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Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes

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Abstract:

A number of functional neuroimaging studies have revealed that regions in and around the intraparietal sulcus (IPS) are parametrically modulated by numerical distance, whereby there is an inverse relationship between distance and levels of activation. These areas are thus thought to contain the internal representation of numerical magnitude. Nevertheless, it has also been suggested that the IPS is involved in response selection during number comparison tasks rather than the representation of numerical magnitude per se. In order to test the independence of the effect of distance on cortical regions we employed a passive viewing paradigm. 16 right-handed male participants viewed rapidly changing slides containing arrays of squares. By varying the distance between the numerosity presented in separate blocks (8 vs. 8, 8 vs. 12, and 8 vs. 16) we examined which regions exhibit a parametric effect of numerical distance. This analysis revealed such effects in the superior part of the IPS bilaterally as well as the superior parietal lobule and the supramarginal gyrus. In contrast, slides rapidly changing in area but not number (Area constant, Area x1 and Area x2) did not yield a parametric effect of distance in these regions. Instead a reverse effect of area was found in a region of the calcarine sulcus. These findings suggest that areas in and around the IPS are involved in numerical magnitude discrimination in the absence of an explicit task and response requirements.
Theme I: The Neural Basis of Behavior

Topic: Cognition

Keywords: Functional MRI; numerical cognition; numerical magnitude; distance effect; intraparietal sulcus
1. Introduction:

How does the brain enable the representation of numerical magnitudes? Much research into the neural basis of numerical magnitude processing today is related to an influential paper by Moyer & Landauer (1967). In this paper, the authors reported that reaction time is inversely related to the distance between numbers when adults perform relative magnitude comparisons. This so-called ‘numerical distance effect’ has since been studied in young children, infants and animals (Brannon & Terrace, 1998; Feigenson, Dehaene, & Spelke, 2004; Huntley-Fenner & Cannon, 2000; Sekuler & Mierkiewicz, 1977; Xu & Spelke, 2000). The distance effect is well replicated and is thought to reveal important characteristics of the semantic organization of numerical magnitudes. The fact that it can be measured in both animals and preverbal infants suggests that it represents a fundamental property of the way in which numerical stimuli are processed. In this vein, it has been hypothesized that numerical magnitudes are represented on a “number line”, where magnitudes close to each other share more variance in representational signal than those relatively far apart and are therefore harder to discriminate.

In addition to the behavioral findings, functional neuroimaging studies have revealed the neural correlates of the numerical distance effect. In a series of studies using both functional Magnetic Resonance Imaging (fMRI) and event-related brain potentials (ERPs), Pinel et al, 1999, 2001 isolated the neural correlates of different stages of processing during number comparison of both number words and Arabic numerals. While identification of Arabic numerals and number words led to activation of different brain areas, the activation converged on areas in and around the intraparietal sulcus (IPS) and precuneus during the numerical magnitude comparison stage. Moreover, activation of
these parietal sites was found to be correlated with numerical distance. In other words, greater parietal activation was observed for close compared with far numerals. Such parametric effects of numerical distance on parietal cortex suggest that the IPS contains the internal representation of numerical magnitude and is involved in the discrimination of numerical stimuli.

In more recent work, Pinel, Piazza, Le Bihan, & Dehaene (2004) have directly contrasted the neural correlates of different comparative judgments. Participants were asked to compare stimuli for size, luminance and number. While the effect of distance on brain activation resulted in different local peaks for each comparison condition, substantial overlap in activation along the IPS between conditions emerged. This may suggest that neurons in and around the IPS contain a distributed and overlapping code for continuous quantity, with an activation peak in the horizontal segment of the right IPS for number comparisons. Thus, while the IPS appears to house the semantic representation of numerical magnitude, its features may overlap with those necessary to perform discrimination of other continuous stimulus variables.

In related work, it has been shown that effects of number discrimination on the IPS are not restricted to symbolic stimuli such as Arabic numerals and number words, but extend to non-symbolic stimuli such as judgments of angle width and line lengths (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003). Such findings have led to the contention that the IPS contains a stimulus-independent representation of numerical magnitude. Moreover, in a task requiring no explicit attention to numerosity, numerical stimuli were found to lead to greater bilateral activation of the IPS than color words or letters (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). Importantly, the response of the IPS was
greater for numerical stimuli regardless of whether these were presented as visual or auditory stimuli. Thus, the representation of numerical magnitude in the IPS appears to be both stimulus-independent and amodal. Recent data from single-cell physiology also supports the involvement of the IPS in numerosity representations (Nieder & Miller, 2004).

However, the IPS is also activated when participants select a response, independently of whether such a response is made in the context of number-related tasks (Culham & Kanwisher, 2001; Jiang & Kanwisher, 2003). This calls into question whether the IPS modulates numerical magnitude processing over and above response selection (Gobel & Rushworth, 2004). In a recent experiment, Gobel, Johansen-Berg, Behrens, & Rushworth (2004) compared activation of the IPS during number comparison with a control task in which participants had to judge whether a vertical line was absent or present. While the contrast of number comparison against rest revealed activation in the IPS, the contrast between the number comparison and control task revealed no significant activation in the IPS. These results suggest that activation in the IPS during number comparison may be related to response selection and task difficulty, rather than semantic processing of numerical magnitude or number-specific discrimination. In other words, greater activation of the IPS for close vs. far numerical distances may reflect nothing more than the increased level of difficulty in response selection.

One way to dissociate processes related to task difficulty and response selection from those involved in the semantic processing of numerical magnitude is to utilize a passive design in which participants are not required to make any active responses. If the IPS contains the semantic representation of numerical magnitude, effects of numerical
distance on this cortical network should be observed even when no active response is required.

To assess this possibility, participants were presented with alternating slides of 8 vs. 8 (distance 0), 8 vs. 12 (distance 4) and 8 vs. 16 (distance 8) squares in separate blocks. We predicted that if distance modulates activation of the IPS in the absence of active decision making and response requirements, a negative, parametric relationship between numerical distance and BOLD signal should emerge in the IPS, whereby rapid changes between 8 & 8 would lead to the greatest responses and stimulus changes between 8 & 16 would lead to the smallest responses. To ascertain whether any effect of distance on neural activation patterns was specific to numerosity, we also presented participants with square stimuli which remained constant in number but varied in area. To match the physical magnitude of change in the area condition with that of the number condition, participants were presented with displays of 8 squares, where each individual square increased in area either by a factor of 1, 1.5 or 2. We predicted that if the presentation of stimuli invoked generalized, higher-level visual discrimination of continuous stimulus attributes, then distance in both the number and area conditions should have similar effects on the neural response. If, however, the rapid changes in numerical stimuli lead to passive discrimination of numerosity, we would expect the effects of numerical distance to differ from those for area.
2. Method:

2.1 Participants

16 healthy, right-handed, male adults (mean age = 20 years; 5 months) participated in this experiment. The procedure was approved by the Committee for the Protection of Human Subjects at Dartmouth College and all participants signed informed consent. Subjects were not told the purpose of the experiment and were simply instructed to fixate on a small white crosshair in the centre of the screen.

2.2 Procedure and Task Design

In each run subjects were presented with blocks of rapidly changing slides of white squares against a black background (see Figure 1). Stimuli were produced using Adobe Photoshop CS™ and were presented with E-Prime (Psychological Software Tools, Pittsburgh, USA). All the squares within a slide were of the same size, and randomly arranged within the constraint that there was no spatial overlap between squares. There were five different types of stimuli blocks: Number x 2.0, Number x 1.5, Constant x 1.0, Area x 1.5, Area x 2.0. Each block contained a total of 80 slides. Each number change (Number x 1.5 and Number x 2.0) and area change (Area x 1.5 and Area x 2.0) block contained two types of slides, 40 of each type. For the number change blocks, there were 40 slides of each number, i.e. 40 slides of 8 squares and 40 slides of 12 squares in each Number x 1.5 block; 40 slides of 8 squares and 40 slides of 16 squares in each Number x 2.0 block. Similarly, for each area change block (Area x 1.5 and Area x 2.0), there were 40 slides for each square size. In the Constant x 1.0 blocks, participants viewed 80 slides of 8 dots with area and number held constant between slides. To ensure
that changes in numerosity were disconfounded from changes in total area occupied by
the squares, the total area occupied by the squares in the numerosity conditions was
equated within and between blocks. To enable a comparison between area changes, the
total area occupied by squares was equated between conditions. In other words, the total
area occupied by the combination of all slides in the Area x1.5 condition was equivalent
to the total area taken up by summing the slides of squares in the Area x2.0 condition.
Moreover, the total area occupied in each of the area conditions was equated with the
total area occupied by squares in the number conditions. Thus, for all conditions the total
area was the same. This enabled comparison between all conditions.

Each slide was presented for a total duration of 250 milliseconds with no fixation
ISI between slides. The order of presentation of the slides within each block was
randomized by the stimulus presentation software. Blocks were separated by 20 seconds
of rest, during which participants fixated on the centrally located white crosshair.
Participants saw a total of 7 repetitions of each block type. The order of the block types
was completely randomized for each run. Each run of stimulation began and ended with
30 seconds of rest. Between runs, participants were reminded by the investigators to
concentrate on the white crosshair and were given a short break.

- FIGURE 1 ABOUT HERE -

2.3 Data Acquisition

Functional images were acquired in a 1.5T General Electric whole body MRI
scanner. A standard birdcage head coil was used and head movements were restricted
through the use of a foam pillow. Using a fast spin echo sequence, 25 T1 weighted
structural slices were acquired in the axial plane. Coplanar to the T1 weighted structural images, functional images were acquired using a gradient echo-planar T2*-sequence sensitive to blood-oxygenation level-dependent (BOLD) contrast. Image volumes consisted of 25 noncontiguous slices (4.5 mm thickness, 1 mm gap, 64 by 64 matrix, repetition time = 2.5 s, TE = 40 ms, flip angle = 90°, field of view = 24 by 24 cm) covering the whole brain. Each run of functional imaging consisted of the acquisition of 96 volumes. Three-dimensional whole-brain high resolution (0.94 X 0.94 1.2), T1 weighted images were acquired in the sagittal plane using a standard GE SPGR 3-D sequence.

2.4 Data Analysis

Structural and functional images were analyzed using Brain Voyager QX 1.2.6 (Brain Innovation, Maastricht, Holland). Functional images were corrected for slice time acquisition differences, head motion and linear trend. Functional images were aligned to the T-1 weighted co-planar images and subsequently to the three-dimensional high-resolution images. The realigned data set was then transformed into Tailarach space (Talairach & Tournoux, 1988).

Following the numerical distance effect, we investigated which areas of the brain exhibited parametric effects of distance (area or number) on BOLD signal. We therefore constructed a parametric general linear model (GLM) design matrix with two predictors: 1. ‘Number Change’ effect, 2. ‘Area Change’ effect and a non-parametric predictor 3. ‘Common Activations’ (see Figure 2). Based on behavioral data and previous neuroimaging studies of the distance effect, we expected smaller signal change for those conditions with greater changes in distance (area or number), and we weighted the
Number Change and Area Change predictors accordingly, e.g. for the Number Change predictor, the smallest weight was given to the Number x2.0 blocks. The Common Activations predictor captures generic task related activation that is not modulated by changes in number or area. Our parametric design matrix was then convolved with the expected BOLD signal. Following Boynton, Engel, Glover, & Heeger (1996), the expected BOLD signal change was modeled using a gamma function (tau of 2.5 seconds and a delta of 1.5). Random-effects analyses were performed to examine the effects of all three predictors in this parametric GLM. Voxels were considered to be significantly activated when they passed a threshold of p<.0001, uncorrected. Using our parametric predictors we identified regions sensitive to 1. Number Change and 2. Area Change. To verify that the parametric predictors in the parametric GLM accurately modeled the signal changes in these regions-of-interest (ROI), we ran a separate, non-parametric, GLM analysis on each ROI, modeling each condition with a separate predictor. The parameter estimate of each predictor from this GLM would yield a more direct estimate of the activation level for each condition. To illustrate graphically how well these two GLMs matched, the results obtained from the parametric GLM was then plotted together with the results from the non-parametric GLM (Figures 3, 4 and 5).

- FIGURE 2 ABOUT HERE -
3. Results:

3.1 Number Change Effect

Bilateral regions in the intraparietal sulcus and the superior parietal lobule were sensitive to the number effect at our selected threshold. Additional activation was observed in the left supramarginal gyrus. See Figures 3

- FIGURE 3 ABOUT HERE -

3.2 Area Change Effect

The only cortical region exhibiting the predicted effect (greater activation for smaller difference in area change) was the right precentral gyrus. In addition, an effect in the reverse direction (greater activation for larger differences in area change) was found in the left calcarine sulcus. See Figure 4.

- FIGURE 4 ABOUT HERE -

3.3 Common Activations

Activations common to all tasks were found in a large network of areas comprising bilateral occipital and parietal, as well as left prefrontal areas. We verified that there were no specific effects of number change and area change in these regions. We present a subset of these regions in Figure 5.

-FIGURE 5 ABOUT HERE -
4. Discussion

We report an effect of numerical distance on regions in and around bilateral intraparietal sulci, as well as in the superior parietal lobules. It is thought that the numerical distance effect on reaction time and accuracy provides important insights into the features of numerical magnitude representations. The distance effect suggests that the representational features of numerical magnitudes close to each other overlap more than those far apart. A number of studies have revealed that areas in and around the IPS are sensitive to numerical distance (Dehaene, 1996; Pinel et al., 2001; Pinel et al., 1999; Pinel et al., 2004). Such findings and the general observation that the IPS is involved in number processing and calculation has led to the suggestion that the IPS contains the internal representation of numerical magnitude. Yet, to date paradigms exploring the numerical distance effect have required participants to make active responses (such as judging whether a number on a screen is larger or smaller than a reference). This has thus far left open the possibility that activation in the IPS and other parietal areas during number discrimination is attributable to response-selection rather than representation and discrimination of numerical magnitude (Gobel et al., 2004; Gobel & Rushworth, 2004). The results reported above throw new light on this debate by revealing a parametric effect of numerical distance on the bilateral IPS and the superior parietal lobules in the absence of any active response. This suggests that the IPS is involved in numerical magnitude discrimination over and above response-related activation.

The areas found to exhibit a significant distance effect overlap closely with those reported to exhibit parametric modulation of distance in active tasks involving symbolic stimuli (Pinel et al., 2001; Pinel et al., 1999; Pinel et al., 2004). Moreover, the bilateral
inferior parietal sites found here are close to the horizontal segment of the intraparietal sulcus (HIPS) which, it has been argued, contains the core representation of numerical quantity (for a review see Dehaene, Piazza, Pinel, & Cohen, 2003).

In addition to areas close to the HIPS, we found superior parietal activations, bilaterally. The role of the superior parietal lobule in number processing is poorly understood, though it has been suggested that its involvement reflects spatial attentional resources both related to and independent of number processing (Dehaene et al., 2003). It is plausible that a superior parietal system for visuo-spatial processing directs attention to numerically relevant dimensions of stimuli and tracks their transformations. In the context of the present findings it might be plausible that greater attentional resources for discrimination of numerical stimulus characteristics are required when the numerical distance is small.

However, these effects cannot be solely attributed to differences in global attention across conditions. If the effect of numerical distance on the parietal areas was merely due to attentional effects independent of number processing, then a similar effect should have been observed for the conditions in which the total number of stimuli remained constant, while the area occupied changed. However, no significant ‘area distance’ effect on parietal regions was observed. An ‘area distance’ effect on parietal regions revealed for the ‘number distance’ effect was also absent at a more generous statistical threshold \( p < .001 \), uncorrected. The only region which was found to exhibit such an effect was the right precentral gyrus. Interestingly, the reverse of the predicted distance effect (i.e. greater activation for large compared with small differences in area) was found in a region of the left calcarine sulcus. The calcarine sulcus is typically
involved in basic visual processing. It therefore seems likely that the greater activation of this region for greater area differences is related to the greater visual discriminability of larger differences in area occupied by squares. Moreover, many cortical regions were activated to similar extents for all conditions, and were not modulated by number or area change in either the predicted or reverse directions. This included regions in the bilateral calcarine sulcus and the inferior parietal lobe which were close to those exhibiting Number Change and Area Change effects, and the dorso-lateral prefrontal cortex, which is often associated with executive functions, cognitive load and attention. Together, these results suggest that the parametric effect of distance on activation in the IPS and superior parietal lobes cannot be explained by global attentional effects. Instead, the data reveal a degree of specificity in response to numerosity changes.

4.1 Passive Activation of Numerosity Representation and Discrimination

The present results show that bilateral parietal regions are involved in the processing and discrimination of non-symbolic numerosity stimuli even during passive viewing. This suggests that previously reported involvement of the IPS in numerosity processing during active tasks was not just due to task difficulty and response selection. This may also explain why Shuman & Kanwisher (2004) did not find any significant difference between number and color discrimination tasks in various parietal regions. Against the background of their results, Shuman and Kanwisher challenge the notion that the IPS is the locus of a domain specific system for number representation. However, in order to equate stimulus properties across the tasks, numerosity changes occurred similarly in all conditions. Given our present findings, it is possible that the same numerosity representation and discrimination mechanisms in the IPS were automatically
activated in both number and color tasks, resulting in the lack of task differences in activation.

4.2 fMR-Adaptation for Numerosity

In the same publication, Shuman and Kanwisher reported another experiment, part of which involved passive viewing of non-symbolic numerosity stimuli. They failed to find a significant fMR adaptation effect of number in the IPS when the same non-symbolic numerosity was presented repeatedly. Interestingly, they found slightly greater activation in a condition in which numerosity was held constant across the block compared to one in which numerosity was varied within the block. The absence of adaptation of the BOLD signal in the IPS to the repetition of numerosity is taken by the authors to indicate a lack of representational specificity for number. However, these findings are actually somewhat comparable to the results reported here, as there was slightly greater activation when numerosity was repeated compared to when it was varied.

In contrast, at the same time as Shuman and Kanwisher reported their negative findings, Piazza, Izard, Pinel, Le Bihan, & Dehaene (2004) revealed fMRI adaptation effects for numerosity repetition in bilateral regions of the IPS when participants passively viewed a stream of stimuli with repeated numerosity (habituation) interspersed irregularly with stimuli of deviant numerosity. Piazza et al. found greater activation during the presentation of the deviant compared with the habituated numerosity stimuli in bilateral regions of the IPS. Furthermore, it was found that the response to the deviant numerosity increased with the degree of deviance. Again, the apparent discrepancy in results may be explained by differences in experimental paradigm. In Shuman and
Kanwisher’s study, the independent variable was simply the number of repetitions in a block. In contrast, Piazza et al. modeled the deviant trials as events of interest. In such a design, the dependent measure may be conceived as dishabituation or change detection. The greater the degree of difference in numerosity in the deviant trial, the less variance it shares with the habituated numerosity, the more salient the change.

In agreement with Piazza et al.’s findings, our data suggest that the IPS is indeed involved in the internal representation and discrimination of numerical magnitude. Yet on closer examination the two sets of results may be perceived as contradictory. While the present results suggest that areas in and around the IPS respond more when the numerical difference between two non-symbolic numerosities is small, Piazza et al.’s results suggest the opposite - greater activation of the IPS for more numerically deviant numerosities. However, it should be noted that while Piazza et al. optimized their experimental design to obtain fMRI adaptation effects (Grill-Spector & Malach, 2001), the present paradigm was not optimized for adaptation and was not designed to test this effect. Each number or area change block contained 40 repetitions of each type of stimulus, while the Constant x1.0 block had 80 repetitions of one type of stimulus. Thus, fMRI adaptation for numerosity should also be expected even in the number and area change conditions, and it is plausible that the Constant x1.0 block did not lead to a significantly greater extent of adaptation than other blocks.

This difference in design offered the opportunity to explore whether the rapid presentation of changing non-symbolic numerosities leads to greater activation of numerosity discrimination processes, exhibiting the distance effect typically observed during active tasks. While representing a well-documented effect, especially for visual
processing, the specific mechanisms and dynamics underlying fMRI-adaption are not clear. It remains for future experiments to establish the conditions under which numerosity adaptation can occur. Moreover, the distance effect and fMRI adaptation appear to generate opposite predictions with regards to functional activation, and there may be interesting interactions between these two effects. The resultant activation profile may be specifically dependent on the task and temporal specifics of stimulus presentation.

The above considerations make it likely that the present data and those reported by Piazza et al are complementary rather than contradictory. While Piazza et al.’s results reveal the degree of overlap in the representation of numerical magnitude, the present findings suggest the existence of neuronal mechanisms for numerosity discrimination that exist in the absence of response requirements.

**Conclusion:**

The numerical distance effect has provided significant insights into the nature of numerical magnitude representations. A number of functional neuroimaging studies have implicated areas in and around the IPS in numerical magnitude processing and have revealed that numerical distance has parametric effects on the activation levels in the IPS. Despite this, there has been controversy over the neural correlates of the numerical distance effect. It has been contended that activation of the IPS during magnitude processing reflects response selection rather than magnitude representation per se. Results from our study suggest that even when participants are not made aware of the purpose of the study and are not required to select a response, the IPS is parametrically
modulated by numerical distance. In contrast, no such parametric effect on the IPS was found when area instead of number was varied. Thus our findings suggest a degree of specificity for the involvement of the IPS in numerical magnitude discrimination.
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References:


Figure Captions

Figure 1
Examples of all stimulus conditions and timings. Every 20s block consisted of 80 randomly presented stimuli, each presented for 250ms.

Figure 2
Schematic of the parametric predictors used in the GLM. Based on the distance effect, greater BOLD signal change is expected for smaller changes in number or area. The Common Activations predictor captures generic task related variance that is not modulated by changes in number or area.

Figure 3
Bilateral parietal regions showing significant (p<.0001, uncorrected) parametric decrease of activation with increasing distance in number change in a random effects GLM. Red lines indicate the effects of Number Change, and green dotted lines indicate the effects of Area Change. Lines were calculated by estimating the three data points from the predictor betas and the weights for each condition. To illustrate the match between the parametric predictors and individual conditions, the z-scores and standard errors for each condition were also calculated. These estimates for each condition are shown in the blue bars. Error bars indicate the standard error of the mean.

Figure 4
Left calcarine region showing significant (p<.0001, uncorrected) parametric increase of activation with increasing distance in area change in a random effects GLM using
parametric predictors. Red lines indicate the effects of Number Change, and green dotted lines indicate the effects of Area Change. Lines were calculated by estimating the three data points from the predictor betas and the weights for each condition. To illustrate the match between the parametric predictors and individual conditions, the z-scores and standard errors for each condition were also calculated. These estimates for each condition are shown in the blue bars. Error bars indicate the standard error of the mean.

*Figure 5*

Activation profiles from some regions that showed significant Common Activations across all conditions (p<.0001, uncorrected) in a random effects GLM, but did not show any modulation with Number Change or Area Change. Red lines indicate the effects of Number Change, and green dotted lines indicate the effects of Area Change. Lines were calculated by estimating the three data points from the predictor betas and the weights for each condition. To illustrate the match between the parametric predictors and individual conditions, the z-scores and standard errors for each condition were also calculated. These estimates for each condition are shown in the blue bars. Error bars indicate the standard error of the mean.
Number x2.0
Number x1.5
Constant x1.0
Area x2.0
Area x1.5

Time
250 msec.
250 msec.
250 msec.
Number Change Effect

Area Change Effect

Common Activations

Area x2.0  Area x1.5  Constant x1.0  Number x1.5  Number x2.0
Parietal Regions Sensitive To Number Change

Right Inferior Parietal
(30, -43, 57)

Left Inferior Parietal
(-26, -47, 58)

Right Superior Parietal
(13, -61, 54)

Left Superior Parietal
(-16, -60, 57)

z-scores

Number Change
Area Change

R

BRES-D-05-00344
Left Calcarine Sulcus
(-12,-66, 6)

- Number Change
- Area Change

BRES-D-05-00344