

1 Attentional amplification of neural codes for number
2 independent of other quantities along the dorsal visual
3 stream

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20 Abstract

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22 Humans and other animals base important decisions on estimates of number, and
23 intraparietal cortex is thought to provide a crucial substrate of this ability. However, it remains
24 debated whether an independent neuronal processing mechanism underlies this “number
25 sense”, or whether number is instead judged indirectly on the basis of other quantitative
26 features. We performed high-resolution 7 Tesla fMRI while adult human volunteers attended
27 either to the numerosity or to an orthogonal dimension (average item size) of visual dot
28 arrays. Numerosity explained a significant amount of variance in activation patterns, above
29 and beyond non-numerical dimensions. Its representation was progressively enhanced along
30 the dorsal visual pathway and was selectively amplified by attention when task relevant.
31 These results reveal a dedicated extraction mechanism for numerosity that operates
32 independently of other quantitative dimensions of the stimuli, and suggest that later stages
33 along the dorsal stream are most important for the explicit manipulation of numerical
34 quantity.

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38 Introduction

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40 One largely debated theme in cognitive neuroscience is how the human brain developed
41 the ability to perform mathematics. While mathematical skills certainly rely on the interplay of
42 a wide range of cognitive functions (De Smedt et al., 2013; Fias, 2016; Luculano and Menon,
43 2018), an influential theory in the field proposes that a necessary prerequisite to develop
44 such a sophisticated uniquely human ability resides in the ‘number sense’ (Dehaene, 1997).
45 This is a phylogenetically ancient competence that enables humans and other animals to
46 assess and mentally manipulate the approximate number of objects in sets. In humans the
47 precision of the number sense (or ‘numerical acuity’, typically measured by visual number
48 discrimination) sharpens with age and with the acquisition of formal mathematical education
49 (Piazza et al., 2013), and correlates with arithmetical skills throughout the life-span (Halberda
50 et al., 2008; Libertus et al., 2011, 2013; Chen and Li, 2014; Anobile et al., 2016a, 2018).
51 Deviations from the typical developmental trend of numerical acuity can be a symptom of
52 developmental dyscalculia (Piazza et al., 2010), a neurodevelopmental disorder that causes
53 specific mathematical learning difficulties.

54 The neural substrate subtending this sense of numerical quantity is thought to be shared
55 across species and has been linked to a network of areas in the frontal and parietal cortices
56 sensitive to changes in numerosity since very early in life (Izard et al., 2008; Hyde and
57 Spelke, 2011; see for reviews: Cantlon, 2012; de Hevia et al., 2017). In these areas
58 electrophysiological recordings in monkeys identified single neurons tuned to specific
59 numerosities of visual arrays (Nieder et al., 2002; Nieder and Miller, 2004; Roitman et al.,
60 2007; Nieder, 2016) and fMRI studies in humans found activation in these areas to be
61 modulated during quantity perception as well as during calculation (for reviews see:
62 Arsalidou and Taylor, 2011; Eger, 2016; Piazza and Eger, 2016). While the first imaging
63 studies in humans were limited by the low spatial resolution and univariate subtraction-based
64 analyses, fMRI adaptation and multivariate pattern analysis methods provide higher
65 sensitivity to finer-scale activity differences (Kourtzi and Grill-Spector, 2005; Norman et al.,
66 2006; Tong and Pratte, 2012). These methods allowed researchers to study the
67 representation of individual numbers by recording the distance-dependent signal release
68 from adaptation (Piazza et al., 2004), or reading out patterns of number-related activity
69 across multiple voxels of the frontal and parietal cortex (Eger et al., 2009). Moreover,
70 population-receptive field mapping (pRF) methods identified individual locations tuned to
71 specific numerosities arranged in spatially organized maps in the parietal cortex (Harvey et
72 al., 2013).

73 While these earlier findings mostly pointed at the key role of parietal and frontal areas in
74 numerical representation, some recent studies found that it is possible to decode the number
75 of items seen by the subjects from the fMRI activity patterns in early visual areas (Bulthé et
76 al., 2014; Eger et al., 2015; Bulthé et al., 2015; DeWind et al., 2018, but see Castaldi et al.,
77 2016). Moreover, spatially organized numerosity maps were recently claimed to extend to the
78 occipital cortex (Harvey and Dumoulin, 2017a) and early ERP components compatible with
79 generators in early visual areas responded to variations in the numerosity of visual arrays
80 (Park et al., 2015; Fornaciai et al., 2017; Fornaciai and Park, 2017).

81 Several properties characterizing numerosity perception, such as being ratio-dependent
82 (Weber's law) and being susceptible to adaptation, led some authors to suggest that number
83 is a "primary" visual property of the image that is directly perceived through specialized and
84 dedicated mechanisms (Burr and Ross, 2008; Ross, 2010; Anobile et al., 2016b). However,
85 in spite of dedicated efforts on modeling the extraction of numerosity from the visual image
86 (Dehaene and Changeux, 1993; Verguts and Fias, 2004; Dakin et al., 2011; Stoianov and
87 Zorzi, 2012; Morgan et al., 2014), the detailed neural processing mechanisms used by the
88 brain to arrive at a representation of numerosity from the visual input remain little understood,
89 and much less understood than the ones for other basic visual features such as orientation,
90 colour, motion, etc. Numerosity is a notoriously difficult feature to study since changes in
91 numerosity tend to be associated with changes in other quantitative features of the sets
92 during natural viewing conditions (e.g., more items tend to occupy a larger area, or be
93 spaced more densely), and it appears impossible to control for all of these associated
94 quantities at the same time. For this reason, in spite of a large body of behavioural and
95 neuroscientific work on this topic, it still remains debated whether the available evidence
96 supports a dedicated neuronal processing mechanism for numerosity. Some have argued
97 instead that numerosity might be judged indirectly by weighing a combination of other, non-
98 numerical, quantitative features of the stimuli (Gebuis and Reynvoet, 2012; Gebuis et al.,
99 2014; Leibovich et al., 2016). For example, numerosity can be mathematically defined as the
100 product of density (number of items per unit of area) by field area; or by the total surface area
101 divided by mean item size. Thus, decisions on numerical quantity could be taken merely
102 indirectly, on the basis of representations of these non-numerical properties, without
103 numerosity being encoded directly by perceptual systems.

104 While this possibility is interesting, several behavioural findings argue against it: (1) the
105 discrimination of numerosity and of one often correlated non-numerical feature (item density)
106 follow different psychophysical laws (Anobile et al., 2016b), and (2) at least for relatively
107 small numbers of not too densely spaced items, perceptual thresholds for numerosity
108 discrimination are typically much smaller than the ones predicted from the thresholds for

109 density and field area together (Cicchini et al., 2016), making it unlikely that estimates of
110 numerosity are based on the latter. For what concerns the neuronal level, a few recent
111 studies have started to directly quantify the effects of non-numerical dimensions of non-
112 symbolic numerical stimuli (e.g. Park et al., 2015; Fornaciai et al., 2017; Harvey and
113 Dumoulin, 2017b; Fornaciai and Park, 2018; DeWind et al., 2018). Those studies found that
114 activity in earlier (occipital) or later (parietal) brain regions appeared to be linked to the
115 numerical content of sets after taking into account effects of certain non-numerical
116 dimensions. However, they mostly only considered the effect of one non-numerical variable
117 at the time and compare it to that of number, without taking into account effects explained by
118 all relevant non-numerical dimensions together. Thus, it still remains unclear to what extent
119 activity evoked by non-symbolic numerical stimuli within early and later regions can be
120 explained by a mechanism that encodes numerosity in itself, or by the ensemble of
121 responses to the different non-numerical dimensions of the stimuli.

122 Here, we implement a new approach to separate brain signals related to numerical and
123 non-numerical quantities and test for a dedicated neuronal mechanism for extracting the
124 numerosity of visual sets. We reasoned that the following signatures would advocate for the
125 existence of such a mechanism:

126 First, information on numerosity should be detectable in activity patterns after multiple
127 important non-numerical quantities are simultaneously (and not only individually) taken into
128 account. Second, and importantly, this information should be specifically amplified depending
129 on whether the numerical dimension of the stimuli is task relevant. If numerosity is an
130 independently encoded perceptual feature, it should be possible to selectively enhance its
131 brain representation by attention, as it has been previously shown for other task-relevant
132 primary features, such as orientation, contrast, color, direction etc. (Jehee et al., 2011; Ester
133 et al., 2016). In other words, tasks involving selective attention to number should enhance
134 the information about numerosity in the relevant brain areas, without affecting the level of
135 information on associated non-numerical dimensions. In fact, we propose that the presence
136 of such attentional amplification is a key criterion in order to identify which brain areas
137 explicitly encode numerosity.

138 On the contrary, if activity patterns could be entirely accounted for by the combination of
139 responses to multiple non-numerical dimensions of the stimuli, no information specifically
140 related to number should be found in the patterns of activity once accounting for the other
141 (non-numerical) dimensions simultaneously. Furthermore, if numerosity was not directly
142 encoded but only indirectly inferred from percepts of non-numerical properties, attentional

143 enhancement should not occur for signals related to numerosity, but if anything, only for
144 other properties (e.g., density and field area) that can jointly define it.

145 To test these predictions, we created a novel stimulus space to disentangle the
146 contribution of numerical and non-numerical dimensions to brain activity patterns, and
147 designed a task where attention is selectively directed towards either of two orthogonal
148 quantitative dimensions of the visual array (number or item size). We exploited the enhanced
149 sensitivity achieved by fMRI at ultra-high field (7 Tesla) and specific multivariate pattern
150 analyses to simultaneously model and separate the contributions of the different numerical
151 and non-numerical quantities to fine-scale activity patterns within multiple regions defined by
152 a probabilistic atlas based on visual topography.

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154 Results

155

156 We scanned twenty healthy adult volunteers while they performed two tasks on arrays of
157 dots varying orthogonally in numerosity (6, 10, or 17 items), average item size (0.04, 0.07, or
158 0.12 visual square degrees - vd^2) and total field area (44 or 20 vd^2) (Fig 1A). Participants
159 alternated between a “number” and a “size” task in different blocks: during the “number”
160 blocks they had to direct attention to the numerosity of each sample stimulus and keep it in
161 memory for comparison with an occasionally following match stimulus, while during “size”
162 blocks they performed the equivalent task on the average item size of the arrays (Fig 1B).
163 When a match stimulus appeared (indicated by a change in color of the fixation point),
164 participants had to decide whether the match stimulus was larger or smaller on the attended
165 dimension than the previous sample held in memory and to respond by button press.

166

167 Behavioral performance and univariate fMRI activation effects

168 Response accuracies for comparison of match stimuli were overall high and not significantly
169 different across tasks (86% for the number task and 85% for the average size task, $t(19) =$
170 0.46 , $p = 0.65$), suggesting that subjects attended to the correct stimulus dimension and the
171 difficulty was on average successfully matched across tasks (Fig 2A).

172 We started the analysis of the functional imaging data by evaluating overall regional
173 activation effects during both tasks. Surface-based random-effects group analysis identified
174 similar bilateral activations in the occipito-parietal and frontal cortex during both tasks for

175 sample stimuli against the implicit baseline (Fig 2B and 2C, thresholded at $p < 0.001$
176 uncorrected). To localize activity in relation to the major sulci and gyri, an anatomical brain
177 parcellation based on the Destrieux Atlas (Fischl, 2004) was superimposed onto the activity
178 maps. In both tasks the activity covered a wide occipito-parietal area starting from the
179 superior occipital and transverse occipital sulci and extending throughout the intraparietal
180 sulcus up to the post-central sulcus. The frontal activity mainly covered the superior frontal
181 gyrus. The direct contrast of sample stimulus-related activity during the number versus the
182 size task revealed no area with significantly stronger activation for either of the two, despite
183 the uncorrected significance threshold (Fig 2D). Altogether, these results suggest that task
184 difficulty was successfully matched and that under these conditions attending to different
185 quantitative dimensions leads to equivalent overall activation of the brain regions involved in
186 the task. Differences in overall activation level can therefore not confound the following more
187 specific results on the within-dimension discriminability of quantitative features.

188

189 Multivariate fMRI Pattern Analyses

190 **Read-out of sample numerosity is modulated by task**

191 Given that the whole brain univariate contrasts had confirmed equivalent activations
192 across the two tasks, we further investigated, using multivariate classification, what was the
193 degree of discriminability of activity patterns evoked by different sample numerosities across
194 different regions of the dorsal visual stream and during the number and size task. In each
195 subject we identified several regions of interest (ROIs) derived from a surface-based
196 probabilistic atlas based on visual topography (Wang et al., 2015, Fig 3A). Within each
197 region, we used an equivalent number of most activated voxels (in the orthogonal contrast
198 'all sample stimuli > baseline') to train and test multivariate classifiers to discriminate
199 between numerosities for each task. Fig 3B shows the across-subject overlap map for the
200 included voxels which mainly highlight the foveal portion of the different ROIs, in line with the
201 central presentation of the dot arrays. We first compared decoding accuracies in three large
202 regions corresponding to early, intermediate and higher level areas (including areas from V1
203 to V3, from V3AB to V7 and from IPS1 to IPS5, respectively). Then, to track the presence of
204 information discriminative of numerosity across the dorsal visual stream more in detail, we
205 further compared the classification accuracies across seven contiguous ROIs from V1 up to
206 IPS345. Fig 3C shows the performance of the classifiers trained to discriminate between
207 different numerosities as a function of task. Overall, the presented sample numerosity could
208 be decoded in all the ROIs and during both the number and size task, however with
209 important differences. When explicitly attending to numerosity, the classification accuracy

210 gradually increased across the dorsal stream (starting to be enhanced from intermediate
211 areas, specifically from V3AB on), and was highest in parietal areas. During the size task,
212 when attention was not explicitly directed towards the numerical aspect of the stimuli, the
213 different numerosities were still decodable, however the classification accuracies were
214 reduced in intermediate and higher regions, while they remained almost unchanged in early
215 visual areas (specifically in V1, V2 and V3).

216 The task-driven modulation of decoding accuracies across the three major ROIs is
217 confirmed by a significant interaction between ROI and task ($F(2,38) = 9.81, p = 0.0004$). For
218 the number task, the classification accuracy progressively increased from the early visual
219 areas (slightly above 60%) to intermediate and higher level regions where it reached almost
220 70% correct. Post-hoc tests showed that the classification accuracy increase in intermediate
221 and higher areas with respect to early areas was very close to or clearly significant ($p =$
222 0.075 and $p = 0.028$ respectively). During the size task, the classification accuracy in the
223 intermediate and higher regions dropped down to 61% and 60% respectively (yet remaining
224 highly significantly above chance in both cases, see p-values in Table 1 in Supplementary
225 materials). The change in classification accuracy across tasks was highly significant both for
226 the intermediate and higher areas ($p = 0.001$ and $p = 0.00001$). On the other hand, the
227 classification accuracy in the early visual areas remained nearly constant (62%) and was not
228 significantly modulated by task ($p = 0.5$).

229 The significant interaction between ROI and task was confirmed when testing the seven
230 individual regions ($F(6,114) = 7.17, p = 0.000002$). Although the post-hoc tests did not show
231 significant differences in classification accuracies across individual ROIs, for the number task
232 the decoding accuracies progressively increased across the visual hierarchy and varied from
233 slightly above 60% in the primary visual areas ($V1 = 62\%$, $V2 = 62\%$, $V3 = 61\%$) up to almost
234 70% in the intermediate and higher ROIs ($V3AB = 64\%$, $V7 = 65\%$; $IPS12 = 67\%$, $IPS345 =$
235 67%). During the size task, decoding accuracies were much reduced in intermediate and
236 higher regions ($V3AB=58\%$, $V7=58\%$; $IPS12=59\%$, $IPS345=58\%$, yet still significantly above
237 chance in all ROIs, see p-values in Table 1 in Supplementary materials), while they remained
238 almost unchanged in the primary visual areas ($V1 = 61\%$, $V2 = 62\%$, $V3 = 60\%$).
239 Accordingly, the post-hoc tests indicated that the classification accuracy in individual regions
240 significantly changed across tasks only from V3AB on ($V1: p = 0.28$; $V2: p = 0.83$; $V3: p =$
241 0.55 ; $V3AB p = 0.0002$; $V7: p = 0.00003$; $IPS12: p = 0.00001$; $IPS345: p = 0.00005$).

242 In sum, multivariate classification analyses revealed that the sample numerosity
243 presented could be read out from brain activity patterns in all ROIs tested during both tasks,
244 although accuracy was enhanced in mid-to-higher level but not in earlier regions when

245 number was the attended feature. However, since in this analysis activations for all sample
246 stimuli for a given numerosity were pooled together, the decoding performance obtained
247 could still be partly driven by features other than numerosity per se.

248

249 **Multiple regression RSA to disentangle the contributions of quantitative** 250 **dimensions**

251 As a critical test of whether the representations of numerical and non-numerical features
252 of the stimuli could be dissociated across the dorsal visual stream, we performed
253 Representational Similarity Analysis (RSA, Kriegeskorte, 2008; Kriegeskorte and Kievit,
254 2013) which, unlike classification-based decoding, allows to assess the effect of multiple
255 quantitative dimensions on activity patterns simultaneously. For each ROI and task, we
256 obtained a neural representational dissimilarity matrix (neural RDM, Fig 4A) by computing
257 the correlation distance between activation patterns for each possible pair of conditions. We
258 then applied multiple regression analysis to test in how far the fMRI pattern dissimilarity
259 structure could be explained by multiple predictor matrices reflecting the stimuli's dissimilarity
260 along several important quantitative dimensions: numerosity, average item size, total field
261 area, total surface area and density (Fig 4B). Of note, our design orthogonally manipulating
262 numerosity, average item size and total field area ensured that numerosity was also partly
263 decorrelated from density and total surface area (as shown by the correlation values in the
264 Predictor Correlation matrix, Fig 4B), allowing for a good dissociation between stimulus
265 descriptors. By using a multiple regression approach we capitalize on the fact that the
266 resulting beta weights reflect only the part of the variance that each one of these stimulus
267 descriptors uniquely explained in the pattern of activity of a given ROI on top of the
268 contribution of all the others. Indeed, by entering numerical and non-numerical dimensions
269 together into a multiple regression, a significantly above zero beta for number would imply
270 that the numerical information is contributing to the pattern of activity within a given ROI, over
271 and above the contribution of the other non-numerical quantitative dimensions.

272 Fig 5 displays the results of the estimated beta weights for various ROIs separately for the
273 number (Fig 4A) and size tasks (Fig 4B). Beta weights for the effect of number independent
274 of the other dimensions (black triangles) were generally positive and progressively explained
275 the activity patterns better when proceeding from lower to higher-level regions when task
276 relevant. The evolution of the numerical information across the visual stream was attenuated
277 during the size task, yet betas remained significantly above zero in all regions (see p-values
278 in Table 2 in supplementary material). Beta weights for the non-numerical dimensions (other

279 shapes in Fig 4) were pronounced predominantly in the earlier visual areas and, importantly,
280 they appeared to be not clearly affected by task.

281

282 **Quantitative dimensions are modulated by task across ROIs to different extent**

283 To statistically test for differential modulation of the contribution of the different
284 quantitative dimensions to activation patterns, beta weights were analyzed with repeated
285 measure ANOVAs with ROI, task and dimension as factors. As for the classification analysis,
286 we first focused on the three large regions corresponding to early, intermediate and higher-
287 level areas and then further on individual ROIs from V1 up to IPS345.

288 The significant triple interaction between ROI, task and dimension confirmed that the beta
289 weights estimated for the different dimensions were differently affected by task across ROIs
290 (for the three large regions: $F(4.42,80.40) = 3.32$, $p = 0.01$; for the individual regions:
291 $F(24,456) = 3.06$, $p = 0.000002$). To identify which dimension was maximally driving this
292 effect, we quantified the changes in beta weights across ROIs and tasks for each dimension
293 separately.

294

295 **Effects of the numerical dimension**

296 Beta values for number were the only ones showing a significant interaction between ROI
297 and task, when comparing the three large subdivisions across the visual stream
298 ($F(1.35,25.61) = 5.97$, $p = 0.015$). During the number task, betas for number were higher in
299 intermediate and higher-level areas with respect to early visual areas (although only the
300 former comparison was significant, $p=0.04$). During the size task the betas for number were
301 significantly lower (significant difference across tasks in early: $p = 0.007$; intermediate: $p =$
302 0.000001 ; higher areas: $p = 0.00001$) and not different across regions.

303 When focusing on the seven individual ROIs, the interaction between ROI and task was
304 significant ($F(2.04,38.83) = 5.29$, $p= 0.009$). Although post-hoc tests did not identify
305 significant differences across ROIs, linear regression showed that the increase in beta
306 weights for number across the dorsal visual stream was significant during the number task
307 only ($F(1,5) = 14.23$, $p = 0.01$, $R^2 = 0.74$), while during the size task betas for number were
308 much more homogenous across ROIs ($F(1,5)=2.37$, $p = 0.18$, $R^2 = 0.32$). Indeed the
309 difference in beta weights between the number and size task was only minor or not
310 significant in V1 and V2, more pronounced in V3, and highly significant from V3AB on

311 (difference across tasks: V1: $p = 0.025$; V2: $p = 0.13$; V3: $p = 0.001$; V3AB $p = 0.000001$; V7:
312 $p = 0.000008$; IPS12: $p = 0.000001$; IPS345: $p = 0.000112$).

313

314 **Effects of the non-numerical dimensions**

315 Different from number, beta weights estimated for the non-numerical dimensions were not
316 modulated by task (no significant interaction between ROIs and task, no significant main
317 effect of task) for any of the dimensions.

318 Independent of the task, total field area best explained activity patterns in early visual
319 areas, while its contribution was reduced when proceeding through intermediate to higher-
320 level areas (significant main effect of ROIs: $F(1.22,23.29) = 35.24$, $p = 0.000002$; significant
321 differences in beta weights between primary and intermediate or higher-level ROIs: $p =$
322 0.000155 , $p = 0.000008$, respectively). Beta values were highly significantly modulated also
323 across the different individual ROIs (main effect of ROIs: $F(2.11,40.11) = 32.27$, $p < 10^{-5}$).
324 Indeed, activity patterns in V1, V2 and V3 were explained equally well by total field area and
325 better than intermediate and higher regions, starting from V3AB on (all $p < 0.01$ at least).

326 Total surface area also most strongly modulated pattern dissimilarity in early visual areas.
327 The significant main effect of ROI ($F(1.4,27.63) = 16.61$, $p = 0.000078$) and the following
328 post-hoc tests showed that beta values for this dimension in the early visual areas were
329 significantly higher than those estimated for the intermediate ($p = 0.000475$) and higher-level
330 ($p = 0.000943$) ROIs, independent of the task. Beta weights for total surface area were
331 comparable in V1, V2 and V3 (no significant difference across these ROIs) and significantly
332 higher than those of the others ROIs starting from V3AB/V7 on (significant main effect of
333 ROI: $F(3.13,59.41) = 13.27$, $p = 0.000001$, comparisons across regions: all $p < 0.01$ at least).

334 Density modulated early visual areas during the number task and both earlier and higher-
335 level areas during the size task. The main effect of ROI was significant ($F(1.41,26.72) = 4.05$,
336 $p = 0.04$), but additional post-hoc tests did not reveal any significant difference across the
337 three large ROIs. Also at the level of individual regions the main effect of ROI was significant
338 ($F(2.55,48.54) = 4.15$, $p = 0.01$) and the strongest difference across ROIs emerged when
339 comparing the lowest beta weights estimated in V3AB with those obtained in V1 ($p = 0.003$)
340 and V7, IPS12 and IPS345 ($p = 0.03$, $p = 0.01$, $p = 0.002$).

341 Surprisingly, effects due to average item size could not be detected in any of the ROIs
342 tested.

343 In sum, while early visual areas contained independent information on multiple
344 quantitative properties of which some explained more variance than numerosity, all regions
345 were modulated to some extent by numerical distance over and above what was explainable
346 by the non-numerical dimensions. Moreover, importantly, explicitly directing attention to
347 number did enhance the representation of numerical information and did so selectively,
348 without altering the representations of non-numerical quantities. Finally, although present
349 starting from the earliest stages of visual analysis, the numerical information at this level was
350 only to a minor extent modulated by task and the greatest contribution to explicit
351 manipulation of numerical quantity was found in intermediate and higher-level regions.

352

353 Discussion

354

355 Our work exploited the enhanced spatial resolution provided by ultra-high field fMRI to
356 reveal how the human brain represents multiple quantitative dimensions of non-symbolic
357 numerical stimuli. Furthermore, we tested whether and at what cortical level the numerical
358 information can be represented and specifically modulated by attention independently of non-
359 numerical visual properties of the image.

360 At the level of overall regional activity, attending to the numerosity or to the average size
361 of the dots in the array recruited largely overlapping occipital and parietal areas, as also
362 previously observed for perception and comparison of different types of quantities (Pinel et
363 al., 2004; Dormal and Pesenti, 2009; Borghesani et al., 2018; for a meta-analysis on other
364 non-numerical representations see: Sokolowski et al., 2017). Only multivariate pattern
365 analysis could detect differences in the way information along the different dimensions was
366 encoded as a function of task in our study. Importantly, the equal percentage of correct
367 responses across tasks ensured that the differences detected could not be attributed to an
368 overall unspecific difference in task difficulty.

369 Multivariate decoding analyses showed that the sample numerosity presented could be
370 read out from brain activity all along the visual stream, however with important differences
371 across regions. When explicitly attended, the numerical information could be read out with
372 gradually higher accuracy following an occipital-parietal gradient, up to a maximum level in
373 the parietal cortices. The effect of attention strongly affected the accuracy of the numerical
374 discrimination in intermediate and higher regions while leaving the accuracy in the early
375 visual areas unaffected. The successful read-out of information related to numerosity from
376 parietal cortices in the current experiment contrasts with some previous studies where fMRI
377 signals discriminative of numerosity information could not be detected in the parietal regions
378 (DeWind et al., 2018; Fornaciai and Park, 2018). Differences in paradigms and sensitivity of
379 the scanners used may account for this discrepancy. Most crucially, in those studies,
380 participants were shown with different numerosities and the task required detecting changes
381 in the colour of the dots. Thus, participants' attention may have not been directed to the
382 numerosity of the visual arrays in that case, and the numerical information may have been
383 reduced when focussing on the dots' colour, similarly to what was observed for the size task
384 in the current experiment. Although in the present study we could still read out numerical
385 information even when it was irrelevant for the task, this signal may have remained
386 undetected by less sensitive MRI scanners.

387 In the current study the number presented could be decoded from the earliest stages of
388 visual processing. However, since this analysis collapsed across the non-numerical
389 dimensions of our stimulus set it is unclear whether the information underlying successful
390 decoding was strictly numerical, especially in earlier regions. Some previous studies have
391 dealt with the problem of correlations between numerical and non-numerical stimulus
392 dimensions by controlling for non-numerical features one at the time and testing for fMRI
393 adaptation effects, or replicability of decoding performance or layouts across conditions
394 where individual non-numerical features were controlled for (Piazza et al., 2004; Eger et al.,
395 2009; Harvey et al., 2013; Harvey and Dumoulin, 2017a; DeWind et al., 2018). When the
396 effects of non-numerical dimensions were measured directly, this was done in some studies
397 by computing the explained variance or classification performance for each feature in
398 isolation and comparing it to the one for number (Harvey and Dumoulin, 2017b; Cavdaroglu
399 and Knops, 2018), leaving open the degree to which the simultaneous contribution of several
400 non-numerical dimensions could account for the findings (Gebuis et al., 2014). Some other
401 previous studies have taken a different approach, by modelling jointly the effects of
402 numerosity and two non-numerical dimensions (termed “size in area” and “spacing”) which
403 were designed to be orthogonal to numerosity but do not necessarily constitute natural,
404 perceptually relevant feature dimensions, but rather mathematically defined constructs
405 (DeWind et al., 2015; Park et al., 2015; DeWind et al., 2018; Fornaciai and Park, 2018). This
406 design also allowed the authors to estimate, from the combined beta weights of numerosity
407 and the mentioned two orthogonal dimensions, which feature represented by different
408 directions in their stimulus space most accounted for the effects in a given ERP component
409 or brain area. However, brain signals can reflect a combination of responses to multiple
410 quantitative dimensions, and this approach does not permit to distinguish, for example, a
411 modulation by numerosity from two independent modulations by field area and density.

412 In our study, on the contrary, we separated the contributions of numerical and non-
413 numerical stimulus dimensions by applying multiple regression to representational distance
414 matrices which allowed us to test for the extent to which numerosity could explain the pattern
415 of activity while taking into account simultaneously the variability explained by several
416 important natural non-numerical features. Indeed estimating significantly above zero beta
417 values for number implies that information about numerosity is present in the pattern of
418 activity over and above the contributions of all the non-numerical features. We found that
419 information specific to number was detectable beyond the information of the other
420 dimensions, and that the numerical information was gradually enhanced when progressing
421 along the visual stream when explicitly task relevant, and much more weakly represented,
422 although still detectable, when not task-relevant. Importantly, the level of information on other

423 quantitative but non-numerical properties of the image, such as total field area, total surface
424 area and density, although reliably detected, especially in earlier brain regions, was not
425 altered when explicitly attending to the numerical quantity. The presence of separable
426 contributions of the representations of numerical and non-numerical dimensions in activation
427 patterns together with the selective attentional modulation of the numerical information
428 provides strong evidence for a specific neuronal extraction mechanism dedicated to the
429 property number. The fact that such specifically numerical information is found from early
430 stages of the cortical hierarchy on, and that attentional modulation does not affect associated
431 non-numerical quantities makes it unlikely that numerical judgements would only be made
432 indirectly on the basis of different non-numerical features.

433 The enhancement of numerical information in activation patterns found here when number
434 was the relevant stimulus dimension is extending a growing body of work on the neuronal
435 correlates of feature-based attention. Neurophysiological studies have shown that attention
436 to basic visual features either increases the gain or sharpens responses of neuronal
437 populations preferentially responsive to these features in different visual areas (e.g. Treue
438 and Trujillo, 1999; McAdams and Maunsell, 2000; Reynolds et al., 2000; Martinez-Trujillo
439 and Treue, 2004; David et al., 2008, see also: Carrasco, 2011 for a review).
440 Correspondingly, fMRI decoding studies have found that directing attention to one feature
441 dimension such as orientation, motion direction or color or to particular values within one
442 given dimension improves the read-out of these features from brain activity in early sensory
443 regions (Kamitani and Tong, 2005, 2006; Serences and Boynton, 2007; Jehee et al., 2011)
444 but in some cases also in higher-level areas (Liu et al., 2011; Ester et al., 2016). According
445 to one influential account, higher-level fronto-parietal areas such as the lateral intraparietal
446 area (LIP) implement spatial “priority maps” in which the level of activity at individual
447 locations depends jointly on the different features of objects at these locations as well as on
448 top-down factors such as their task relevance, associated reward, etc (Itti and Koch, 2001;
449 Thompson and Bichot, 2005; Gottlieb, 2007; Sapountzis et al., 2018). Independent of spatial
450 priority, LIP neurons have also been found to represent higher-level factors such as learned
451 category membership and other non-spatial information (Freedman and Assad, 2009) and to
452 flexibly switch between encoding of different visual features, such as color or motion,
453 depending on the task (Toth and Assad, 2002; Ibos and Freedman, 2014). The idea of a role
454 for intraparietal areas as mere “priority maps” or reflecting entirely flexible encoding of
455 information on task-relevant features (without intrinsic selectivity) can insufficiently account
456 for our results, since it would predict an equivalent amplification of the representation of
457 average size when this is the attended feature instead of number. This is not what we
458 observed. Our results are thus more compatible with an enhancement of the responses of

459 neuronal populations with intrinsic selectivity to the feature numerosity in these areas
460 (comparable to the one observed for other features in lower-level visual regions).

461 While the existence of individual neurons tuned to different numbers of items in
462 intraparietal cortex is well established (Nieder and Miller, 2004; Roitman et al., 2007), the
463 only electrophysiological study that recorded from neurons in the ventral intraparietal (VIP)
464 cortex in macaque monkeys under changing task conditions (Viswanathan and Nieder, 2015)
465 found that neurons encoded numerosity to the same extent, regardless of whether the task
466 required to attend to the number or the color of the items. This differs from our results which
467 show a clear attentional amplification of numerosity information. Given that the human IPS 1-
468 5 investigated in the current work is usually considered to be the equivalent of the macaque
469 LIP/VIP complex (Kastner et al., 2017), the difference between results may be due to a
470 difference across species, but differences in paradigms and in the nature of the signal
471 recorded in the two studies make it difficult to directly relate the two findings. For example,
472 monkeys were trained initially with the color match to sample task, then re-trained to respond
473 to number, thus implying comparisons across an extended time period and different context,
474 whereas our participants switched between the two tasks within the same scanning session.
475 In addition, it is possible that the color task with a single color per stimulus and a small
476 number of highly distinguishable alternatives placed lower demands on attentional load
477 compared to our average size task, therefore leaving number processing unaltered.
478 Nevertheless, as a common denominator both studies agree on pointing to some degree of
479 spontaneous encoding of numerosity in intraparietal areas under conditions of attention to an
480 orthogonal stimulus dimension.

481 The gradual enhancement of numerosity information observed by us in the number task
482 when progressing along the dorsal visual stream is compatible with a multi-stage process of
483 the extraction of numerosity where attention may operate at multiple levels over which
484 attentional enhancements accumulate. If numerosity information can be retrieved from
485 multiple levels of the cortical hierarchy, this does not need to imply that this features is
486 encoded by individual neurons at all these levels, but it may be detectable by multivariate
487 methods even if it existed only in distributed form across the population of neurons. As one
488 speculative interpretation, the numerical information read out from early visual areas could
489 reflect a location map (Dehaene and Changeux, 1993), or the process of object
490 segmentation where different individual items start to be separately represented, but this
491 representation may not yet be in a form that is most easily read out for numerical
492 discrimination. Higher areas may progressively transform and concentrate the initially
493 distributed information onto individual neurons, which most likely constitute the base on
494 which we operate when comparing numbers. This interpretation is in line with a recent study

495 showing that although different numerosities could be discriminated based on the pattern of
496 activity in early visual areas and parietal cortex, the behavioral precision of numerical
497 discrimination was correlated with the decoding accuracy only in the latter region (Lasne et
498 al., 2018).

499 A surprising result of the current experiment is that we could not find information about
500 average item size in the pattern of activity in any of the regions examined, even though this
501 feature's perceptual discriminability was equated with the one of numerosity. This suggests
502 that the neural mechanisms supporting average size representation may differ from those
503 engaged during single object size analysis which has been shown to overlap partly with
504 numerosity maps in parietal regions (Harvey et al., 2015). Mechanisms for average size
505 perception, and in general for ensemble statistics are still unclear. It has been previously
506 suggested that average item size perception, like density perception, may rely on texture
507 processing mechanisms rather than individual item identification (Im and Halberda, 2013).
508 Various regions along the ventral visual stream have been implicated in texture perception.
509 In particular, adaptation studies have identified recovery of fMRI signal in the medial part of
510 the posterior collateral sulcus that was selective for texture as opposed to color or shape of
511 3D irregular objects (Cavina-Pratesi et al., 2010) and the parahippocampal place area (PPA)
512 showed equal release from adaptation for object ensemble and surface textures, suggesting
513 that ensembles and textures are processed similarly (Cant and Xu, 2012). It is possible that
514 average size is also represented in the ventral stream which was not covered here, and
515 future studies should focus on these regions to try to detect a representation of average size.
516 What we observed, however, was that beta weights for density obtained from RSA
517 regression became significant in the parietal regions during the size task, suggesting that
518 texture processing mechanisms may be automatically activated during the average size task.
519 This interpretation, however, has to remain speculative and future studies should investigate
520 neural mechanisms relating texture, density and average size processing.

521 In conclusion, with this study using high-resolution, high-field fMRI we provide direct
522 neuroscientific evidence for a processing mechanism dedicated to visual numerosity which is
523 separable from the ones underlying the processing of non-numerical quantities from early
524 stages of cortical processing on, and independently and progressively amplified across the
525 dorsal visual stream when numerical information is explicitly processed. An important goal for
526 the future will be to better understand what are the processing steps and transformations
527 occurring at the different levels of the cortical hierarchy that characterize this specific sense
528 of numerosity, for example by comparing fMRI data against computational models simulating
529 the visual extraction of numerosity.

530

531 Methods

532

533 Subjects and MRI acquisition

534 Twenty healthy adults with normal or corrected vision (10 males and 10 females, mean
535 age 24 years) participated in the study. The study was approved by the regional ethical
536 committee (Hôpital de Bicêtre, France) and all participants gave written informed consent.
537 Functional images were acquired on a SIEMENS MAGNETOM 7T scanner with head
538 gradient insert (Gmax 80mT/m and slew rate 333T/m/s) and adapted 32-channel head coil
539 (Nova Medical, Wilmington, MA, USA) as T2*-weighted fat-saturation echo-planar image
540 (EPI) volumes with 1.3 mm isotropic voxels using a multi-band sequence (Moeller et al.,
541 2010) (<https://www.cmrr.umn.edu/multiband/>, multi-band [MB] = 2, GRAPPA acceleration
542 with [IPAT] = 2, partial Fourier [PF] = 7/8, matrix = 120 x 150, repetition time [TR] = 2 s, echo
543 time [TE] = 22 ms, echo spacing [ES] = 0.71 ms, flip angle [FA] = 68°, bandwidth [BW] =
544 1588 Hz/px, phase-encode direction left>>right). Calibration preparation was done using
545 Gradient Recalled Echo (GRE) data. Sixty oblique slices covering the occipital, parietal and
546 partially the frontal cortex were obtained in ascending interleaved order. Before the
547 experimental runs two single volumes were acquired with the parameters listed above but
548 with opposite phase encode direction to be used for distortion correction in the later analysis
549 (see Image Processing and Data Analysis). T1-weighted anatomical images were acquired
550 at 0.8 mm isotropic resolution using an MP2RAGE sequence (GRAPPA acceleration with
551 [IPAT] = 3, partial Fourier [PF] = 6/8, matrix = 281 x 300, repetition time [TR] = 6 s, echo time
552 [TE] = 2.92 ms, time of inversion [TI] 1/2 = 800/2700 ms, flip angle [FA] 1/2 = 4°/5°,
553 bandwidth [BW] = 240 Hz/px.). During scanning participants wore a radiofrequency
554 absorbent jacket (Accusorb MRI, MWT Materials Inc., Passaic, NJ, USA) to minimize so-
555 called “third-arm” or “shoulder” artifacts due to regions where the head gradient is unable to
556 unambiguously spatially encode the image (Wald et al., 2005). Head movement was
557 minimized by padding and tape. Visual stimuli were back-projected onto a translucent screen
558 at the end of the scanner bore and viewed through a mirror attached to the head coil.
559 Participants held two response buttons in their left and right hands.

560

561 Stimuli and procedure

562 During fMRI scanning participants were centrally presented with heterogeneous arrays of
563 dots, half black, and half white, on a mid-gray background. The generated sets of dots were
564 orthogonally varied in number, average item size and total field area for a total of 18
565 conditions: six, ten or seventeen dots were presented with either small, medium or large
566 average item area (0.04, 0.07, 0.12 visual squares degree) and designed to fall within a
567 small or large total field area (defined by a virtual circle of either about 5 or 7.5 visual degree
568 diameter). Numbers and average item sizes were chosen to be perceptually equally
569 discriminable based on a previous behavioral study (Castaldi et al., 2018). Total field areas
570 were chosen so that arrays of dots could be sufficiently sparse (~ 1 dot/vd²) to target the
571 'number regime' (Anobile et al., 2013, 2015).

572 Within each run participants performed two tasks in different blocks, as indicated by the
573 written task instructions provided at the beginning of each block. Instructions were shown for
574 2 s and specified whether participants had to attend either to the number of dots (number
575 task) or to the average item size of the dots (size task) in the array. Six seconds after the
576 instruction a delayed comparison task started with brief presentation (500 ms) of a sample
577 dot array stimulus. At each trial participants attended to the cued dimension of the sample
578 stimulus and held this information in memory until the following trial was presented, knowing
579 that a comparison response with the following trial may be required. After a variable ISI of 3.5
580 – 5.5 s, a second dot array was presented. If the color of the fixation point remained
581 unchanged (green), no comparison was required and participants only had to update their
582 memory with the new sample stimulus. If instead the fixation point changed color (turning to
583 red 1 s before the stimulus presentation) participants had to compare the current stimulus
584 (match stimulus) with the one held in memory and decide whether the current stimulus was
585 larger or smaller (on the attended dimension) than the previous one. Response was provided
586 by button press and after 5.5 s the next sample stimulus was presented and the whole
587 procedure started again. Match stimuli were designed to be ~ 2 JNDs larger or smaller than
588 the previously presented sample stimulus on the attended dimension, based on each
589 participant's Weber fraction as measured in a behavioral test prior to the fMRI scanning,
590 while the unattended dimension was the same as the previous sample stimulus.

591 Twenty trials were presented in each block: one trial for each one of the 18 sample
592 stimulus conditions (3 numerosity x 3 sizes x 2 total field areas) and two match trials. The
593 hands assigned to either the 'smaller' or 'larger' response were inverted in the middle of the
594 scanning session, i.e. after the third run, and counterbalanced across subjects. Within the
595 scanning session participants performed six runs of ~ 7 min and 44 s. Each run included four
596 blocks where the two tasks alternated. The type of task with which the run started was
597 balanced across runs and participants.

598 To measure their numerical and average size acuity, participants performed a behavioral
599 test prior to the fMRI scanning. In different sessions participants were shown two consecutive
600 centrally presented arrays of dots and were required to perform a discrimination task on the
601 attended dimension (either numerosity or average item size) by pressing the left or the right
602 arrow (to choose the first or the second stimulus respectively). The set of stimuli used
603 included arrays of 5,7,9,11,15 and 20 dots (ratios 0.5, 0.7, 0.9, 1.1, 1.5 and 2 with respect to
604 the reference of 10 dots) that could be displayed with the average dot areas of 0.05, 0.06,
605 0.08, 0.11, 0.15 and 0.2 visual square degrees (ratios 0.5, 0.6, 0.8, 1.1, 1.5 and 2 with
606 respect to the reference of 0.1 visual square degrees). Dots were randomly drawn within two
607 possible virtual circles of ~5.8 and 7.6 visual degrees diameter. Reference and test stimuli
608 could appear either as first or as second stimulus. After task instructions and twelve practice
609 trials, participants performed three sessions of one task and three sessions of the other, with
610 counterbalanced order across subjects. For each task participants performed a total of 432
611 comparisons (6 numerosities x 6 average item sizes x 2 total field areas x 2 presentation
612 order x 3 sessions). To quantify participants' precision in number and size judgments, we
613 computed the JND for each task. The percentage of test trials with "greater than reference"
614 responses was plotted against the log-transformed difference between test and reference
615 and fitted with a cumulative Gaussian function using Psignifit toolbox (Schütt et al., 2016).
616 The difference between the 50% and the 75% points yielded the JND.

617 Stimuli and paradigms were generated and presented under Matlab 9.0 using
618 PsychToolbox routines (Brainard, 1997).

619

620 Image Processing and Data Analysis

621 EPI images were motion-corrected and co-registered to the first single band reference
622 image using statistical parametric mapping software (SPM12,
623 <https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). The single-band reference images of the
624 two initial volumes acquired with opposite phase encode directions served to estimate a set
625 of field coefficients using topup in FSL (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL>), which was
626 subsequently used to apply distortion correction (apply_topup) to all EPI images. Cortical
627 surface reconstruction and boundary based registration of single band reference images to
628 each subject's cortical surface, as well as a minimal amount of surface constrained
629 smoothing (FWHM = 1.5 mm) for noise reduction were performed in Freesurfer
630 (<https://surfer.nmr.mgh.harvard.edu/>).

631 The preprocessed EPI images (in subjects' native space) were entered into a general
632 linear model separately modeling the effects of the 36 sample conditions (3 numerosities x 3
633 average item sizes x 2 total field areas x 2 tasks, within each run the two repetitions for each
634 condition were pooled together), the match stimulus separately for left and right hand and the
635 written instructions at the beginning of the block as stick functions (using the default of 0
636 duration for events) convolved with the standard hemodynamic response function. The six
637 motion parameters were included in the GLM as covariate of no interest. An AR(1) model
638 was used to account for serial auto-correlation and low-frequency signal drifts were removed
639 by a high-pass filter with a cutoff of 192 s. In each subject we contrasted the activation
640 elicited by: all the sample stimuli during the number tasks against the implicit baseline
641 (contrast name: 'Judge Number > Baseline'); all the sample stimuli during the size tasks
642 against the implicit baseline (contrast name: 'Judge Size > Baseline'); all the sample stimuli
643 during the number tasks against all the sample stimuli during the size tasks (contrast name:
644 'Judge Number > Judge Size). After creating the contrasts in each single subject's volume
645 space, the contrast images were projected onto the surface with Freesurfer, aligned to
646 fsaverage and smoothed with a 3-mm fwhm Gaussian kernel. The second-level group
647 analysis was then performed in the surface space.

648 The beta estimates for the sample stimulus conditions from the first-level analysis (1 beta
649 estimate per run and condition) were entered into pattern recognition analysis. In each
650 subject we defined anatomical regions of interest (ROIs) derived from a surface based
651 probabilistic atlas (Wang et al., 2015) where regions are defined based on retinotopy. ROIs
652 for V1 to IPS5 were created on the Freesurfer surface and projected back into each subject's
653 volume space. For each ROI we merged the left and right hemisphere. ROIs were further
654 merged into three large ROIs corresponding to early (V1 to V3), intermediate (V3A, V3B and
655 V7, also known as IPS0) and higher-level (IPS 1 to IPS5) areas. In addition we focused the
656 analysis on individual regions: V1, V2, V3, V3AB (merging V3A and V3B), V7, IPS12
657 (merging IPS 1 and 2), IPS345 (merging IPS 3, 4 and 5). Within each one of these bilateral
658 regions we selected on a subject-by-subject basis an equal number of 800 voxels that
659 responded most strongly to the orthogonal contrast 'all sample stimuli > baseline' for pattern
660 recognition analysis. To evaluate the degree of spatial consistency of the selected voxels
661 across subjects we created an overlap map with Freesurfer (Fig 3B): single subjects' ROIs
662 were aligned to fsaverage and the number of subjects for which a given location was
663 included in their specific ROI was represented by a heat map (with yellow color meaning that
664 a given location was selected in all subjects).

665 Pattern classification analysis was performed in scikit-learn (Pedregosa et al., 2011) using
666 beta estimates after subtracting the voxel-wise mean across conditions by applying linear

667 support vector machines (SVM) with regularization parameter $C=1$. Classification analysis
668 was performed leaving patterns of one run out at each loop of the 6-fold cross-validation
669 cycle. This implies that classifiers were trained on five betas per condition and tested with the
670 left out beta images (one per condition). The classification accuracies obtained for each cycle
671 were then averaged together. Pairwise classification was performed for all pairs of
672 numerosities collapsing across the size and total field area dimensions, but keeping patterns
673 separated by task. Classification accuracy was then averaged across all pairs of
674 numerosities for each task. A one-sample t-test against the theoretical chance level of 50%
675 was performed to evaluate significance of discrimination. Repeated measures ANOVAs
676 were then performed on classification accuracies with ROI and task as factors.

677 For representational similarity analysis (RSA, Kriegeskorte, 2008; Kriegeskorte and Kievit,
678 2013) the GLM was performed concatenating the runs and obtaining one single beta per
679 condition, task and subject. Comparable to the procedure of the pattern classification
680 analysis, voxel-wise scaling was applied by subtracting the mean across conditions. Neural
681 representational dissimilarity matrices (neural RDMs) for each task and ROI were created by
682 computing the correlation distance ($1 - \text{Pearson correlation}$ across voxels) between
683 activity patterns associated with all possible pairs of conditions using CoSMoMvpa Toolbox
684 (Oosterhof et al., 2016). The neural RDMs were then entered in a multiple regression with
685 five predictors corresponding to matrices encoding the distance on a logarithmic scale for the
686 different quantitative dimensions defining the dot arrays: number, average item size, total
687 field area, total surface area and density. In the multiple regression analysis all distance
688 matrices were z-transformed before estimating the regression coefficients. The obtained beta
689 weights for each dimension and ROI were tested with one-sample t-tests against zero across
690 subjects. The effects of ROI, dimension and task were analyzed with repeated measures
691 ANOVAs.

692

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694

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699 References

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701 Anobile, G., Cicchini, G.M., and Burr, D. (2013). Separate mechanisms for perception of numerosity
702 and density. *Psychological Science* 0956797613501520.

703 Anobile, G., Turi, M., Cicchini, G.M., and Burr, D. (2015). Mechanisms for perception of numerosity or
704 texture-density are governed by crowding-like effects. *Journal of Vision* 15, 4.

705 Anobile, G., Castaldi, E., Turi, M., Tinelli, F., and Burr, D. (2016a). Numerosity but not texture-density
706 discrimination correlates with math ability in children. *Developmental Psychology* 52, 1206–1216.

707 Anobile, G., Cicchini, G.M., and Burr, D. (2016b). Number As a Primary Perceptual Attribute: A
708 Review. *Perception* 45, 5–31.

709 Anobile, G., Arrighi, R., Castaldi, E., Grassi, E., Pedonese, L., M. Moscoso, P.A., and Burr, D. (2018).
710 Spatial but Not Temporal Numerosity Thresholds Correlate With Formal Math Skills in Children.
711 *Developmental Psychology*.

712 Arsalidou, M., and Taylor, M.J. (2011). Is $2+2=4$? Meta-analyses of brain areas needed for numbers
713 and calculations. *NeuroImage* 54, 2382–2393.

714 Borghesani, V., de Hevia, M., Viarouge, A., Chagas, P., Eger, E., and Piazza, M. (2018). Processing
715 number and length in the parietal cortex: Sharing resources, not a common code. *Cortex*.

716 Brainard, D.H. (1997). The psychophysics toolbox. *Spatial Vision* 10, 433–436.

717 Bulthé, J., De Smedt, B., and Op de Beeck, H.P. (2014). Format-dependent representations of
718 symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern
719 analyses. *NeuroImage* 87, 311–322.

720 Bulthé, J., De Smedt, B., and Op de Beeck, H.P. (2015). Visual Number Beats Abstract Numerical
721 Magnitude: Format-dependent Representation of Arabic Digits and Dot Patterns in Human Parietal
722 Cortex. *Journal of Cognitive Neuroscience* 27, 1376–1387.

723 Burr, D., and Ross, J. (2008). A Visual Sense of Number. *Current Biology* 18, 425–428.

724 Cant, J.S., and Xu, Y. (2012). Object Ensemble Processing in Human Anterior-Medial Ventral Visual
725 Cortex. *Journal of Neuroscience* 32, 7685–7700.

726 Cantlon, J.F. (2012). Math, monkeys, and the developing brain. *Proceedings of the National Academy*
727 *of Sciences* 109, 10725–10732.

728 Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research* 51, 1484–1525.

729 Castaldi, E., Aagten-Murphy, D., Tosetti, M., Burr, D., and Morrone, M.C. (2016). Effects of adaptation
730 on numerosity decoding in the human brain. *NeuroImage*.

731 Castaldi, E., Mirassou, A., Dehaene, S., Piazza, M., and Eger, E. (2018). Asymmetrical interference
732 between number and item size perception provides evidence for a domain specific impairment in
733 dyscalculia. *PLOS ONE* 13, e0209256.

- 734 Cavdaroglu, S., and Knops, A. (2018). Evidence for a Posterior Parietal Cortex Contribution to Spatial
735 but not Temporal Numerosity Perception. *Cerebral Cortex*.
- 736 Cavina-Pratesi, C., Kentridge, R.W., Heywood, C.A., and Milner, A.D. (2010). Separate Channels for
737 Processing Form, Texture, and Color: Evidence from fMRI Adaptation and Visual Object Agnosia.
738 *Cerebral Cortex* 20, 2319–2332.
- 739 Chen, Q., and Li, J. (2014). Association between individual differences in non-symbolic number acuity
740 and math performance: A meta-analysis. *Acta Psychologica* 148, 163–172.
- 741 Cicchini, G.M., Anobile, G., and Burr, D. (2016). Spontaneous perception of numerosity in humans.
742 *Nature Communications* 7, 12536.
- 743 Dakin, S.C., Tibber, M.S., Greenwood, J.A., Kingdom, F.A.A., and Morgan, M.J. (2011). A common
744 visual metric for approximate number and density. *Proceedings of the National Academy of Sciences*
745 108, 19552–19557.
- 746 David, S.V., Hayden, B.Y., Mazer, J.A., and Gallant, J.L. (2008). Attention to Stimulus Features Shifts
747 Spectral Tuning of V4 Neurons during Natural Vision. *Neuron* 59, 509–521.
- 748 De Smedt, B., Noël, M., Gilmore, C., and Ansari, D. (2013). How do symbolic and non-symbolic
749 numerical magnitude processing skills relate to individual differences in children’s mathematical
750 skills? A review of evidence from brain and behavior. *Trends in Neuroscience and Education* 2, 48–55.
- 751 Dehaene, S. (1997). *The number sense: how the mind creates mathematics* (New York: Oxford
752 University Press).
- 753 Dehaene, S., and Changeux, J. (1993). Development of Elementary Numerical Abilities: A Neuronal
754 Model. *Journal of Cognitive Neuroscience* 5, 390–407.
- 755 DeWind, N.K., Adams, G.K., Platt, M.L., and Brannon, E.M. (2015). Modeling the approximate number
756 system to quantify the contribution of visual stimulus features. *Cognition* 142, 247–265.
- 757 DeWind, N.K., Park, J., Woldorff, M.G., and Brannon, E.M. (2018). Numerical encoding in early visual
758 cortex. *Cortex*.
- 759 Dormal, V., and Pesenti, M. (2009). Common and specific contributions of the intraparietal sulci to
760 numerosity and length processing. *Human Brain Mapping* 30, 2466–2476.
- 761 Eger, E. (2016). Neuronal foundations of human numerical representations. In *Progress in Brain*
762 *Research*, (Elsevier), pp. 1–27.
- 763 Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., and Kleinschmidt, A. (2009). Deciphering
764 Cortical Number Coding from Human Brain Activity Patterns. *Current Biology* 19, 1608–1615.
- 765 Eger, E., Pinel, P., Dehaene, S., and Kleinschmidt, A. (2015). Spatially Invariant Coding of Numerical
766 Information in Functionally Defined Subregions of Human Parietal Cortex. *Cerebral Cortex* 25, 1319–
767 1329.
- 768 Ester, E.F., Sutterer, D.W., Serences, J.T., and Awh, E. (2016). Feature-Selective Attentional
769 Modulations in Human Frontoparietal Cortex. *Journal of Neuroscience* 36, 8188–8199.

770 Fias, W. (2016). Neurocognitive Components of Mathematical Skills and Dyscalculia. In *Development*
771 *of Mathematical Cognition*, (Elsevier), pp. 195–217.

772 Fischl, B. (2004). Automatically Parcellating the Human Cerebral Cortex. *Cerebral Cortex* *14*, 11–22.

773 Fornaciai, M., and Park, J. (2017). Distinct Neural Signatures for Very Small and Very Large
774 Numerosities. *Frontiers in Human Neuroscience* *11*.

775 Fornaciai, M., and Park, J. (2018). Neural Sensitivity to Numerosity in Early Visual Cortex Is Not
776 Sufficient for the Representation of Numerical Magnitude. *Journal of Cognitive Neuroscience* 1–15.

777 Fornaciai, M., Brannon, E.M., Woldorff, M.G., and Park, J. (2017). Numerosity processing in early
778 visual cortex. *NeuroImage* *157*, 429–438.

779 Freedman, D.J., and Assad, J.A. (2009). Distinct Encoding of Spatial and Nonspatial Visual Information
780 in Parietal Cortex. *Journal of Neuroscience* *29*, 5671–5680.

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

783 Gebuis, T., Gevers, W., and Kadosh, R.C. (2014). Topographic representation of high-level cognition:
784 numerosity or sensory processing? *Trends in Cognitive Sciences* *18*, 1–3.

785 Gottlieb, J. (2007). From Thought to Action: The Parietal Cortex as a Bridge between Perception,
786 Action, and Cognition. *Neuron* *53*, 9–16.

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

789 Harvey, B.M., and Dumoulin, S.O. (2017a). A network of topographic numerosity maps in human
790 association cortex. *Nature Human Behaviour* *1*, 0036.

791 Harvey, B.M., and Dumoulin, S.O. (2017b). Can responses to basic non-numerical visual features
792 explain neural numerosity responses? *NeuroImage* *149*, 200–209.

793 Harvey, B.M., Klein, B.P., Petridou, N., and Dumoulin, S.O. (2013). Topographic Representation of
794 Numerosity in the Human Parietal Cortex. *Science* *341*, 1123–1126.

795 Harvey, B.M., Fracasso, A., Petridou, N., and Dumoulin, S.O. (2015). Topographic representations of
796 object size and relationships with numerosity reveal generalized quantity processing in human
797 parietal cortex. *Proceedings of the National Academy of Sciences* *112*, 13525–13530.

798 de Hevia, M.D., Castaldi, E., Streri, A., Eger, E., and Izard, V. (2017). Perceiving numerosity from birth.
799 *Behavioral and Brain Sciences*,40.

800 Hyde, D.C., and Spelke, E.S. (2011). Neural signatures of number processing in human infants:
801 evidence for two core systems underlying numerical cognition: Neural signatures of number in
802 infants. *Developmental Science* *14*, 360–371.

803 Ibos, G., and Freedman, D.J. (2014). Dynamic Integration of Task-Relevant Visual Features in
804 Posterior Parietal Cortex. *Neuron* *83*, 1468–1480.

805 Im, H.Y., and Halberda, J. (2013). The effects of sampling and internal noise on the representation of
806 ensemble average size. *Attention, Perception, & Psychophysics* 75, 278–286.

807 Itti, L., and Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews*
808 *Neuroscience* 2, 194–203.

809 Luculano, T., and Menon, V. (2018). Development of Mathematical Reasoning. In *Stevens’ Handbook*
810 *of Experimental Psychology and Cognitive Neuroscience*, p.

811 Izard, V., Dehaene-Lambertz, G., and Dehaene, S. (2008). Distinct cerebral pathways for object
812 identity and number in human infants. *PLoS Biology* 6, e11.

813 Jehee, J.F.M., Brady, D.K., and Tong, F. (2011). Attention Improves Encoding of Task-Relevant
814 Features in the Human Visual Cortex. *Journal of Neuroscience* 31, 8210–8219.

815 Kamitani, Y., and Tong, F. (2005). Decoding the visual and subjective contents of the human brain.
816 *Nature Neuroscience* 8, 679–685.

817 Kamitani, Y., and Tong, F. (2006). Decoding Seen and Attended Motion Directions from Activity in the
818 Human Visual Cortex. *Current Biology* 16, 1096–1102.

819 Kastner, S., Chen, Q., Jeong, S.K., and Mruzek, R.E.B. (2017). A brief comparative review of primate
820 posterior parietal cortex: A novel hypothesis on the human toolmaker. *Neuropsychologia* 105, 123–
821 134.

822 Kourtzi, Z., and Grill-Spector, K. (2005). fMRI Adaptation: A Tool for Studying Visual Representations
823 in the Primate Brain. In *Fitting the Mind to the World Adaptation and After-Effects in High-Level*
824 *Vision*, (Clifford Colin W. G., Rhodes Gillian), p.

825 Kriegeskorte, N. (2008). Representational similarity analysis – connecting the branches of systems
826 neuroscience. *Frontiers in Systems Neuroscience*.

827 Kriegeskorte, N., and Kievit, R.A. (2013). Representational geometry: integrating cognition,
828 computation, and the brain. *Trends in Cognitive Sciences* 17, 401–412.

829 Lasne, G., Piazza, M., Dehaene, S., Kleinschmidt, A., and Eger, E. (2018). Discriminability of
830 numerosity-evoked fMRI activity patterns in human intra-parietal cortex reflects behavioral
831 numerical acuity. *Cortex*.

832 Leibovich, T., Katzin, N., Harel, M., and Henik, A. (2016). From ‘sense of number’ to ‘sense of
833 magnitude’—The role of continuous magnitudes in numerical cognition. *Behavioral and Brain Sciences*
834 1–62.

835 Libertus, M.E., Feigenson, L., and Halberda, J. (2011). Preschool acuity of the approximate number
836 system correlates with school math ability: Approximate number system and math abilities.
837 *Developmental Science* 14, 1292–1300.

838 Libertus, M.E., Feigenson, L., and Halberda, J. (2013). Is approximate number precision a stable
839 predictor of math ability? *Learning and Individual Differences* 25, 126–133.

840 Liu, T., Hospadaruk, L., Zhu, D.C., and Gardner, J.L. (2011). Feature-Specific Attentional Priority
841 Signals in Human Cortex. *Journal of Neuroscience* 31, 4484–4495.

842 Martinez-Trujillo, J.C., and Treue, S. (2004). Feature-Based Attention Increases the Selectivity of
843 Population Responses in Primate Visual Cortex. *Current Biology* 14, 744–751.

844 McAdams, C.J., and Maunsell, J.H.R. (2000). Attention to Both Space and Feature Modulates
845 Neuronal Responses in Macaque Area V4. *Journal of Neurophysiology* 83, 1751–1755.

846 Moeller, S., Yacoub, E., Olfman, C.A., Auerbach, E., Strupp, J., Harel, N., and Uğurbil, K. (2010).
847 Multiband multislice GE-EPI at 7 tesla, with 16-fold acceleration using partial parallel imaging with
848 application to high spatial and temporal whole-brain fMRI. *Magnetic Resonance in Medicine* 63,
849 1144–1153.

850 Morgan, M.J., Raphael, S., Tibber, M.S., and Dakin, S.C. (2014). A texture-processing model of the
851 “visual sense of number.” *Proceedings of the Royal Society B: Biological Sciences* 281, 20141137–
852 20141137.

853 Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience* 17, 366–382.

854 Nieder, A., and Miller, E.K. (2004). A parieto-frontal network for visual numerical information in the
855 monkey. *Proceedings of the National Academy of Sciences of the United States of America* 101,
856 7457–7462.

857 Nieder, A., Freedman, D.J., and Miller, E.K. (2002). Representation of the quantity of visual items in
858 the primate prefrontal cortex. *Science* 297, 1708–1711.

859 Norman, K.A., Polyn, S.M., Detre, G.J., and Haxby, J.V. (2006). Beyond mind-reading: multi-voxel
860 pattern analysis of fMRI data. *Trends in Cognitive Sciences* 10, 424–430.

861 Oosterhof, N.N., Connolly, A.C., and Haxby, J.V. (2016). CoSMoMvPA: Multi-Modal Multivariate
862 Pattern Analysis of Neuroimaging Data in Matlab/GNU Octave. *Frontiers in Neuroinformatics* 10.

863 Park, J., DeWind, N.K., Woldorff, M.G., and Brannon, E.M. (2015). Rapid and Direct Encoding of
864 Numerosity in the Visual Stream. *Cerebral Cortex* bhv017.

865 Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M.,
866 Prettenhofer, P., Weiss, R., Dubourg, V., et al. (2011). *Scikit-learn: Machine Learning in Python*. 7.

867 Piazza, M., and Eger, E. (2016). Neural foundations and functional specificity of number
868 representations. *Neuropsychologia* 83, 257–273.

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

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

874 Piazza, M., Pica, P., Izard, V., Spelke, E., and Dehaene, S. (2013). Education Enhances the Acuity of the
875 Nonverbal Approximate Number System. *Psychological Science* 24, 1037–1043.

876 Pinel, P., Piazza, M., Le Bihan, D., and Dehaene, S. (2004). Distributed and Overlapping Cerebral
877 Representations of Number, Size, and Luminance during Comparative Judgments. *Neuron* 41, 983–
878 993.

879 Reynolds, J.H., Pasternak, T., and Desimone, R. (2000). Attention Increases Sensitivity of V4 Neurons.
880 *Neuron* 26, 703–714.

881 Roitman, J., Brannon, E.M., and Platt, M.L. (2007). Monotonic Coding of Numerosity in Macaque
882 Lateral Intraparietal Area. *PLoS Biology* 5, e208.

883 Ross, J. (2010). Vision senses number directly. *Journal of Vision* 10, 1–8.

884 Sapountzis, P., Paneri, S., and Gregoriou, G.G. (2018). Distinct roles of prefrontal and parietal areas in
885 the encoding of attentional priority. *Proceedings of the National Academy of Sciences* 115, E8755–
886 E8764.

887 Schütt, H.H., Harmeling, S., Macke, J.H., and Wichmann, F.A. (2016). Painfree and accurate Bayesian
888 estimation of psychometric functions for (potentially) overdispersed data. *Vision Research* 122, 105–
889 123.

890 Serences, J.T., and Boynton, G.M. (2007). Feature-Based Attentional Modulations in the Absence of
891 Direct Visual Stimulation. *Neuron* 55, 301–312.

892 Sokolowski, H.M., Fias, W., Bosah Ononye, C., and Ansari, D. (2017). Are numbers grounded in a
893 general magnitude processing system? A functional neuroimaging meta-analysis. *Neuropsychologia*.

894 Stoianov, I., and Zorzi, M. (2012). Emergence of a “visual number sense” in hierarchical generative
895 models. *Nature Neuroscience* 15, 194–196.

896 Thompson, K., and Bichot, N. (2005). A visual salience map in the primate frontal eye field. *Prog Brain*
897 *Res.* 147:251-62.

898 Tong, F., and Pratte, M.S. (2012). Decoding Patterns of Human Brain Activity. *Annual Review of*
899 *Psychology* 63, 483–509.

900 Toth, L.J., and Assad, J.A. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex.
901 *Nature* 415, 165–168.

902 Treue, S., and Trujillo, J.C.M. (1999). Feature-based attention influences motion processing gain in
903 macaque visual cortex. *Nature* 399, 575–579.

904 Verguts, T., and Fias, W. (2004). Representation of Number in Animals and Humans: A Neural Model.
905 *Journal of Cognitive Neuroscience* 16, 1493–1504.

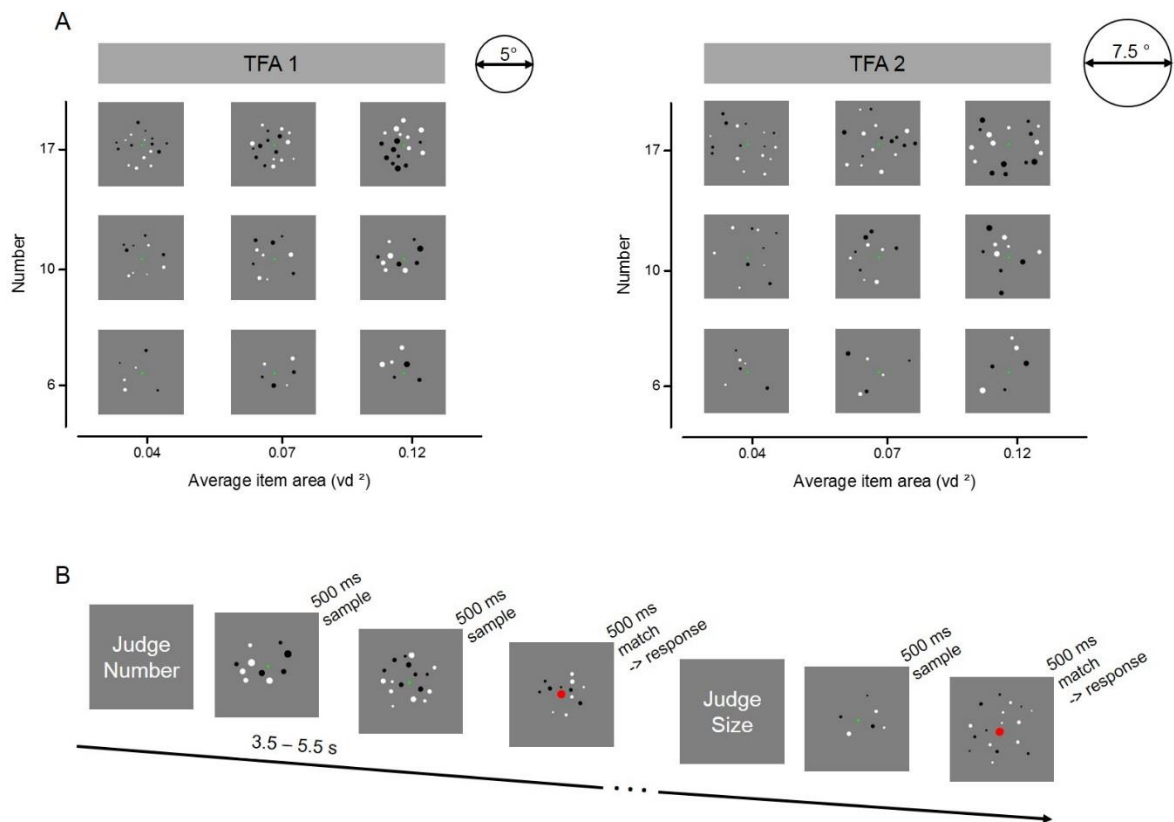
906 Viswanathan, P., and Nieder, A. (2015). Differential Impact of Behavioral Relevance on Quantity
907 Coding in Primate Frontal and Parietal Neurons. *Current Biology* 25, 1259–1269.

908 Wald, L.L., Wiggins, G.C., Potthast, A., Wiggins, C.J., and Triantafyllou, C. (2005). Design
909 Considerations and Coil Comparisons for 7 Tesla Brain Imaging. *Proc. Intl. Soc. Mag. Reson. Med.* 13,
910 1.

911 Wang, L., Mruczek, R.E.B., Arcaro, M.J., and Kastner, S. (2015). Probabilistic Maps of Visual
912 Topography in Human Cortex. *Cerebral Cortex* 25, 3911–3931.

913

914 **Figures**



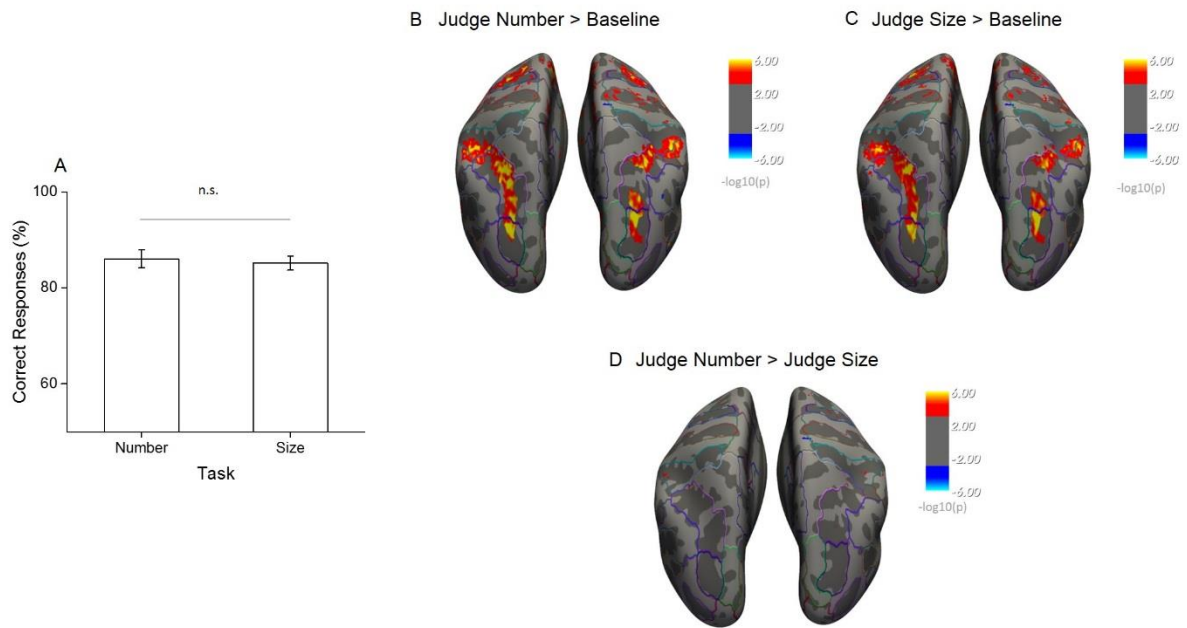
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916 Fig 1 Stimulus set and design for the fMRI experiment

917 (A) Example of the full set of stimulus conditions. Arrays of six, ten or seventeen dots were
 918 created with three average item areas (0.04, 0.07 and 0.12 visual degree²) and displayed
 919 within two total field areas, enclosed by imaginary circles of 5° (TFA 1) and 7.5° (TFA 2)
 920 diameter. (B) Illustration of the trials' temporal presentation and paradigm during scanning. At
 921 the beginning of each block, written instructions informed participants about the dimension to
 922 attend: either the numerosity or the average size of the dots arrays. Participants were
 923 instructed to keep in memory the relevant dimension of each sample trial until the following
 924 trial was shown (after a variable time interval of 3.5 - 5.5 s). The color of the fixation point in
 925 the upcoming trial provided further instruction: if it remained green, participants had to update
 926 their memory with the new stimulus (new sample trial), while if it turned red, participants had
 927 to compare the current stimulus (match trial) with the one kept in memory, and to indicate by
 928 button press whether the match stimulus was larger or smaller than the sample on the
 929 attended dimension. After the response a new sample stimulus appeared after at least 8
 930 seconds. fMRI analyses focused on activity evoked by sample stimuli only.

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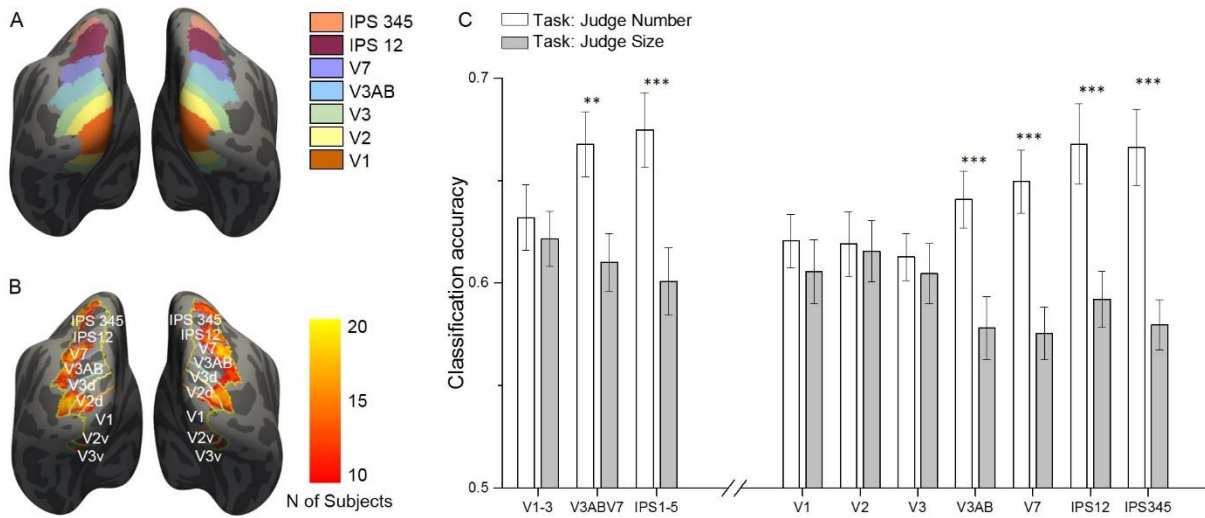


933
 934 Fig 2 Behavioral performance during scanning and univariate effects of task

935
 936 (A) The percentage of correct responses to match stimuli for the two tasks performed during
 937 scanning shows that task difficulty was successfully matched. (B-D) Statistical results
 938 obtained from the surface based group analysis (n=20). The maps show the activation
 939 elicited for all sample trials during the number task (B) and the size task (C) when contrasted
 940 against the implicit baseline and against each other (D). Activation maps are thresholded at
 941 $p < 0.001$, uncorrected for multiple comparison, and displayed on Freesurfer's fsaverage
 942 surface with outlines identifying the major sulci and gyri based on the Destrieux Atlas.

943

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946

947 Fig 3 ROI localization and results of multivariate classification for discrimination between
948 numerosities as a function of the task

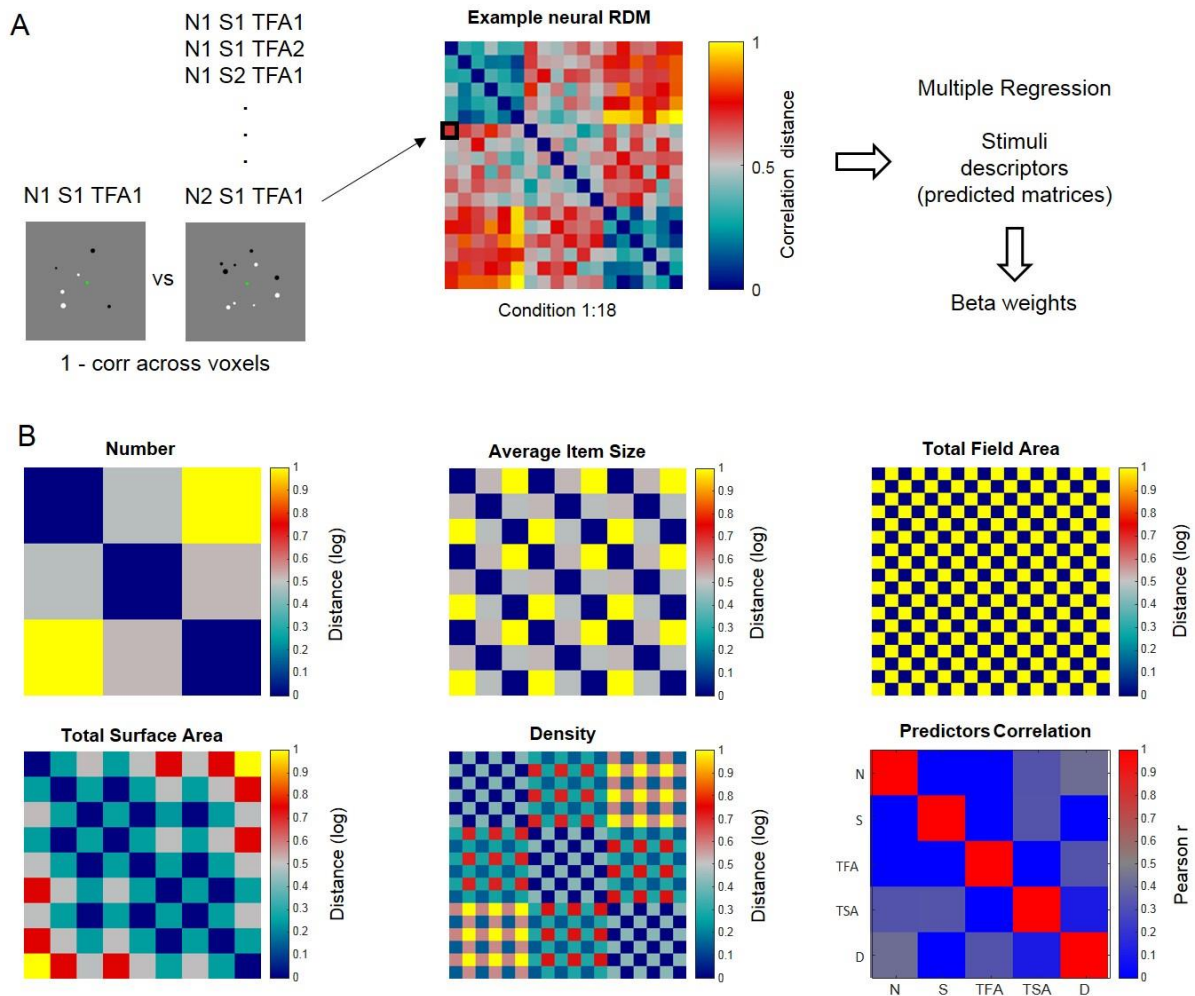
949 (A) Color-coded ROIs defined by the probabilistic atlas are shown on the inflated brain
950 template. (B) Across-subject overlap map of the most activated voxels in the contrast all
951 sample>baseline. For each subject the most activated voxels were selected from each ROI
952 (outlines) and hemisphere and the color map shows the number of subjects for which a given
953 location was selected. (C) Sample numerosities could be classified significantly above
954 chance across all the combined (left side) and individual (right side) ROIs, both during the
955 number (white bars) and size (gray bars) task. The classification performance is strongly
956 modulated by task only in the intermediate and higher-level ROIs, starting from V3AB on, but
957 not in the early areas (V1, V2 and V3). Results show mean classification accuracy across
958 subjects ($n=20$) \pm standard error of the mean (SEM).

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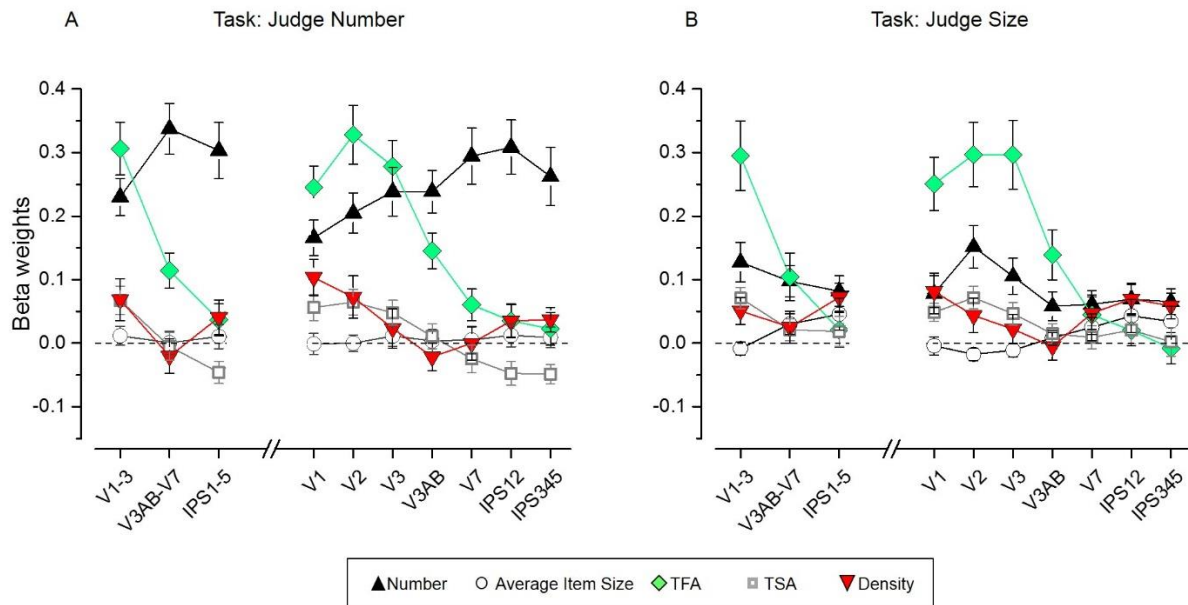
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963

964 Fig 4 Schematic Illustration of Representational Similarity Analysis

965 Neural representational dissimilarity matrices (RDM) derived from fMRI were entered in a
 966 multiple regression where predictors corresponded to five matrices describing the
 967 dissimilarities across stimulus conditions along numerical and non-numerical dimensions. (A)
 968 Example neural RDM, quantifying the correlation distance (1 – Pearson correlation) between
 969 the patterns of activity elicited by all possible pairs of stimulus conditions across voxels within
 970 a given ROI (matrix scaled between 0 and 1 for visualization purposes). Each cell represents
 971 the correlation distance between activity patterns associated with a given pair of stimulus
 972 conditions (relatively lower values indicate more similar, and higher values more dissimilar
 973 patterns, respectively). (B) The five dissimilarity matrices used as predictors in the multiple
 974 regression analysis represent the logarithmic distance between pairs of stimuli in terms of
 975 number, average item size, total field area, total surface area and density (all matrices scaled
 976 between 0 and 1 for visualization purposes). The correlation across these five predicted
 977 matrices is shown in the ‘predictor correlation’ matrix. The orthogonal combination of number
 978 (N), average item size (S) and total field area (TFA) levels in our design ensured that number
 979 was also partially de-correlated from total surface area (TSA) and density (D).



980

981 Fig 5 Results of the Representational Similarity Analysis

982 Beta weights obtained from the RSA multiple regression analysis for number (black
 983 triangles), average item size (circles), total field area (TFA, diamonds), total surface area
 984 (TSA, squares) and density (red triangles) for the number (A) and size (B) task. While the
 985 fMRI pattern dissimilarity in early visual areas reflected contributions of multiple properties
 986 (TFA, density, TSA, but also number on top of these), when attending to number (A) the
 987 dissimilarity matrix for number increasingly better explained the fMRI pattern dissimilarity
 988 when progressing towards higher areas of the dorsal visual stream, where the contribution of
 989 non-numerical dimensions was smaller. The dissimilarity matrix for number however,
 990 contributed much less to explain neural dissimilarity in mid- and higher-level ROIs during the
 991 size task (B). The contribution of the non-numerical dissimilarity matrices remained mostly
 992 unaffected in most of the ROIs, with only a slightly enhanced contribution of the dissimilarity
 993 matrix for density which significantly contributed to explain the neural RDMs in higher areas
 994 during the size judgments. Data points show mean beta weights across subjects ($n=20$) \pm
 995 standard error of the mean (SEM). P-values testing the significance of the beta coefficients
 996 for each dimension and ROI are reported in Table 1 in Supplementary Material.

997

998

999 **Supplementary Material**

1000 **Tables**

Task: Judge Number										
Stat\ROI	V1-3	V3AB-V7	IPS 1-5	V1	V2	V3	V3AB	V7	IPS12	IPS345
t-value	39.38	42.13	37.00	47.64	39.36	53.33	45.95	42.17	34.12	35.76
Dof	19	19	19	19	19	19	19	19	19	19
p-value	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
Task: Judge Size										
Stat\ROI	V1-3	V3AB-V7	IPS 1-5	V1	V2	V3	V3AB	V7	IPS12	IPS345
t-value	46.75	43.47	36.38	38.81	41.11	41.21	37.43	45.20	43.56	47.82
Dof	19	19	19	19	19	19	19	19	19	19
p-value	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005

1001

1002 Table 1 Statistical results for the performance of the classifiers trained to discriminate
 1003 between different numerosities.

1004 The table reports t-values, degrees of freedom (Dof) and p-values of the two-tailed t-tests
 1005 against zero used to evaluate the accuracies of number classification for every ROI and task.

1006

Task: Judge Number										
Dim\ROI	V1-3	V3AB-V7	IPS 1-5	V1	V2	V3	V3AB	V7	IPS12	IPS345
N	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
S	.447	.972	.587	.946	.996	.495	.836	.818	.500	.587
TFA	<.0005	.001	.157	<.0005	<.0005	<.0005	<.0005	.025	.185	.392
TSA	.007	.815	.016	.014	.005	.026	.580	.271	.021	.005
D	.052	.456	.151	.002	.043	.464	.339	.998	.200	.075
Task: Judge Size										
Dim\ROI	V1-3	V3AB-V7	IPS 1-5	V1	V2	V3	V3AB	V7	IPS12	IPS345
N	.001	.001	.003	.024	<.0005	.001	.020	.010	.013	.005
S	.405	.086	.083	.777	.085	.339	.459	.243	.119	.155
TFA	<.0005	.012	.445	<.0005	<.0005	<.0005	.002	.170	.419	.747
TSA	<.0005	.238	.439	.003	.001	.017	.361	.622	.352	.921
D	.025	.328	.004	.004	.127	.348	.821	.083	.007	.009

1007

1008 Table 2 Statistical results for beta weights obtained from the RSA multiple regression.

1009 The table shows p-values of two-tailed t-tests against zero across subjects for every ROI and
 1010 dimension (N: number, S: average item size, TFA: total field area, TSA: total surface area, D:
 1011 density) for the number (upper table) and size (lower table) tasks.

1012