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Corrigendum

Corrigendum to "Overlapping and distinct brain regions involved in estimating the spatial position of numerical and non-numerical magnitudes: An fMRI study" [Neuropsychologia 51 (2013) 979–989]

Stephan E. Vogel [a,g], Roland H. Grabner [b,e,g], Michael Schneider [c], Robert S. Siegler [d,f], Daniel Ansari [a,*]

[a] Numerical Cognition Laboratory, Department of Psychology & Brain and Mind Institute, The University of Western Ontario, Westminster Hall, Room 325, London, Ont., Canada N6A3K7
[b] Institute for Behavioral Sciences, ETH, Zurich, Switzerland
[c] Department of Psychology, University of Trier, Germany
[d] Department of Psychology, Carnegie Mellon University, United States
[e] Department of Psychology, Georg-August-University of Göttingen, Germany
[f] SCIL Center, Beijing Normal University, Beijing, China
[g] Educational Neuroscience, Institute of Psychology, University of Graz, Austria

The authors wish to report an error in the method section of this manuscript. In this manuscript we mistakenly reported "… that the visual indicator of the trackball was reset to the center of the screen (i.e., same location as the presented probe) after each trial in all experimental conditions (p.982)." Contrary to what is reported in the method section, the position of the trackball-cursor was set to a randomly selected position, excluding the correct position of the probes, along the number line at the start of every trial. As such the distance from the starting point of the trackball-cursor to the correct position of the probe on the physical line was randomly distributed across the experiment. The authors would like to apologise for any inconvenience caused.

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* Corresponding author.
E-mail addresses: daniel.ansari@uwo.ca, daniel.ansari@gmail.com (D. Ansari).

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Overlapping and distinct brain regions involved in estimating the spatial position of numerical and non-numerical magnitudes: An fMRI study

Stephan E. Vogel [a], Roland H. Grabner [b,e], Michael Schneider [c], Robert S. Siegler [d,f], Daniel Ansari [a,*]

[a] Numerical Cognition Laboratory, Department of Psychology & Brain and Mind Institute, The University of Western Ontario, Westminster Hall, Room 325, London, Ont., Canada N6A 3K7
[b] Institute for Behavioral Sciences, ETH, Zurich, Switzerland
[c] Department of Psychology, University of Trier, Germany
[d] Department of Psychology, Carnegie Mellon University, United States
[e] Department of Psychology, Georg-August-University of Göttingen, Germany
[f] SCIL Center, Beijing Normal University, Beijing, China

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ABSTRACT

How are numerical and non-numerical magnitudes processed in the brain? Brain imaging research, primarily using comparison paradigms (i.e. judging which of two magnitudes is larger), has provided strong evidence demonstrating that the intraparietal sulcus (IPS) is a key region for processing both numerical (e.g. Arabic numerals, arrays of dots) and non-numerical magnitudes (e.g. height, brightness). These studies have suggested that there is both activation overlap and segregation in the brain regions involved in processing different dimensions of magnitude. In the present functional Magnetic Resonance Imaging (fMRI) study, we extended this line of investigation by probing the brain mechanisms underlying the mapping of numerical (Arabic numerals) and non-numerical magnitudes (brightness levels) onto a number line. Consistent with previous studies the present results revealed that number and brightness estimation was associated with overlapping activation within right lateralized areas of the posterior IPS. In addition, the contrast between number and brightness estimation revealed that bilateral anterior regions of the IPS are specifically involved in the process of estimating the position of symbolic numbers onto a number line. Furthermore, we found a significant influence of landmark reference points (0, 50 and 100) on brain activation in the right IPS for number estimation only. No regions were found to be specifically associated with brightness estimation. The results of this study reveal that the estimation of both numerical and non-numerical magnitude are associated with the engagement of a right lateralized magnitude system, but that symbolic number estimation is associated with additional engagement of bilateral regions of the anterior IPS.

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1. Introduction

Research into the neural correlates of numerical cognition has implicated the parietal lobe, and more specifically the intraparietal sulcus (IPS), as a critical brain region for processing the abstract meaning of numerical magnitude (the total number of items in a set). Brain activity in this region is consistently activated whenever participants are presented with symbolic (e.g., Arabic digit) or non-symbolic (e.g., dot arrays) numerical magnitudes (for a review see Nieder & Dehaene, 2009).

Most tasks that have investigated the neural correlates of numerical magnitude processing have focused on the comparison of symbolic and/or non-symbolic numerical magnitudes. In such comparison tasks, numerical symbols or non-symbolic object arrays are presented on a screen and participants are either asked to decide which of two simultaneously presented digits/dot arrays is numerically larger/smaller, or whether a presented numeral/dot array is numerically larger/smaller than a non-presented reference number (e.g., 5). The results of such imaging studies have shown that the comparison of pairs of number separated by relatively smaller numerical distances are associated with greater activation in the IPS compared to number pairs that are separated by large distance. This evidence has been taken to suggest that numbers that are close together share more representational variance than numbers that are relatively further apart (Ansari & Dhital, 2006; Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Kaufmann et al., 2005; Pinel, Dehaene, Riviere, & Le Bihan, 2001). This reliable activation pattern has since been taken as evidence for the idea that numerically close distances (e.g., 4 and 5) exhibit a greater representational overlap compared to relatively large distances (e.g., 2 and 8; Moyer & Landauer, 1967).

* Corresponding author. Tel.: +1 519 661 2111.
E-mail addresses: daniel.ansari@uwo.ca, daniel.ansari@gmail.com (D. Ansari).

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In addition to the frequently used number comparison tasks, passive tasks such as fMRI adaptation – in which participants solely attend to the presentation of stimuli without any overt task demand – have recently been used to investigate the neural correlates of numerical magnitude processing. Convergent with activations found in the number comparison task and the theory of a distance dependent representational overlap, results of such studies have revealed that areas in and around the IPS habituate to numerical magnitudes in response to both symbolic and non-symbolic numerical stimuli, and exhibit a greater signal recovery (following the presentation of novel numerical magnitudes) for numerical magnitudes that are relatively distant from the original (adapted) numerical magnitude compared to when the numerical distance between the adapted and novel numerical magnitude is relatively small (Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Notebaert, Nelis, & Reynvoet, 2011; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007).

Another task that has proved useful for generating behavioral evidence regarding basic numerical representation is the number line estimation task (Siegler & Opfer, 2003). In this paradigm, participants are asked to estimate the spatial position of a number on a physical number line. More specifically, participants are presented with a horizontal line that is flanked by a 0 on the left and, for example, a 100 on the right, thus constructing a number line that is restricted to a specific range of numerical values. Then, a numerical probe (e.g., 67) is presented and participants are asked to indicate the spatial position of this number on the given physical number line. This task involves the mental activity of taking an internal representation of numerical magnitude and estimating its relative position on a spatial reference frame. Thus, the number line task has been argued to index numerical magnitude processing in the context of a spatial framework, representing a core property of estimation — the translation between representations of number and space (Sigler & Opfer, 2003). Behavioral studies of number line estimation have revealed that children's performance on the number line estimation task changes over developmental time and that individual differences in estimation accuracy correlate with children's proficiency in arithmetic, memory for numbers, standardized mathematical achievement test scores, and mathematical school grades (Booth & Siegler, 2006; Schneider, Grabner, & Paetsch, 2009; Schneider et al., 2008; Siegler & Booth, 2004; Thompson & Siegler, 2010). Furthermore, interventions that increase the accuracy of children's estimates on the number line, cause increases in children's arithmetic competence (Booth & Siegler, 2008; Siegler & Ramani, 2009). Moreover, recent research has demonstrated that participants implicitly divide the number line into specific landmarks, which are used as reference guides for estimating the position of the probe on the line (Siegler & Opfer, 2003). As such, participants are more accurate to place a number onto the line when the probe is numerically closer to a landmark – such as 0, 50, 100 – compared to when the probe is numerically farther away (e.g., Schneider et al., 2008; Sullivan, Juhasz, Slattery, & Barth 2011). The neurocognitive mechanism that underlie the use of landmark reference points remain, however, unknown. Besides its frequent and successful use in behavioral research, the number line task is also highly ecological relevant since number lines are introduced in schools and may help to enhance children's symbolic number representation as a result of experience by using numbers within a spatial context. Given the significance of the number line task in the literature and its significant association with mathematical relevant measurements, it is a logical and important next step to uncover the neural correlates associated with this task in order to further increase our understanding of the neural circuitry underlying different components of symbolic number processing.

Moreover, in addition to providing another tool to investigate number processing in the brain, the number line task also allows for the investigation of differences and commonalities of brain regions that are involved in estimating the spatial position of numerical and non-numerical magnitudes such as brightness. While early theoretical approaches debated whether numerical and non-numerical magnitudes – such as number, time and space – are processed via independent and fully distinct magnitude systems (Murphy, 1996, 1997), or a fully shared magnitude representation (Meck & Church, 1983; Moyer & Landauer, 1967), more recent work argued that multiple magnitude dimension rely on a "partly-shared" magnitude representation (Walsh, 2003). More specifically, the latter theory postulates that numerical as well as non-numerical magnitudes may share a common representation of magnitude, but, critically, also engage additional, dimension specific (i.e., numerical and non-numerical specific) representations.

Evidence in favor of a partly-shared magnitude systems was recently provided by neuropsychological studies with patients (e.g., Cappelletti, Freeman, & Cipolotti, 2009, 2011), as well as from neuroimaging studies that showed activation in similar as well as dissociated regions in the parietal lobe when magnitudes of different kinds are compared. For example, Pinel, Piazza, Le Bihan, and Dehaene (2004) investigated brain activity while participants decided which of two simultaneously presented numerals was brighter, physically larger, or numerically larger. Judgments of number and area were associated with overlapping responses in the IPS, while comparisons of brightness and size were found to share activation in regions of the occipito-temporal cortex. This evidence suggests, that at least some regions of the parietal cortex are involved in the processing of both numerical and non-numerical magnitudes, but also, that other non-numerical magnitudes may draw upon distinct magnitude representations.

Cohen Kadosh et al. (2005) used similar comparisons tasks as those that were used by Pinel et al. (2004) and showed overlapping brain representations for size, brightness, and numerical magnitude in frontal, parietal and occipitotemporal regions of the cortex. However, in addition to these common effects across different magnitude comparison tasks, the authors found that the left IPS was uniquely engaged in numerical comparison it was the only region that showed significant task-specific activation (i.e., number > size and number > -brightness) as well as a numerical distance effect. Thus, besides showing an overlap between different magnitude dimensions, the results also imply the involvement of dimension specific mechanisms. Interestingly, dimension specific effects were especially pronounced for the numerical comparison, suggesting that numbers may play a special role amongst other magnitude dimensions.

In a similar vein, Dormal and Pesenti (2009) found common as well as segregated brain activations in the left and right parietal lobe when numerical and non-numerical magnitudes were compared. Participants were asked to compare the number of dots in two linear arrays, the physical length of two linear arrays of dots, or the physical length of two continuous rectangles. In all cases, the stimuli being compared were simultaneously presented on a computer screen. Analyses of the fMRI data revealed that both the left and the right anterior IPS were specifically engaged when participants compared the amount of dots in the arrays. In addition to the number-related activations, the right IPS was also activated for the comparison of length, leading the authors to suggest that the right IPS is involved in general magnitude processing, while the left IPS may be particularly important for the processing of numerical magnitudes.

Taken together, these data suggest that magnitudes of different kinds neither fully rely on independent magnitude systems, nor on one single magnitude representation. Rather, the evidence points towards a co-involvement of common and distinct magnitude related

representations, particularly within the numerical domain. Furthermore, the data suggest that differences and commonalities between numerical and non-numerical magnitudes may be related to particular locations within the left and right IPS. More specifically, common effects of magnitude processing are predominantly found in regions along the right IPS, while the processing of discrete numerical magnitudes also involves regions of the left anterior IPS. These insights have been gleaned from experiments using comparison tasks and little is known about such commonalities and differences in the context of other numerical processing tasks, such as estimation.

Therefore, in the present study, a number line estimation task with numbers from 0 to 100 was administered to investigate which brain regions are involved in estimating the spatial position of numbers on a horizontal number line. In addition, to probe commonalities and differences between numerical and non-numerical estimation, a brightness estimation task was administered which required participants to estimate the spatial position of probes (swatches of different levels of brightness) on a horizontal line ranging from white to black.

In sum, the present study investigated the following questions. First of all, we were interested in uncovering the neural architecture involved in estimating the spatial position of symbolic numbers on a number line. Since the number line task is thought to measure numerical magnitude representations, we predicted that, consistent with the literature, the IPS would play a vital role in estimating the spatial position of symbolic numerical magnitudes on a physical number line. Alternatively, if the task access different representations of numerical magnitude, or relies on different brain mechanisms than numerical magnitude comparison and adaptation, one might expect activations that deviate from regions typically found in numerical magnitude processing. In addition, we were interested in whether the neural circuits underlying estimation differ between numerical and non-numerical estimation. Particularly, we aimed to investigate the relationship between landmark reference points and the extent to which the distance of the probe, to its closest landmark (i.e., "landmark distance"), modulates brain activation in the parietal lobe, and how such brain activation may differ between numerical and non-numerical estimation. Against the background of the literature from numerical and non-numerical comparison studies reviewed above, we expected that both similar and distinct brain regions are involved when numerical and non-numerical magnitudes are estimated. More specifically, we predicted to find overlapping activation in the right IPS when numerical and non-numerical magnitudes are mapped into space, and additional, number specific activation in the left IPS. This evidence would speak in favor of the "partly-shared magnitude" theory. Alternatively, if the estimation of numerical and non-numerical magnitudes onto a spatial reference frame is sub served by (a) fully distinct or (b) fully overlapping magnitude mechanisms, we expect to find (a), no significant overlap between the two magnitude tasks, but strong dimension-specific activation for number and brightness, or, in the case of (b), a significant overlap between the two magnitude tasks, but no significant activation difference in the format specific contrasts. In addition, if landmark reference points significantly influenced numerical magnitude processing in the brain, we expected to see a parametric modulation of the IPS related to "landmark distance" in the numerical condition only.

2. Materials and methods

2.1. Participants

Participants were 14 healthy, right-handed adult participants: 7 females (mean age=24.86 years; SD=5.40; range=18–33) and 7 males (mean age=24.29 years; SD=2.87; range=19–28).

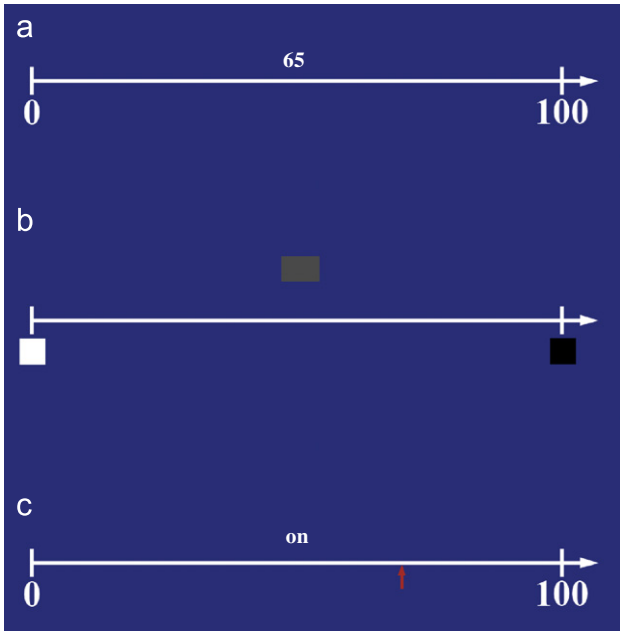

Fig. 1. Example stimuli used in the three different experimental conditions: (a) number line estimation, (b) brightness estimation and (c) word control task.

2.2. Task design and stimuli

Two experimental conditions – number line estimation (NLE) and brightness estimation (BE) – and one control condition were used in this experiment (see Fig. 1 for example of stimuli).

2.2.1. Number line estimation (NLE)

A white horizontal line was presented on a blue screen to visually map out a spatial reference frame from left to right (see Fig. 1a). The spatial reference line was supplemented in such a way that two Arabic numerals – 0 at the left end and 100 on the right end – were presented as flankers below the horizontal line. The purpose of the two numerals was to indicate the spatial-numerical extent of the reference line ranging from 0 on the left to 100 on the right.

Arabic numerals, ranging within 1–99 (Table 1), were randomly ordered as probes in the NLE condition. Furthermore, all stimuli probes were chosen in such a way that the numerical distances of the probe to its closest landmark (i.e., 0, 50, and 100) was uniformly distributed over the range of all possible distances (see also Table 1). In the present manuscript we will refer to this estimate as "*landmark distance*". Probes were presented for 5000 ms at the center of the screen and above the spatial reference line. Each probe was presented 3 times using 3 different jitter intervals after stimulus presentation. Participants were instructed to indicate the spatial position of the numerical value on the number line by clicking a trackball at the desired location.

2.2.2. Brightness estimation (BE)

The same visual reference line as in the NLE condition was used for the BE condition. However, instead of 0 and 100 anchoring the line, two square boxes, one filled with the brightness level of white and the other filled with the brightness level of black[1] were presented below the vertical line and were used to indicate the brightness range of the reference line, from white on the left to black on the right (see Fig. 1b). The same experimental procedure as in the NLE condition was used for the BE task. However, instead of Arabic digits, brightness levels (Table 1) were presented randomly on the screen at the same location as the numeric probe in the NLE task. Participants needed to indicate with the trackball the spatial position on the reference line at which they would place the presented brightness.

[1] All brightness levels were generated with the computer program Borland Delphi. Shades of gray were specified with the RGB color system. Within this format, each color value (R, G and B) was coded within in a range from 0 to 255. Using the formula [(100−*n*)*255/100] different gray levels (100 in total) were generated, with white (0, 0, 0) and black (100, 100, 100) on the two ends of the range.

Table 1
List of stimuli used in the experimental and in the control conditions, as well as the numerical distance of each probe to the next closest landmark reference point (i.e., "landmark distance"). Note that the brightness values in the BE task correspond to the numerical values used in the NLE task in such a way that the steps between brightness levels and numerical levels are equivalent. For example, the magnitude difference between the 1st number (i.e., 3) and the 2nd number (i.e., 7) in the list is the same as the magnitude difference between the 1st and 2nd brightness swatch in the list.

Numbers in the NLE	Brightness in the BE	Words in the control	Landmark distance
3		on	3 (to 0)
7		in	7 (to 0)
11		to	11 (to 0)
13		at	13 (to 0)
21		me	21 (to 0)
28		we	22 (to 50)
33		he	17 (to 50)
36		it	14 (to 50)
42		no	8 (to 50)
45		so	5 (to 50)
56		by	6 (to 50)
57		go	7 (to 50)
60		do	10 (to 50)
65		am	15 (to 50)
74		as	24 (to 50)
77		my	23 (to 100)
83		or	17 (to 100)
85		ox	15 (to 100)
90		if	10 (to 100)
98		be	2 (to 100)

2.2.3. Control condition

The same reference line as in the NLE condition was used in the control condition (see Fig. 1c). In contrast to the two experimental conditions, two-letter words (Table 1) were used as probes. The rationale for using two-letter words in the control condition was to equate visual complexity across the word and number conditions. The task was to move the trackball to the location on the line indicated by an arrow, and to click on it. The presented arrows indicated the locations of correct estimates in the other two conditions, thus requiring the same hand movements in all three conditions. Please note that the letter probes were irrelevant to task performance in the control condition and were only used to equate the complexity of visual input.

Also note that the visual indicator of the trackball was reset to the center of the screen (i.e., same location as the presented probe) after each trial in all experimental conditions. In addition, the spatial locations of the correct answers on the reference line were matched across identical trials between conditions. For example, the correct position on the reference line for the numerical probe 36 was identical to the correct position of the corresponding gray shade (see Table 1 for the correspondence between numerical and brightness values) and the arrow in the word control condition. This standardized procedure ensured that hand movements were matched as best as possible across the three experimental conditions.

Since the word control task did not involve explicit processing of the two-letter words presented in the middle of the screen, additional dummy trials were included in all conditions. On these trials, numbers, brightness stimuli, and dummy words were crossed out with two red lines. Whenever dummy trials appeared on the screen, participants were asked to indicate the presence of such a trial with a button press. The inclusion of these additional trials ensured that participants paid attention to the dummy words in the word control condition and that perceptual processing mechanisms across all tasks were at least roughly comparable.

2.3. Experimental procedure

Before entering the scanner, participants were told about the fMRI environment and the experimental task procedure. Once in the scanner, participants were presented with 12 blocks – 4 for NLE, 4 for BE, and 4 for the word controls – divided into four functional runs (3 blocks per run). The order of the 12 blocks was counterbalanced across the four runs. Thus the block presentation order from one run to the next was not predictable for participants. Within each block, 15 stimuli of the same task were presented, resulting in a total of 45 trials per run (see also Table 1) and 180 trials for the four runs. Thus, each stimuli was presented three times (20 stimuli per condition), resulting in a total of 60 stimuli per experimental condition when combining all functional runs. Stimuli were presented in a pseudo-random order, with the rule that the same stimulus must not be presented on consecutive trials. Between stimuli, a jitter interval of 5000 ms, 7500 ms and

10,000 ms was used to optimize the sampling of the hemodynamic response function (HRF). Jitter time was balanced in such a way that the same jitter-time was never presented on consecutive trials.

2.4. Data acquisition

Functional and structural imaging data were acquired using a whole-body MRI scanner (3T GE). A standard echo-planar imaging (EPI) T2* sequence was used in order to measure and quantify the blood-oxygen-level-dependent (BOLD) functional response. In each run, 444 functional volumes were collected. One volume consisted of 36 slices (3.4 mm slice thickness; flip angle: 59°) and was acquired using an interleaved ascending order. Timing parameter for this paradigm were set to a time to repetition (TR) of 2100 ms and a time to echo (TE) of 31 ms. T1 whole-brain high-resolution pictures for each subject were acquired with an axial FSPGR BEAVO sequence with a TR of 8836 ms and a TE of 3504. Each 3D volume consisted of 140 horizontal slices (1.2 mm slice thickness, flip angle: 13°).

2.5. Data analysis

All functional and structural imaging data were pre-processed and analyzed with the software package Brain Voyager QX 2.3 (Brain Innovation, Maastricht, The Netherlands). Participants' functional runs were first corrected for slice time acquisition (cubic spline, images were acquired in an ascending-interleaved order) and head motion (trilinear/sinc interpolation). Furthermore, a High-Pass filter (GLM-Fourier, 2 sine/cosine cycles) was applied to remove frequencies related to physiological noise, such as breathing and the heart beat. Finally, all functional runs were spatially smoothed using a kernel of 6 mm full width at half maximum (FWHM). Individual's structural 3D images and individual functional runs were co-registered. This was attained by mapping the individual functional runs onto the anatomical 3D image until a maximum of spatial overlap of anatomical landmarks was achieved. To maximize the accuracy of the functional-to-structural alignment, all anatomical images were stripped from the skull and only the remaining brain tissue was used for the co-registration process. After all the functional images were aligned to their corresponding anatomical image, the data were transformed into Talairach space (Talairach & Tournoux, 1988) for group statistical analysis.

Functional events were modeled as an event-related design using a random effects (RFX) general linear model (GLM) with the three tasks as predictors. The design matrix contained, therefore, predictors for the NLE, BE and control conditions. All predictors were convolved with a two-gamma hemodynamic response gamma function (HRF) to model the expected (BOLD) function (Friston et al., 1998).

2.5.1. Tasks > control condition

The initial analysis aimed to investigate brain areas that were significantly modulated by the experimental conditions compared to the word control condition. Contrasts of "[NLE > control]" and "[BE > control]" were calculated separately.

2.5.2. Conjunction analysis to probe neural circuits commonly engaged by number and brightness estimation

To examine regions that showed a significant common neural response to number and brightness estimation, a conjunction of RFX analysis was calculated over the contrasts "[NLE > control]∩[BE > control]".

2.5.3. Number and area-specific activation

To evaluate numerical and non-numerical task specific brain activation patterns, two conjunction of RFX analyses were calculated. To investigate number specific activation, the conjunction of "[NLE > BE]∩[NLE > control]" was calculated. To calculate brightness specific activation, the conjunction of "[BE > NLE]∩[BE > control]" was calculated. These analyses ensured that activation differences between the two experimental estimation conditions (i.e., NLE and BE) were over and above activation of the word control task.

For all analyses, an initial, uncorrected threshold of $p < 0.001$ was used to identify regions that showed a significant difference. The resulting maps were subsequently corrected for multiple comparisons using cluster size thresholding (Forman et al., 1995; Goebel, Esposito, & Formisano, 2006). In this method, an initial voxel-level (uncorrected) threshold is set. Then, the thresholded maps are submitted to different correction criteria, based on the estimates of the map's spatial smoothness and on an iterative procedure (Monte Carlo simulation) for estimating cluster-level false-positives rates. After 1000 iterations, the minimum cluster-size that yielded a cluster-level false—positive rate (α) of 0.05 was used to threshold the statistical maps. Only activations whose size met or exceeded the cluster threshold were allowed to remain on the statistical maps.

3. Results

3.1. Behavioral results

Reaction times (RT) in the three conditions were subjected to an analysis of variance (ANOVA) with repeated measurements. This analysis indicated a difference in median RT's among the three tasks (NLE = 3367 ms, SD = 266 ms; BE = 3264 ms, SD = 376 ms; Word Control = 3106, SD = 303 ms, ($F(2,13) = 5.541$, $p = 0.015$). To identify the source of this effect, we calculated three paired sample t-tests between the conditions. After correcting for multiple comparisons (Bonferroni Correction), this analysis revealed a difference between the NLE and Word control reaction times ($t(13) = 3.661$, $p = 0.003$). The contrast between NLE and BE conditions was non-significant ($t(13) = 1.491$, $p = 0.160$), as was the contrast between BE and Word control conditions ($t(13) = 1.679$, $p = 0.117$).

We also compared the mean percent absolute errors[2] (PAEs) for the three conditions. The PAEs were 2.43 (SD = 0.71) for the NLE condition, 17.32 (SD = 7.00) for the BE condition, and 0.41 (SD = 0.17) for the word condition, where participants only needed to duplicate the position of the arrow on the number line. An ANOVA with repeated measurements showed a significant difference across the three conditions ($F(2,13) = 70.803$, $p < 0.001$). Post-hoc t-tests for paired samples revealed significant differences for all possible combinations: NLE versus BE $t(13) = -7.735$, $p < 0.001$; NLE versus Control $t(13) = 10.896$, $p < 0.001$; BE versus Control $t(13) = 9.056$, $p < 0.001$).

Furthermore, we investigated the extent to which "*landmark distance*" influenced the precision with which numerical and brightness probes were placed onto the number line. For this analysis, we first calculated the sample mean PAE for each "*landmark distance*" across all individuals and for each experimental condition. Next, we quantified the relationship between the sample mean PAE and "*landmark distance*" by performing a correlation analysis. As expected, Pearson correlation coefficients revealed a strong association between PAE and "*landmark distance*" for the number ($r = 0.601$; $p < 0.001$) but not for the brightness condition ($r = 0.411$; $p = 0.072$). In other words, the further away the number to be estimated was from the closest landmark the greater the PAE. Thus, participants estimation errors increase as you get further away from the landmark. This result is consistent with previous findings that showed a significant influence of landmark reference points on the precision with which numerals are placed onto number lines (e.g., Schneider et al., 2008; Siegler & Opfer, 2003; Sullivan et al., 2011).

3.2. fMRI results

3.2.1. Number and brightness versus control

The aim of the first analysis was to identify brain regions that showed stronger activation for the numerical and brightness estimation tasks than for the word control. The numerical estimation task revealed greater activations than the control task in frontal, parietal and occipital areas (see Fig. 2, activations displayed in red). Activations within the parietal lobe were restricted to the IPS in both hemispheres and to the left posterior superior parietal lobe (PSPL, more specifically the precuneus). Similarly, the brightness estimation task produced greater activations within frontal, parietal and occipital regions than the control (see Fig. 2, activation displayed in blue). In this contrast however,

[2] Percent absolute errors were calculated by the formula (estimate − estimated quantity/scale of estimates). For example, if a participant was to estimate the number 35 on a number line trial and placed the number on the position 15, the percent absolute error would be 20% [35–15)/100] (see also Booth & Siegler, 2006).

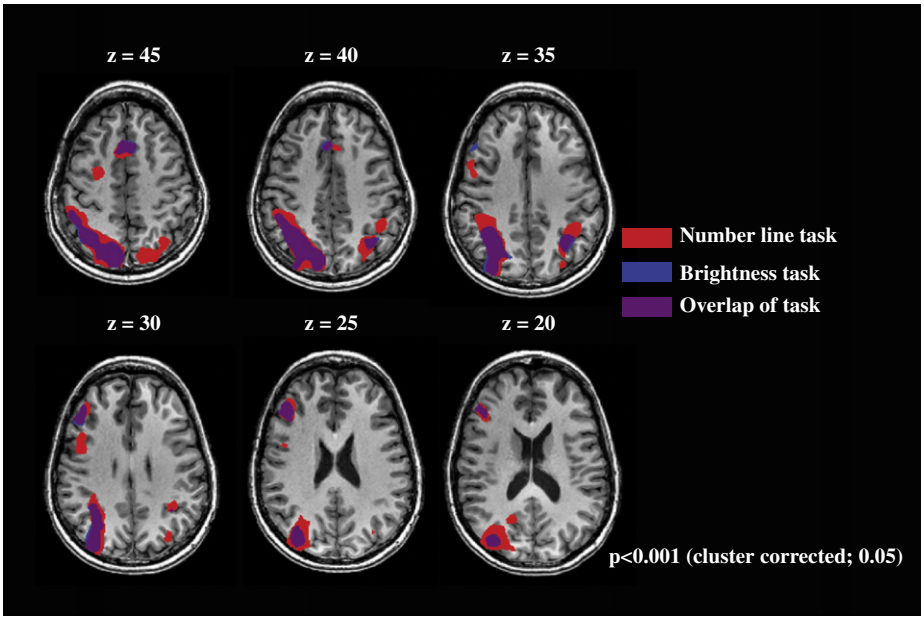

Fig. 2. Activations of the "Number line task > word control" and the "Brightness task > word control" are displayed in six transversal sections of the brain. Number related activations are shown in red while Brightness related activations are shown in blue. Overlapping regions are shown in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

parietal activations in the IPS were more pronounced in the right hemisphere, covering the IPS and the PSPL (precuneus) (see Tables 2 and 3 for Talairach coordinates of the contrasts).

3.2.2. Common activations for number and brightness

To analyze the extent to which the neural correlates of the experimental tasks overlapped, a whole-brain conjunction analysis between "[NLE > control]∩[BE > control]" was performed. Results of this contrast showed a significant overlap in the right hemisphere of the parietal cortex and the frontal lobe (see Fig. 3, activation displayed in blue; for Talairach coordinates see Table 4). Activation overlap between NLE and BE tasks in the parietal lobe spanned the right IPS extending to the PSPL, while activation in the frontal lobe was found in the dorsolateral prefrontal cortex (DLPFC) and the right middle frontal gyrus.

3.2.3. Number specific activations

This analysis was designed to reveal brain regions that showed activation specifically modulated by the number line estimation task. For the contrast "[NLE > BE]∩[NLE > control]", number specific activations were found in bilateral regions of the anterior IPS and the left PSPL. In addition to the activation clusters in the parietal lobe, right lateralized activations were found in the DLPFC and occipital-parietal junction (see Fig. 3, activation displayed in red; also for Talairach coordinates see Table 5).

To investigate regions specifically modulated in response to brightness estimation, a conjunction of the contrasts "[BE > control]∩[BE > NLE]" was performed. No significant differences in activation were found.

3.2.4. Influence of landmark reference points

To better characterize the neurocognitive processes involved in estimating the position of a numerical and non-numerical probe onto a number line, we investigated whether reference points (i.e., 0, 50, 100) along the number line significantly influenced participants brain activation while placing the probe onto the line. As such, we first calculated the numerical distance of each probe to its next closest reference point. For example, the distance for the numeral 28 (and for the corresponding brightness probe) is 22 since the next closest landmark is 50. However, for the numeral 21 (and for the corresponding brightness probe) the closest reference point on the number line is 0 and its distance is 21. To investigate whether "*landmark distances*" significantly

Table 2
List of those areas that showed a significant difference between the number line estimation task and the word control task (i.e., NLE > control). Coordinates are given in Talairach space (Talairach & Tournoux, 1988). Activations are reported at a threshold level of $p < 0.001$ (0.05 corrected on cluster level).

	Hemisphere	Stereotaxic coordinates		
		X	*Y*	*Z*
Precuneus	R	8	−77	48
Intraparietal sulcus	R	29	−62	36
Middle occipital gyrus	R	35	−77	21
Middle frontal gyrus	R	32	1	51
Superior frontal gyrus	R	8	10	48
Superior frontal gyrus	R	41	37	27
Cuneus	L	−16	−95	9
Precuneus	L	−13	−80	48
Intraparietal sulcus	L	−31	−68	42
Middle frontal gyrus	R	47	13	33

Table 3
List of those areas that showed a significant difference between the brightness estimation task and the word control task (i.e., BE > control). Coordinates are given in Talairach space (Talairach & Tournoux, 1988). Activations are reported at a threshold level of $p < 0.001$ (0.05 corrected on cluster level).

	Hemisphere	Stereotaxic coordinates		
		X	*Y*	*Z*
Intraparietal sulcus	R	32	−56	39
Sub-gyral	R	29	1	54
Precuneus	R	8	−80	48
Intraparietal sulcus	L	−34	−59	36
Medial frontal gyrus	L	−4	19	45
Lingual gyrus	R	14	−89	0
Middle frontal gyrus	R	48	31	30

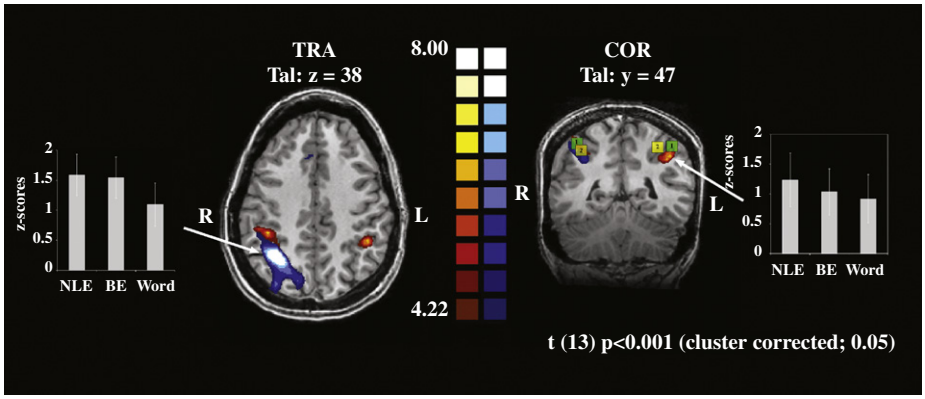

Fig. 3. The blue areas represent areas that were involved both when participants mapped number and brightness into space. Areas in red display number specific regions that were activated only when the position of numbers were estimated. The coronal section displays in addition gravity centers of two meta-analysis of numerical magnitude processing—green square (1): Cohen Kadosh, Lammertyn, and Izard (2008); in yellow square (2): Dehaene, Piazza, Pinel, and Cohen (2003). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
List of those areas that showed a significant overlap for the number line estimation and brightness estimation task (i.e., [NLE > control]∩[BE > control]. Coordinates are given in Talairach space (Talairach & Tournoux, 1988). Activations are reported at a threshold level of $p < 0.001$ (0.05 corrected on cluster level).

	Hemisphere	Stereotaxic coordinates		
		X	*Y*	*Z*
Intraparietal sulcus	R	32	−56	39
Sub-gyral	R	29	1	54
Precuneus	R	8	−80	48
Middle frontal gyrys	R	47	31	27
Middle frontal gyrus	R	5	19	45

Table 5
List of brain regions that showed a significant number specific activation (i.e., [NLE > BE]∩[NLE > control]). Coordinates are given in Talairach space (Talairach & Tournoux, 1988). Activations are reported at a threshold level of $p < 0.001$ (0.05 corrected on cluster level).

	Hemisphere	Stereotaxic coordinates		
		X	*Y*	*Z*
Intraparietal sulcus	R	38	−38	36
Intraparietal sulcus	L	−43	−44	39
Middle temporal gyrus	R	35	−71	15
Middle frontal gyrus	R	23	−5	48
Precuneus	L	−10	−81	51

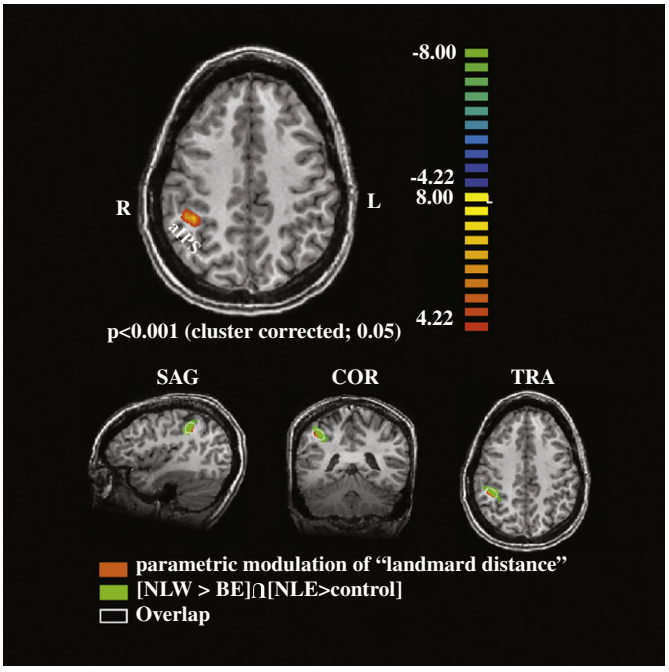

Fig. 4. The figure shows the parametric modulation of the right anterior IPS as a factor of "*landmark distance*" with greater activation the further away the estimated number is from the closest landmark. In addition, the Sagittal, Coronal and Transverse view below the main image visualize the overlap between the number specific contrast "[NLE > BE]∩[NLE > control]" and the parametric activation of the anterior IPS. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

modulated brain activation, we entered "*landmark distances*" for each magnitude condition (i.e., number and brightness) as parametric regressor into a whole brain RFX-GLM analysis. All predictors were convolved with a two-gamma hemodynamic response gamma function (HRF) to model the expected (BOLD) function (Friston et al., 1998). The same statistical criteria as in the preceding analyses were applied. An initial uncorrected statistical threshold of $p < 0.001$ was chosen, and subsequently adjusted for multiple comparisons (cluster level false—positive rate of $p < 0.05$) using a Monte-Carlo simulation (Forman et al., 1995; Goebel et al., 2006).

Results for the NLE contrast revealed that the right IPS (Talairach coordinates: $x = 38$, $y = -41$, 39) of the parietal lobe was the only region that was parametrically modulated by "*landmark distance*" (see Fig. 4). In addition to the right IPS, two regions of the frontal lobe (Talairach coordinates: $x = 32$, $y = -2$, $z = 54$/Middle Frontal Gyrus; $x = -25$, $y = -11$, $z = 45$/Middle Frontal Gyrus) and one region in the occipital lobe (Talairach coordinate: $x = 11$, $y = -71$, $z = -6$/Lingual Gyrus) were also modulated by the distance between the probe and the reference points on the number line. No significant parametric modulation in response to "landmark distance" was found in the BE condition.

The parametric modulation of the right IPS perfectly overlapped with the number specific activation found in the conjunction contrast "[NLE > BE]∩[NLE > control]" (see Fig. 4). In other words, the reverse landmark distance effect was found within the same brain region that was found to respond more to the number line than the brightness estimation task. Moreover, note that the parametric "*landmark distance*" effect is the reverse of the numerical distance effect, which is typically found in numerical comparison tasks. Therefore, the "*landmark distance*" effect is not indicative of a numerical comparison (i.e., the probe and the landmark), but rather

indicates the engagement of quantitative mechanisms that is modulated by the distance of the probe and the closest landmark.

4. Discussion

Number lines are used to externally represent numerical magnitudes and are frequently employed in developmental research to examine how number processing changes over the course of learning and development (e.g., Booth & Siegler, 2006; Siegler & Booth, 2004). Although many studies have examined the neuronal correlates of numerical comparison (e.g., Ansari et al., 2005; Pinel et al., 1999, 2001) and number adaptation (e.g., Cohen Kadosh et al., 2007; Notebaert, Nelis, & Reynvoet, 2010; Piazza et al., 2007, 2004), the brain regions that are involved placing numerals onto physical number lines are currently unknown. To fill this gap, the present study explored the neural correlates that can be associated with estimating the spatial position of numerical magnitudes on horizontally oriented reference lines (i.e., number line). Furthermore, in order to better characterize the neural architecture that is specifically involved in placing numerical symbols onto number lines, we contrasted the brain correlates of numerical magnitudes with the estimation of a non-numerical dimension — brightness. By doing so, we were able to investigate the extent to which the neural correlates of estimating the spatial position of symbolic numerical magnitudes draw upon neuronal processes that are either partly shared with non-numerical magnitudes and/or are number specific.

As predicted at the outset, results of the present study demonstrated that the parietal lobe plays a critical role in estimating the spatial position of discrete, numerical and continuous, non-numerical quantities onto physical reference lines. These are, to the best of our knowledge, the first empirical data to show that number line estimation engages regions similar to those revealed in other number processing paradigms (such as comparison and adaptation). By doing so the present data suggest that the parietal activation underlying the processing of numerical and non-numerical magnitude are process rather than task-specific. In other words, by being convergent with findings from other paradigms measuring numerical magnitude processing, the present data provide compelling evidence in support of task independent mechanisms in the IPS when numerical and non-numerical magnitude are processed.

In addition to providing evidence to demonstrate that number and brightness estimation independently activated the parietal cortex, a conjunction analysis of number and brightness revealed an extensive activation overlap of activation correlated with number and brightness estimation in the right IPS. Moreover, a second analysis, contrasting the brain activation evoked by the number line estimation task with those correlated with each of the other tasks, revealed number specific activations within bilateral regions of the anterior IPS. Therefore, by demonstrating that estimating the spatial position of symbolic numerals encompasses additional regions of the bilateral anterior IPS, above and beyond the common activation in the right hemisphere, the present study provides data that necessitate an account that goes beyond the notion of a single common magnitude code. Furthermore, a parametric analysis, which aimed to investigate the influence of "landmark distance" on brain activation, revealed that the right anterior IPS of the parietal cortex was significantly modulated by the distance of the probe to its closest reference point in the NLE condition. Thus, demonstrating that the right IPS is critically involved when participants are asked to estimate the position of a numerical probe along the number line and that its activation is dependent on the distance between the probe and its closest landmark. Given that the right IPS has been revealed here and in other studies as being a region that is critical for the basic processing of magnitude, the landmark distance effect findings may reflect an increasing engagement of approximate quantity processing as a function of how informative (distant) the landmarks are. In other words, when the number to be estimated is close to a landmark, less magnitude related processes in the right IPS are engaged compared to when the difference between the number and the closest landmark is relatively large. Furthermore, the data show a critical difference between processing of numerical and non-numerical estimates, since the brightness estimates were not subject to a landmark distance effect at either the brain or behavioral levels of analyses. While the absence of a landmark effect in the BE task does not exclude the possibility that participants used other landmarks to inform their brightness estimates, it does, however highlight, that the mechanisms underlying the estimation of brightness and symbolic numerical magnitudes along a number line differ significantly.

Similar hemispheric dissociations for the processing of discrete numerical and continuous non-numerical magnitudes were revealed in previous functional imaging studies using comparison, but not estimation tasks. One of the earliest studies, to find hemispheric differences across magnitude dimensions, employed number, brightness and size comparison tasks (Cohen Kadosh et al., 2005). Results of this study showed that the right IPS was engaged to the same extent across all three comparison conditions, whereas the left IPS was more strongly activated in the numerical condition, providing initial evidence for possible hemispheric differences for the processing of numerical and non-numerical magnitudes.

Moreover, significant activation overlap between numerical and non-numerical magnitudes in the right IPS was also found in studies that contrasted neural correlates of number and length comparisons using linear dot arrays (Dormal & Pesenti, 2009), the comparison of physical size of disks, number of dots in arrays, as well as positive and negative integers (Chassy & Grodd, 2011), as well as judging the numerosity of flashed dot sequences in contrast to estimating how long a dot was presented on a screen (Dormal, Dormal, Joassin, & Pesenti, 2011). All of these studies strongly point to the right IPS as a region that is engaged during the processing of both numerical and non-numerical dimensions. Also consistent with the present data, these studies revealed that in addition to the overlapping activation of the right IPS in response to different magnitude tasks, significant number specific activation was associated with activation of the left IPS. The present results, therefore, strengthen the hypothesis that the processing of numerical magnitudes is associated with the additional engagement of left IPS regions, and that the numerical domain should be treated as a special domain amongst other magnitudes.

Taken together, the hemispheric differences revealed in the present study are strikingly similar to a growing body of studies that probe the neural correlates of numerical and non-numerical magnitude processing. This convergence of evidence across findings with different methods and stimuli, provide strong support for hemispheric differences in the processing of numerical and non-numerical magnitudes. By doing so, the present data suggest that these activations are not task specific but may be category specific (discrete vs. continuous) and demonstrate that these differences generalize across number processing paradigms. A similar sensitivity of the bilateral IPS has been demonstrated in adults in response to numerical and non-numerical discrete dimensions. Fias et al. (2007) asked participants in three tasks to decide which of two simultaneously presented numerals is larger, which of two simultaneously presented letters comes later in the alphabet, and which of two simultaneously presented colored squares was most saturated. Results of this imaging study revealed brain responses in regions of

the bilateral anterior IPS in the number and letter task, but not for the saturation task. Thus, the results of this study suggested that similar regions in the brain respond to the comparison of discrete dimensions regardless of the format. However, using the same dataset and a multivariate approach (i.e., multi-voxel pattern analysis (MVPA) using a support vector machine) in order to further investigate representational similarities or differences between these dimensions, Zorzi, Di Bono, and Fias (2011) demonstrated that distinct sets of voxel discriminate between numerical and non-numerical categories within the anterior IPS. Together, the data suggest that discrete dimensions regardless of format exhibit a similar activation topography when analyzed in a univariate approach, but distinct pattern can be found for numbers and letters within these regions.

In addition to hemispheric differences, the results of the present data revealed an interesting anterior-to-posterior organization, with number specific activations being associated with anterior portions of the IPS, while activation common to both numerical and non-numerical estimation was associated with more posterior sections of the right IPS. A similar anterior-to-posterior distribution was found in the above-discussed study by Dormal and Pesenti (2009). Specifically, the authors showed a number specific activation within anterior bilateral regions of the IPS, and an activation overlap for number and length at posterior sections of the IPS. Similarly, Pinel et al. (2004) found overlapping activation for size and brightness comparison in bilateral regions of the posterior IPS, while numerical comparison was associated with activation in more anterior regions of the IPS. These data are therefore consistent with the present findings in suggesting the existence of an anterior-to-posterior organization of the IPS for processing numerical and non-numerical magnitudes. One possible explanation for such activation differences is, that numbers undergo a crucial process of enculturation, which reorganizes the functional brain architecture for processing numerical information substantially. Such reorganization might be driven by a process of abstracting numerical from non-numerical magnitudes. In this context it should also be considered that there considered there were no regions specifically associated with brightness estimation. While it is hard to interpret such a null result, one might speculate that numerical magnitudes are associated with specialized brain circuits that are abstracted (though not fully) from those associated with the processing of non-numerical magnitudes, which share a common set of brain circuitry in the right parietal cortex.

It should be noted that in addition to demonstrating parietal activation, the present results also revealed activation differences and commonalities of the brightness and number estimation task in a number of frontal areas. More specifically, we found number specific as well as common activation for numerical and brightness estimation in two distinct regions of the right middle frontal gyrus (MFG; see also Tables 4 and 5). Prefrontal activations are commonly found in numerical tasks. However, while the functional role of the IPS in symbolic numerical representation is well established, the role of the frontal cortex is less well understood. Neurobiological evidence from single-cell recording in monkeys has suggested that the prefrontal cortex (PFC) may be related to high-order associations between numerical quantities and their symbolic referents (Diester & Nieder, 2007). Developmental studies have frequently found stronger recruitment of prefrontal regions in children compared to adults (Ansari et al., 2005; Kaufmann et al., 2006). This evidence suggests an ontogenetic shift from prefrontal regions towards parietal regions for numerical magnitude processing but also points towards the frontal cortex as important structure for number processing. However, alternatively it has been contested that prefrontal activation in numerical tasks might be related to non-numerical mechanisms such as working memory or attention, and that activation of this regions are not directly linked to numerical representations per se (Kaufmann et al., 2006; Rivera, Reiss, Eckert, & Menon, 2005). In addition to the number related activation, the conjunction analysis of number and brightness revealed joint activation in the right MFG. The region to be found modulated by both tasks was centered anterior and directly adjacent to the number-specific activation, an activation pattern that mirrors a recently proposed cognitive control hierarchy in which abstract, high-order control is functionally organized along the posterior-to-anterior axis of the prefrontal cortex (e.g., Badre, 2008). Functional imaging work and neurophysiological studies with monkeys have both reported activation in frontal regions in response to the processing of different magnitudes such as line length and number (e.g., Pinel et al., 2004; Tudusciuc & Nieder, 2009). However, a recent neurophysiological study could demonstrate that prefrontal neurons, which are tuned for the processing of space and time, are linked by prospective goals rather than common representation of magnitude (Genovesio, Tsujimoto, & Wise, 2012). This finding suggests that common magnitude related activation in prefrontal regions, which are often observed in fMRI studies, may be related to non-numerical processes and can be distinguished from representational activation. Whether activations of the frontal cortex in the present study can be directly linked to magnitude representations, or whether such activation patterns are due to the involvement of additional non-numerical cognitive resources cannot be answered with this study. The involvement of frontal regions in magnitude related tasks needs to be further explored in order to tease apart the above discussed possibilities.

Besides investigating the commonalties and differences in the brain responses associated with number and brightness estimation, we investigated the neural effects that reference points in the number line tasks exerted on the brain. For this we conducted a parametric landmark reference point analysis in which we analyzed the effect of distance of each numeral to the closest reference point (i.e., 0, 50, 100) on brain activation. Results of this whole-brain analysis revealed a significant modulation of the right IPS in the number condition only. In other words, the acquired BOLD signal in the number task was larger for trials in which the numerals were farther away from landmarks (i.e., 0, 50, 100) compared to trials in which the numerals were closer to the landmarks. Behavioral studies have frequently reported the influence of landmarks in number line tasks, demonstrating that placing a numeral onto the number line is less accurate when the numeral is farther away from a reference point (e.g., Siegler & Opfer, 2003). However, the cognitive mechanism that underlie this process are largely unknown. The present study provides evidence, for the first time, that landmarks have a significant impact on signals of the parietal cortex. Recent developmental studies have suggested an early sensitivity of the right parietal cortex towards non-symbolic magnitudes such as dot arrays. For example, Cantlon, Brannon, Carter, and Pelphrey (2006) were able to demonstrate a neural adaptation effect in the right parietal cortex in response to a passive presentation of dot-arrays (non-symbolic numersoities). Moreover, a recent imaging study that used Near-Infrared Spectroscopy (NIRS) was able to find an early specialization of the right parietal cortex in 6-month old pre-verbal infants (Hyde et al., 2010) in response to the presentation of non-symbolic numerosities. These studies provided compelling evidence that the right parietal cortex, and more specifically the right IPS, is engaged in basic non-symbolic numerical processes from early on in life. The parametric modulation of the right IPS found in the present tasks suggests the involvement of such basic numerical processes when numerals are placed onto number lines. More specifically, the stronger engagement of the IPS in trials in which numerals were farther apart from landmarks,

might be indicative of a greater involvement of basic numerical estimation processes that are needed in order to better judge the actual position of the numeral on the line. This argument is in line with the idea that reference points provide additional guidance for placing numerals onto a number line and that less numerical estimation processes are needed to find the right location on the number line for numerals for which a reference is close by. Interestingly, a reverse numerical distance effect (that is more activation for far distances compared to close distances) on brain activation in the IPS was also found in a numerical ordinality task, in which participants were asked to decide whether three simultaneously presented numerals were presented in "correct ascending order" (e.g., 22 23 25) or not (Franklin & Jonides, 2009). The authors suggested, that the presence of the reverse distance effect in brain activation is further evidence that different neurocognitive mechanisms are in engaged depending upon whether numerical magnitude or numerical order information is accessed.

While the reverse distance effect in the ordinality task is similar to the landmark distance effect revealed here, it is important to note that there are important differences between these tasks. Specifically, the number line task involves the mental act of estimating the correct position of a given numeral on the number line and the reverse distance effect may reflect the degree to which quantitative information is being drawn upon to make this judgement. In contrast, the reverse distance effect in the ordinality task is thought to reflect the sequential nature of the numerical set and the fact that ordinality can be processed more easily when numbers are presented in a correct order with close distances between the numbers. Interestingly, the neural correlates of the reverse distance effect in the ordinality task by Franklin and Jonides (2009) was found to be left lateralized, whereas the reverse landmark distance effect in the present study, was found to be lateralized to the right hemisphere. These hemispheric differences might be reflective of different underlying processes given rise to a similar behavioral pattern. As such it would be an interesting study to compare and contrast the reverse distance effect obtained from different tasks directly. Taken together, the present findings help to further unravel the neurocognitive mechanisms that are involved in the number line estimation task and how these converge with and differ from the estimation of continuous magnitudes, such as brightness.

A few potential limitations deserve some discussion. Specifically, the behavioral data revealed that there were significant differences in reaction time and accuracy between some of the conditions. In view of this it might be argued that differences in performance between conditions are confounding the neuroimaging findings. While such an argument is legitimate, there are several reasons that speak against this concern. First, significant differences in reaction times were only found between the NLE and word control condition, but no such differences was found between the NLE and BE condition. Number specific activations, which were based on the conjunction of "[NLE > BE]∩[NLE > control]" are therefore very unlikely to be attributable to task difficulty, since the contrast between NLE > BE in this conjunction cannot be explained by reaction time differences. Thus, it seems very unlikely that the number specific activation as revealed by the conjunction is solely driven by task difficulties between NLE and the control condition. The same argument can be applied to the common activation of number and brightness, in which the statistical test used to reveal areas commonly modulated by both task was based on a conjunction of "[NLE > control]∩[BE > control]". Again, only one contrast within this analysis could be potentially explained by reaction time differences. Since a conjunction necessitates that both contrasts significantly modulate activity in a particular region, the joint activation cannot be explained by one of the contrasts alone. Thus the activations revealed by these conjunctions must be driven by factors other than reaction time differences between conditions in one of the contrasts used to define the conjunction.

Another issue that merits discussion in this context is the fact that the percent absolute errors (PAEs) differed across all conditions. In the behavioral number line literature PAEs measurements are used to estimate the precision of the representation underlying the mappings of numerical magnitude representations into space. In other words, the smaller the difference between the estimate and the estimated quantity is, the more precise the underlying representation (Booth & Siegler, 2006). Thus, it could be argued that differences in PAEs reflect natural characteristics in the noisiness of the underlying representations. In other words, the task of estimating the spatial position of continuous non-numerical dimension such as brightness may inherently differ in their noisiness, therefore in their PAEs, from that of discrete numerical magnitudes and by extension also from the control task in which an arrow is pointing to the correct position, leading to very small PAEs. Such a difference might not be seen as a confound but rather as particular characteristic differences of the processes elicited by the two tasks. However, since the number related activation is based on the conjunction contrast "[NLE > BE]∩[NLE > control]", in which number is more accurate in comparison to brightness but less accurate in comparison to the word control condition, PAE's cannot by themselves explain the number specific activation difference observed. In other words, the conjunction contrast is defined on the basis of one contrast in which number accuracy is higher compared to a control (NLE > BE), and another contrast in which number accuracy is lower compared to a control (NLE > control). Therefore, the joint activation of these contrasts "[NLE > BE]∩[NLE > control]" cannot solely be explained by differences in accuracy. Given this, we suggest that the observed differences and commonalities between the tasks can be, with some confidence, attributed to specific differences and commonalities between numerical and non-numerical magnitudes.

5. Conclusion

A large body of evidence suggests that brain regions in and around the IPS are involved in processing the quantity information of number symbols However, the brain regions that are involved in the mapping of discrete numbers onto an external reference space such as the number line are currently unknown.

The present study addressed this gap in the literature by probing the brain regions associated with number line estimation. We examined the neural correlates that are involved when numerical positions are estimated on an external reference frame, and compared them to the areas involved in estimating the spatial position of a continuous non-numerical dimension—brightness. Results showed common activation for estimating numerical magnitudes and brightness onto a spatial continuum (the line) in the right IPS. In addition, bilateral anterior regions of the IPS were specifically involved when the spatial position of numerical magnitudes was estimated. The present data extend our current knowledge of the neural basis for numerical and non-numerical magnitude processing. Specifically, consistent with the present literature, common as well as number-specific activations within regions of the IPS were found for estimating numerical and non-numerical magnitudes. These data provide further evidence to suggest that the processing of numerical magnitude, over and above the engagement of a common magnitude representation, recruits additional representational resources, especially regions of the bilateral anterior IPS, which may specialize for symbolic

number processing over the course of developmental time. Future studies should explore this possible functional specialization and how it may be constructed over the course of developmental time. In addition, the present study provides data to demonstrate that the number line task is a valid paradigm for investigating basic numerical processing in functional brain imaging research.

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