even when they are irrelevant to the task (e.g., whether numerical magnitude interferes with judgments of nonnumerical magnitudes and vice versa), we found a general effect of congruity on regions typically associated with cognitive control and possibly the inhibition of task-irrelevant information. This suggests that both numerical and nonnumerical magnitudes are processed regardless of whether they are task relevant. Importantly, we also found that activity in the rTPJ, a region associated with stimulus-driven attention, was differentially modulated depending on whether numerical or nonnumerical magnitudes were the task-irrelevant dimension. Specifically, the data revealed a

Task × Congruity interaction in the rTPJ; the processing of numerical magnitudes, when nonnumerical magnitudes conflicted with numerical magnitude processing, activated this region significantly more than vice versa—during processing of nonnumerical magnitudes, when numerical magnitudes conflicted with nonnumerical magnitudes. Thus, it seems that both numerical and nonnumerical magnitudes are being processed automatically through mechanisms of cognitive control, as evidenced by the functional main effect of congruity. Irrelevant nonnumerical magnitudes, however, activated a region known to be critical in the reorienting of attention to stimulus parameters more so than irrelevant numerical magnitudes.

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