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1 Increased functional connectivity of the intraparietal sulcus underlies the

2 attenuation of numerosity estimations for self-generated words

3

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4 Abbreviated title: Attenuation of numerosity estimations

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- 41

42 ABSTRACT

43	Previous studies have shown that self-generated stimuli in auditory, visual, and
44	somatosensory domains are attenuated, producing decreased behavioral and neural
45	responses compared to the same stimuli that are externally generated. Yet, whether such
46	attenuation also occurs for higher-level cognitive functions beyond sensorimotor processing
47	remains unknown. In this study, we assessed whether cognitive functions such as
48	numerosity estimations are subject to attenuation in 56 healthy participants (32 women).
49	We designed a task allowing the controlled comparison of numerosity estimations for self
50	(active condition) and externally (passive condition) generated words. Our behavioral results
51	showed a larger underestimation of self- compared to externally-generated words,
52	suggesting that numerosity estimations for self-generated words are attenuated. Moreover,
53	the linear relationship between the reported and actual number of words was stronger for
54	self-generated words, although the ability to track errors about numerosity estimations was
55	similar across conditions. Neuroimaging results revealed that numerosity underestimation
56	involved increased functional connectivity between the right intraparietal sulcus and an
57	extended network (bilateral supplementary motor area, left inferior parietal lobule and left
58	superior temporal gyrus) when estimating the number of self vs. externally generated
59	words. We interpret our results in light of two models of attenuation and discuss their
60	perceptual versus cognitive origins.

61

62 SIGNIFICANCE STATEMENT

63 We perceive sensory events as less intense when they are self-generated compared to externally-generated ones. This phenomenon, called attenuation enables us to distinguish 64 sensory events from self and external origins. Here, we designed a novel fMRI paradigm to 65 assess whether cognitive processes such as numerosity estimations are also subject to 66 attenuation. When asking participants to estimate the number of words they had generated 67 68 or passively heard, we found bigger underestimation in the former case, providing behavioral evidence of attenuation. Attenuation was associated with increased functional 69 70 connectivity of the intraparietal sulcus, a region involved in numerosity processing. Together, our results indicate that attenuation of self-generated stimuli is not limited to 71 72 sensory consequences but also impact cognitive processes such as numerosity estimations.

74 INTRODUCTION

75	The ability to distinguish self- versus externally-generated stimuli is crucial for self-
76	representation (Kircher and David, 2003; Legrand, 2006). A typical mechanism by which
77	stimuli generated by oneself and those caused by external sources are distinguished is
78	sensory attenuation, whereby self-generated stimuli are perceived as less intense. Indeed,
79	previous studies have shown that self-produced stimuli in the auditory (Baess et al., 2011;
80	Timm et al., 2014), visual (Hughes and Waszak, 2011; Benazet et al., 2016) and
81	somatosensory domains (Shergill et al., 2013; Kilteni and Ehrsson, 2020), are perceived as
82	less intense compared to the same stimuli when they are externally generated. Such
83	attenuation was shown at the behavioral level and at the neural level in sensory cortical
84	regions (e.g., auditory cortex (Rummell et al., 2016; Whitford, 2019)) as well as the
85	thalamus, cerebellum, supplementary motor area and inferior parietal cortex (Hickok, 2012;
86	Lima et al., 2016; Bansal et al., 2018; Brooks and Cullen, 2019).
87	
88	Previous studies have shown that attenuation not only applies to stimuli that are generated
89	by overt actions, but also extends to covert processes such as motor imagery (Kilteni et al.,
90	2018) or inner speech (Scott et al., 2013; Whitford et al., 2017). In the latter case,
91	attenuation of the electrophysiological (Whitford et al., 2017; Jack et al., 2019) and
92	behavioral (Scott et al., 2013) responses corresponding to the test stimulus (phoneme) was
93	observed when it matched the imagined cued phoneme. These studies used phonemes that
94	are integrated into the early stages of hierarchical speech processing implying primary

96 effects have been demonstrated (Rummell et al., 2016). An outstanding question is whether

attenuation of self-generated stimuli is limited to sensory consequences (e.g., weakened 97 percept) or whether it can also impact cognitive processes that are non-perceptual in nature 98 99 such as abstract judgments or performance monitoring. 100 To answer this question, we investigated the cognitive function of numerosity estimations, defined as approximate judgments when counting is not involved (Dehaene, 1997). 101 102 Properties of numerosity estimations such as innateness, amodality, or precision that 103 linearly decreases with increasing numerosity have been described (Anobile et al., 2016; 104 Burr et al., 2018). Extensive neuroimaging work has also established that brain areas in the intraparietal sulcus (IPS) region play a key role in numerosity processing (for review, see 105 Arsalidou & Taylor, 2011). If attenuation for self-related functions extends to higher-level 106 107 cognitive processes such as numerosity estimations, we would expect the number of items that are self-generated to be underestimated compared to externally-generated items in 108 109 relation to modulation of IPS activity. Thus, this study aimed at investigating whether numerosity estimations of self-generated words were attenuated compared to numerosity 110 estimations of passively heard words, thereby demonstrating that self-attenuation applies 111 112 to cognitive processes beyond sensory processing. To investigate which brain regions and networks showed activity related to attenuation 113 processes, we designed a functional magnetic resonance imaging (fMRI) paradigm allowing 114 115 the controlled comparison of numerosity estimations of either self-generated words (active condition) during a phonetic verbal fluency task or externally-generated words (passive 116 117 condition) while passively listening to a stream of words. Additionally, we asked participants to evaluate the error they could have made in their estimation (performance monitoring). 118

119 Assuming that attenuation occurs during numerosity estimations (active condition), we

120	predicted that participants would underestimate the number of self- vs. externally-
121	generated words and explored possible effects on performance monitoring. As performance
122	monitoring is better for self-initiated vs. observed processes (Pereira et al., 2020), we
123	expected to find a stronger relationship between the reported and actual number of words
124	in the active vs. passive condition. At the neural level, considering that sensory attenuation
125	of self-generated stimuli involves the corresponding sensory brain regions (e.g., primary
126	auditory cortex for attenuated sounds, see Rummell et al., 2016; Whitford, 2019), we
127	expected to find reduced BOLD signal during the active vs. passive condition in areas
128	responsible for numerosity processing including the IPS.

129 METHODS

130 Participants

131	Three independent participant groups were tested in this study. First, we performed a
132	behavioral pilot experiment in a mock scanner, where we tested 17 (6 women) participants
133	(age range: 18 – 28 years; M = 23 years, CI(95%) = [23, 24]); schooling level varied between
134	13 and 21 years; M = 17 years, CI(95%) = [16, 18]). During the main fMRI experiment, we
135	studied 25 (14 women) participants (age range: 18 – 37 years; M = 23 years, CI(95%) = [22,
136	26]; schooling level varied from 12 to 22 years: M = 17 years, CI(95%) = [16, 18]). An
137	additional control experiment in the mock scanner was performed, where 14 (12 women)
138	participants were tested (age range: 18 – 29 years; M = 24 years, CI(95%) = [22, 26]);
139	schooling level varied between 10 and 23 years; M = 16 years, CI(95%) = [14, 18]). All
140	participants were right-handed according to the Edinburgh Hand Preference Inventory
141	(Oldfield, 1971) and native French-speaking healthy volunteers with no history of
142	neurological or psychiatric disease and no recent reported history of drug use. Participants
143	had normal or corrected-to-normal vision and no claustrophobia. All participants were naive
144	to the purpose of the study, gave informed consent in accordance with institutional
145	guidelines and the Declaration of Helsinki, and received monetary compensation (20 CHF /
146	hour). The study was approved by the local ethical committee of the canton Geneva
147	(protocol ID: 2015-00092).

148 Experimental task

The experiment was performed in a mock scanner environment (both for the behavioralpilot experiment and the training for the main fMRI experiment) and in the MRI scanner

151	(main fMRI experiment). The task consisted in phonetic verbal fluency and passive word
152	listening parts, followed by numerosity and error estimations (Figure 1). The task comprised
153	two conditions (20 trials each) during which participants either covertly generated words
154	(active condition) or listened to pre-recorded words (passive condition). Each trial started
155	with a randomly jittered inter-trial interval varying between 4 s and 4.75 s, followed by an
156	audio cue (2 s) indicating which of the active or passive condition will follow, and a recorded
157	cue letter (2 s). Next, the word generation phase lasted between 20 s and 35 s; in the active
158	condition, participants had to covertly generate words starting with the cued letter (Figure
159	1, top). For each word they covertly generated, participants were asked to press a response
160	button, which gave us access to the actual number of generated words. In the passive
161	condition, a series of pre-recorded audio words were played to the participants, who were
162	asked to press the response button for every word that contained the cue letter (Figure 1,
163	bottom). We avoided asking participants to detect words starting with the cued letter, as
164	this could have influenced word generation in the next active trials with the same cued
165	letter. In both conditions, the end of the generation/listening phase was indicated by an
166	audio cue (0.5 s). After that, participants first reported the estimation of a total number of
167	words generated (active condition) or heard (passive condition). For this, they used two
168	buttons that moved a slider displayed on the screen. The slider was presented as a random
169	integer (ranging from 0 to 20), which could be changed in value by pressing the response
170	box buttons (left button – decrease the value, right button – increase the value). This was
171	followed by an error estimation, where participants were asked to evaluate their
172	performance on the numerosity estimation by estimating the magnitude of the error they
173	thought they might have made (in number of words). For this, an automatically sliding bar
174	was presented, and the participant had to select with one button press the desired value

(e.g., +/- 2 words error). Values varied from +/- 0 words (e.g., numerosity response judged
as correct) to +/- 5 words mistaken. The total time for numerosity and error estimations
were restricted to a maximum of 7 s. Except for the numerosity and error estimation
periods, participants were asked to perform the task with eyes closed.

179

180 Stimuli

181 All stimuli were prepared and presented using Matlab 2016b (mathworks.com) and the Psychtoolbox-3 toolbox (psychtoolbox.org; Brainard 1997; Kleiner et al. 2007; Pelli 1997). 182 183 Twenty different cue letters were used for active and passive conditions. The same cue 184 letter was used once during the active and once during the passive condition in the counterbalanced order. Played back words during the passive condition were chosen from a 185 list of 420 French words (Ferrand and Alario, 1998). The audio stimuli presented during the 186 187 task were recorded by male and female native French speakers in a neutral manner and registered in wav format with 11025Hz sampling frequency. The gender of the voice 188 pronouncing words in the passive condition was matched to the participants' gender. During 189 190 the experiment, participants were equipped with MRI compatible earphones and report 191 buttons for the right hand.

192 Procedure

Participants were trained in a mock scanner prior to the main fMRI experiment in order to familiarize themselves with the task. They were asked to perform four trials of the task during the training (twice for each condition), with the cue letters 'j' and 'k'. These letters were not used later during the main fMRI experiment. We note that participants were

197	instructed by the experimenter not to count nor use any strategy to try to remember the
198	number of words generated/heard while performing numerosity and error estimations.
199	The main experiment consisted of three runs lasting approximately 15 min, each with short
200	breaks in-between. The total duration of a trial varied between 40 and 55 s due to
201	pseudorandomized time for the word generation/listening phase. This time variability was
202	introduced to avoid habituation and predictability for the number of generated/heard
203	words and to decorrelate hemodynamic activity related to word generation/listening and
204	numerosity estimations. The experiment was designed in 10 blocks with 4 trials of the same
205	condition per block. The blocks of the active condition trials always preceded the blocks of
206	the passive condition, allowing us to use the number and pace of generated words that
207	were recorded based on participant's button presses to playback the words during the next
208	block of the passive condition. The order of the number of words played with their
209	corresponding pace during the passive condition was shuffled within the block. This was
210	done to ensure that participants could not recognize whether the number and pace of the
211	played words matched the preceding active condition block. Additionally, to avoid repetition
212	effects between blocks, the cue letters between two consecutive blocks were different,
213	meaning that the cue letters in a given active block were not used in the following passive
214	block.
215	After the main experiment, a standard phonemic verbal fluency (generation time of 60 s,

cue letter 'p') test (Lezak, 1995) was performed overtly to verify that subjects understood
the task correctly. Overall, the experiment lasted approximately 1h 30 min (MRI session)
and 1h in the mock scanner (pilot session). The pilot mock scanner study contained the

same procedure as the main MRI experiment, except for the shorter breaks between theruns since there was no scanning involved.

The sample size for the main fMRI experiment was based on a recent study from our group in which similar conditions were contrasted (e.g., judgement of self-generated vs. observed decisions; Pereira et al., 2020).

224 Control order experiment

225 An additional control experiment in the mock scanner was performed to rule out the 226 possibility that repetition effects occurred between consecutive blocks. It consisted only of 227 passive condition trials, which were divided into 'random' and 'repeated' blocks. The 'random' block trials were designed by pseudo-randomly generating the number of words 228 played (mean of 10 words/block ranging from 6 to 20 words per trial) and their playing pace 229 230 (total time of playing varied between 20 s and 35 s) to match the main fMRI experiment. 'Repeated' blocks consequently followed 'random' blocks, with the same number of words 231 and word playing pace as in the preceding random block but with a shuffled order. This 232 control experiment consisted of 2 'random' and 2 'repeated' blocks, with 4 trials/block, and 233 234 lasted approximately 30 min.

235

236 Behavioral performance measures

Most statistical frameworks to analyze performance monitoring have been developed for discrimination tasks with a binary response (e.g., Fleming and Lau, 2014 for a review). In the following, we propose two indices of numerosity performance and performance monitoring to analyze ordinal data (e.g., number of words). In addition to the prerequisites described

243	The numerosity performance index is a normalised accuracy ratio reflecting how correctly
244	participants estimated the number of words during the generation/listening phase. For each
245	trial, we wanted signed numerosity performance to be proportional to the difference
246	between the reported number of generated/heard words (numerosity estimation; [N]) and
247	the actual number of words generated/heard [W]. We normalized this difference by the
248	sum of numerosity estimation and actually generated/heard number of words [N+W]
249	(equation 1) to give more weight to errors made about low numbers of words (e.g., an error
250	of +/- 2 given a numerosity estimation of 8 has higher magnitude than an error of +/-2 given
251	a numerosity estimation of 16; Figure 1-1 A). This normalization allowed us to assess
252	attenuation effects independent of the number of generated words, given that the precision
253	of numerosity estimation linearly decreases with increasing number of items (e.g., Piazza et
254	al., 2004). Negative numerosity performance values thus reflected an underestimation of
255	generated/heard words, and positive values reflected an overestimation of
256	generated/heard words. In contrast, null numerosity performance values reflected correct
257	answers about the number of generated/heard words.
258	numerosity performance = $\frac{N-W}{N+W}$ (equation 1)

Additionally to the numerosity performance index, we derived separate measures of

261 accuracy [N-W] and accuracy ratio [(N-W)/W] to assess the generalizability of our findings.

262	Performance monitoring reflected how well participants estimated an error about their
263	previous performance. We defined it as the absolute value of the difference between the
264	error estimation [E] and (accuracy [N-W]), normalized by the sum of the numerosity
265	estimation and words generated/heard [N+W]) (equation 2). Normalization was done in
266	order to consider the difficulty; the same error made when estimating the low number of
267	words or high number of words should be penalized proportionally. A performance
268	monitoring value of 0 reflected ideal error tracking, whereby participants correctly
269	estimated the error made during the numerosity estimation. An increase in performance
270	monitoring value represented an increase in error magnitude while estimating the
271	difference between numerosity estimation and the actual number of words
272	generated/heard (Figure 1-1 B).

273 *performance monitoring* =
$$\left|\frac{E - |N - W|}{N + W}\right|$$
 (equation 2)

Data cleaning was performed prior to statistical analysis: trials for which participants did not
generate at least five words or failed to answer numerosity or error estimations within the
time limit were excluded from behavioral and fMRI analysis (in total, 2.44 ± 1.87
trials/subject were excluded). The threshold of 5 words was selected according to the
working memory capacity of 5 ± 2 items (Cowan, 2010). Considering all participants' data,
6.1% of all trials were discarded.

281 Behavioral data analysis

- 282 All continuous variables (numerosity performance, accuracy, accuracy ratio and
- 283 performance monitoring) were analyzed using linear mixed-effects regressions with

284	condition ("active", "passive" or "random", "repeat" for the control order experiment) as a
285	fixed effect and a random intercept by participant and condition. The inclusion of additional
286	random effects was guided by model comparison and selection based on Bayesian
287	Information Criteria. Analyzes were performed using the Ime4 (Bates et al., 2015) and
288	ImerTest (Kuznetsova et al., 2017) packages in R (R-project.org). The significance of fixed
289	effects was estimated using Satterthwaite's approximation for degrees of freedom of F
290	statistics (Luke, 2017).

291 Bayesian analysis was performed using the brms package (Bürkner, 2017) in R to examine the occurrence of possible repetition effects between random and repeated passive blocks 292 in the control experiment. Namely, we conducted a Bayesian linear model of numerosity 293 294 performance with condition ("random", "repeated") as fixed effects and a random intercept by participant and condition with four chains of 10000 iterations including 2000 warmup 295 296 samples. We made a prior assumption that underestimation would be observed in the passive condition (prior with Gaussian distribution of mean = -0.032 and SD = 0.156), based 297 on the difference between numerosity performance during the active and passive 298 conditions observed in the main fMRI experiment. 299

300 Data simulation of absolute accuracy during numerosity estimations

302 generated/heard) of numerosity estimations observed in the experimental data may be

To examine weather absolute accuracy (correct numerosity estimations of words

- 303 approximated by a noisy sampling process rather than counting, we performed data
- 304 simulations. More specifically, we simulated 1000 numerosity estimations (as the main
- 305 experiment contained 40 trials/subject * 25 subjects) from a normal distribution centred on
- 306 10 and standard deviation (SD) varying from 0.5 to 6 with 0.1 steps. We rounded each item

to the nearest integer and counted how many times the number 10 was obtained. The
simulation was iterated 10000 times.

309 fMRI data acquisition

- 310 MRI data were acquired using a Siemens Magnetom Prisma 3 T scanner with a 64-channel
- head coil. T1 weighted (1 mm isotropic) scans were acquired using a Magnetization
- 312 Prepared Rapid Acquisition Gradient Echo (MPRAGE) sequence (TR = 2300 ms; TI = 900 ms;

313 TE = 2.25 ms; flip-angle = 8 degrees; GRAPPA = 2; FOV = 256 × 256 mm; 208 slices).

- 314 Functional scans were obtained using echo-planar (EPI) sequence (multiband acceleration =
- 315 6; TR = 1000 ms; TE = 32 ms; flip-angle = 58 degrees; FOV = 224 × 224 mm; matrix = 64 x 64;
- 316 slice thickness = 2 mm; number of slices = 66). The number of functional image volumes
- varied according to the experiment duration (2278 ± 61 volumes).

318 fMRI data preprocessing

Anatomical and functional images were processed and analyzed using SPM-12 (Welcome 319 Centre for Human Neuroimaging, London, UK). Pre-processing steps included slice time 320 321 correction, field-map distortion correction, realignment and unwarping to spatially correct for head motions and distortions, co-registration of structural and functional images, 322 323 normalization of all images to common Montreal Neurological Institute (MNI) space, and spatial smoothing with a Gaussian kernel with a full-width at half maximum (FWHM) of 4 324 mm. Quality assurance of all EPI images was performed with the criteria of maximum 2 mm 325 translation and 2° rotation between volumes. In addition, an excessive movement was 326 estimated with the mean framewise displacement (FD) (Power et al., 2012) with the 327 328 exclusion threshold of 0.5 mm. None of the subjects had a higher mean FD (0.2 ± 0.06 mm) 329 than the set threshold.

330 fMRI data analysis

331	We used a two-level random-effects analysis. In the first-level analysis, condition-specific
332	effects were estimated according to a general linear model (GLM) fitted for each subject. An
333	average mask of grey matter from all subjects was built using FSL (fsl.fmrib.ox.ac.uk/fsl) and
334	used to mask out white matter and non-brain tissues. The GLM was built using six boxcar
335	regressors corresponding to the duration of the word generation/listening phase,
336	numerosity estimation and error estimation in the active and passive conditions. Parametric
337	modulators of numerosity performance and performance monitoring were included in the
338	numerosity estimation and error estimation regressors, respectively. Further, we added
339	regressors of no interest corresponding to audio instructions, button presses and excluded
340	trials, plus six regressors for head motion (translation and rotation).
2/1	At the second level (group level), we performed a one way analysis of variance (ANOVA)
541	At the second-level (group level), we performed a one-way analysis of variance (ANOVA)
342	with F-tests to assess main effects common to active and passive conditions and t-tests to
343	analyze the difference between conditions (active vs. passive) for each regressor of interest:
344	numerosity estimation and error estimation. We used a voxel-level statistical threshold of
345	p<0.001 and corrected for multiple comparisons at the cluster level using family-wise error
346	(FWE) correction with the threshold of p<0.05. We used the anatomical automatic labelling

(AAL) atlas for brain parcellation (Tzourio-Mazoyer et al., 2002). 347

Functional connectivity analysis 348

Psychophysiological Interaction (PPI) analysis was employed to identify modulations of 349 350 functional coupling between a seed region and other brain regions by experimental conditions (active vs. passive) (Friston et al., 1997). To perform this analysis we used 351

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generalized psychophysiological interaction (gPPI) toolbox version 13.1 (McLaren et al.,
2012). Spheres of 6 mm radius were formed around the peak coordinates of the right IPS (x
= 29; y = -65; z = 50) and the left IPS (x = -27; y = -66; z = 47) clusters that were identified in
the second-level analyses. First-level (individual) GLM analyses were performed, including
task regressors of numerosity estimation or error estimation (psychological term) and time
course of the seed region (physiological term). As for other aforementioned fMRI analyses,
we performed t-tests to compare the differences between conditions.

359 Data and code availability

360 The MRI data that support the findings of this study is available on a public repository on

361 zenodo.org (https://doi.org/10.5281/zenodo.4925909). Behavioral data, analysis and task

362 codes are available here: https://gitlab.epfl.ch/lnco-public/cognitive-attenuation.

363 RESULTS

364 Behavioral results

365 By design, the number of generated and heard words was matched between conditions

366 (active: M = 10.7, SD = 3.6, CI(95%) = [10.4, 11.1]; passive: M = 10.7, SD = 3.5, CI(95%) =

367 [10.4, 11.0], $F_{(1.884)} = 0.005$, p = 0.94). The duration of word generation and listening did not

differ between conditions either (active: M = 27.4, SD = 5.6, CI(95%) = [26.9, 27.9]; passive:

369 M = 28.4, SD = 7.0, CI(95%) = [27.7, 29.0], $F_{(1.26)} = 2.04$, p = 0.16). Having shown that

370 conditions were similar in terms of difficulty, we turned to the analysis of numerosity

371 performance and performance monitoring.

372 Numerosity performance indices revealed that globally, participants underestimated the

373 number of words (M = -0.05, SD = 0.11, Cl(95%) = [-0.06, -0.05]). This underestimation was

374	significantly larger ($F_{(1,24)} = 5.85$, p = 0.023, 18 subjects out of 25 showed the effect) in the
375	active condition (M = -0.07, SD = 0.11, CI(95%) = [-0.08, -0.06]) compared to the passive
376	condition (M = -0.04, SD = 0.12, Cl(95%) = [-0.05, -0.03]) (Figure 2 A). Comparable results
377	were obtained during the pilot experiment in the mock scanner in an independent group of
378	subjects (active: M = -0.05, SD = 0.01, CI(95%) = [-0.06, -0.03]); passive: M = -0.03, SD = 0.10,
379	CI(95%) = [-0.04, -0.02]; $F_{(1,16)}$ = 5.80 p = 0.016). These two experiments suggest that
380	numerosity estimations for self-generated words are attenuated.
381	We further show that the larger underestimation in the active compared to the passive
382	condition was also found when considering the measures of accuracy (active: $M = -1.48$, SD
383	= 2.38, CI(95%) = [-1.69, -1.26]); passive: M = -0.94, SD = 2.59, CI(95%) = [-1.17, -0.71];
384	F(1,24) = 4.43 p = 0.045) and accuracy ratio as dependent variables (active: M = 0.89, SD =
385	0.20, Cl(95%) = [0.87, 0.91]); passive: M = 0.95, SD = 0.23, Cl(95%) = [0.93, 0.97]; F(1,24) =
386	7.44 p = 0.011).
387	We then assessed the linear relationship between the reported (numerosity estimation) and
388	actual number of words (Figure 2 B). Besides a main effect of words ($F_{(1,908)}$ = 1042, p <
389	0.001) and of condition ($F_{(1,198)}$ = 8.25, p = 0.0045), we found an interaction between
390	condition and generated/heard words ($F_{(1,802)}$ = 4.3, p = 0.038). This interaction was driven
391	by a steeper slope in the active condition (M = 0.62, CI(95%) = [0.57, 0.67]) compared to the
392	passive condition (M = 0.55, CI(95%) = [0.50, 0.60]) (Figure 2 C), which indicates better
393	numerosity tracking for self-generated words during the main fMRI experiment (a slope of
394	value 1 reflecting ideal performance). We note that this interaction did not reach
395	significance in our pilot experiment ($F_{(1,350)}$ = 1.10, p = 0.66), which calls for interpreting this
396	result with caution.

397	Next, we investigated whether performance monitoring varied between conditions, by
398	quantifying how well participants were able to track the error made when estimating the
399	number of generated/heard words. We found no differences in performance monitoring
400	$(F_{(1,24)} = 1.09, p = 0.3)$ between the active (M = 0.07, SD = 0.06, CI(95%) = [0.07, 0.08]) and
401	passive (M = 0.08 , SD = 0.06, CI(95%) = [0.07, 0.09]) conditions during the main fMRI
402	experiment, nor during the mock scanner pilot experiment ($F_{(1,16)} = 0.78$, p = 0.39; active: M
403	= 0.07, SD =0.06, CI(95%) = [0.06, 0.08]; passive: M = 0.06, SD =0.06, CI(95%) = [0.06, 0.07]).
404	This confirms the absence of evidence supporting an effect of attenuation on performance
405	monitoring.

Finally, we carried out a control task for word generation outside the scanner, during which
participants had to perform a standard verbal fluency task overtly with the cue letter 'p'.
Comparing the number of words generated, starting with the letter 'p' overtly (outside the
scanner) and covertly (during the scanning), we did not observe any significant differences
between the number of words generated overtly (M = 12.6, SD = 3.79, Cl(95%) = [10.9,
14.1]) and covertly (M = 12.3, SD = 3.96, Cl(95%) = [10.6, 13.9]; paired t-test; t₍₂₄₎ = -0.4;

412 p=0.69). This control task confirms that subjects did generate words covertly and

- 413 comparably to overt fluency, as instructed.
- 414 Control order experiment. The global underestimation (M = -0.06, SD = 0.11, CI(95%) = [-
- 415 0.08, -0.05]) was replicated as in the main experiment. This underestimation was not

417 0.09, -0.04]) and 'repeated' (M = -0.07, SD = 0.12, CI(95%) = [-0.09, -0.04]) blocks, with a

418 Bayes factor BF10 = 0.09 supporting the absence of difference between conditions.

Data simulation of absolute accuracy during numerosity estimations. As can be seen on the
Figure 3, the value of 10 occurred in 19.5% of all data points when drawn from a normal
distribution with SD = 2, similarly to the observed empirical data.

422

423 fMRI results

424 Numerosity performance

425 Brain activity during the numerosity estimation phase was widespread, irrespective of the

426 experimental condition (Table 1-1). Differences between conditions revealed widespread

427 relative deactivations in the active compared to the passive condition in the bilateral

428 parietal cortex including IPS, middle-superior temporal gyri, precuneus, cerebellum, middle

429 cingulate gyri, SMA, insula, middle-superior frontal gyri, hippocampus, caudate nucleus,

430 putamen (for the detailed list of all areas see Table 1).

To avoid contaminating the results with inherent differences between the active and passive 431 432 conditions that are not specific to numerosity processes, we looked for brain activity parametrically modulated by numerosity performance. We found a single brain region with 433 such a pattern of activity, namely the right IPS, whose activity was negatively correlated 434 with numerosity performance (main effect F = 20.0, $p_{FWE} = 0.042$, $k_{vox} = 148$, x = 29, y = -65, z 435 436 = 50; Figure 4 A, B). The same pattern was found bilaterally when using a less stringent threshold (p<0.005 peak level uncorrected; Figure 4 C, Table 2). Unlike our prediction, IPS 437 activation did not differ between the active and passive conditions ($p_{FWE} > 0.05$), suggesting 438 that this effect was independent of whether words were heard or actively generated. 439

440	Using PPI analysis, we investigated whether the functional connectivity of the right IPS with
441	other brain regions differed between the active and passive conditions. This analysis
442	revealed that bilateral supplementary motor area (SMA), left inferior parietal lobule (IPL)
443	and left superior temporal gyrus (STG) had increased connectivity with the right IPS in the
444	active compared to the passive condition (Figure 5, Table 3). No effect in the other direction
445	was observed.

447 Performance monitoring

448 Besides numerosity performance, we also quantified brain activity during the error

449 estimation phase. We found widespread cortical and subcortical activations during this

450 phase compared to baseline, irrespective of the experimental condition (Table 4-1).

451 Moreover, bilateral insula and right putamen were significantly less active during the active

452 compared to the passive condition (Figure 6, Table 4). The left caudate nucleus showed the

453 opposite pattern, with higher activity in the passive than in the active condition.

454 To avoid confounding factors between the active and passive condition, we looked more

- 455 specifically at parametric modulations of error monitoring. We observed that BOLD signal in
- 456 the left IPS was more related to performance monitoring in the active compared to the

457 passive condition (t = 4.02, p_{FWE} = 0.041, k_{vox} = 198, x = -27, y = -66, z = 47; Figure 7).

458 Interestingly, this activation cluster spatially overlapped with the observed activation cluster

- 459 related to the main effect of numerosity performance when applying a lower statistical
- 460 threshold (exploratory analysis, p<0.005 peak level uncorrected, pFWE < 0.05 cluster level)

461 (see Figure 4 C).

- Lastly, results from the PPI analysis using the left IPS as a seed ROI did not reveal any
- 463 functional connectivity differences between the active and passive conditions during error

464 estimation.

465

467 **DISCUSSION**

468	The present study examined whether attenuation of self-generated stimuli impacts
469	cognitive processes beyond the traditionally investigated sensory processes, namely
470	numerosity estimations and performance monitoring. To this end, we developed an
471	experimental paradigm allowing the controlled comparison of numerosity estimations and
472	performance monitoring regarding self- and externally-generated words while acquiring
473	fMRI data. We found that participants more strongly underestimated the number of self-
474	compared to externally-generated words, providing behavioral evidence that numerosity
475	estimations are indeed subject to attenuation. As expected, numerosity performance was
476	associated with hemodynamic activity changes in IPS. Furthermore, a network including the
477	bilateral SMA, left IPL and left STG showed increased functional connectivity with the right
478	IPS during numerosity estimations for self-generated words, suggesting that numerosity-
479	related attenuation involves this neural network. Finally, by asking participants to monitor
480	the accuracy of their own numerosity estimations, we found equivalent performance
481	monitoring for self- and externally-generated words. Although no difference was found at
482	the behavioral level, we found that performance monitoring was associated with increased
483	IPS activity in the active vs. passive condition.

484 Behavioral and neural markers of attenuated numerosity estimations

Participants underestimated the number of words they generated or heard. Such
underestimations were previously described regarding the numeric estimation of perceptual
quantities (e.g., number of dots or sequences of sounds) to discrete measures (e.g., Arabic
numeral) (Castronovo and Seron, 2007; Reinert et al., 2019). In the present study, we found
that word numerosity underestimation was stronger in the active compared to the passive

490 condition, in line with our hypothesis that attenuation of self-generated stimuli may extend
491 to higher-level cognitive functions (Kilteni et al., 2018; Jack et al., 2019). Of note, this
492 underestimation could not be due to simple repetition effects between successive blocks of
493 active and passive condition trials, as a control experiment showed no differences in
494 numerosity estimations between repeated blocks of passive condition trials.

495

Attenuation of self-generated stimuli has been mostly investigated for sensory processes 496 497 and refers to the diminished behavioral and neural responses associated with self-498 generated compared to externally-generated stimuli (Timm et al., 2014; Benazet et al., 499 2016). Importantly, attenuation has recently also been described for imagined actions in the absence of overt actions (e.g., Kilteni et al., 2018; Jack et al., 2019;). For example, imagined 500 self-touch was felt as less intense compared to externally applied touch (Kilteni et al., 2018). 501 Similarly, imagined speech elicited reduced electrophysiological signals related to auditory 502 503 processing (Whitford et al., 2017). These studies, however, investigated cognitive processes intimately linked to sensorimotor systems (e.g., imagined movement and touch), yet, to the 504 505 best of our knowledge, it was unknown whether comparable mechanisms of attenuation 506 also affect cognition beyond sensorimotor processing, such as numerosity estimations with no or less obviously implicated sensorimotor processes (e.g., Dehaene, 1997). Here we show 507 508 that differential attenuation can be observed for cognitive processes such as numerosity estimations that depend on whether they are self-generated or not. As of today, there is no 509 510 consensus to explain how the brain attenuates expected (e.g., self-generated) stimuli while remaining sensitive to unexpected ones (for a recent review and unifying theoretical 511 512 account see Press et al., 2020). Among the so-called cancellation theories, the internal

513	forward model (Farrer and Frith, 2002; Miall and Wolpert, 1996) proposes that corollary
514	discharges related to action are used to predict the sensory consequences of that action.
515	When such predictions match the actual sensory feedback from the action, its sensory
516	consequences are attenuated, and the action is perceived as self-generated (Wolpert and
517	Flanagan, 2001). The forward model thus proposes to link sensory attenuation to the
518	sensory predictions generated by a neural comparator. An analogous mechanism has been
519	proposed to account for attenuation for covert actions such as motor imagery (Kilteni et al.,
520	2018) or inner speech (Tian and Poeppel, 2010). The present data show that attenuation
521	exists beyond overt and covert actions, raising the possibility that the forward model
522	extends to repetitive cognitive activity (e.g., fluency and related numerosity estimations).
523	One possibility, similar to what has been described for inner speech, would be that
524	numerosity underestimation stems from a weaker perceptual representation of self-
525	generated words. In other words, attenuation may not impact numerosity estimations
526	directly, but rather through a decreased representation of self-generated words, which in
527	turn may lead to attenuation of numerosity estimations.
528	A second account could be that mental operations have a gating effect (Cromwell et al.,
529	2008), independent from predictive mechanisms, thereby directly affecting the strength of
530	the mental representations of self-generated words. A similar gating mechanism has
531	recently been shown to offer a plausible alternative to forward model accounts of sensory
532	self-attenuation (Thomas et al., 2020). Finally, the general mechanisms put forward by the
533	predictive coding account of active inference to explain sensory attenuation may also apply
534	to non-perceptual cognitive attenuation such as the one we observed (Brown et al. 2013)

535	At the neural level, the IPS showed activity related to numerosity performance, in line with
536	previous studies (Cohen and Dehaene, 1996; Piazza et al., 2006). This relation, however, was
537	not modulated by condition (active vs. passive), as one could have expected based on
538	previous reports showing that sensory attenuation coincides with decreased activity in the
539	corresponding sensory area (e.g., attenuation in primary auditory cortex during self-
540	generated auditory stimuli; Rummell et al., 2016; Whitford, 2019). Importantly, we found
541	differences in functional coupling during numerosity estimations of the IPS with a network
542	of brain regions between the active and passive conditions. The increase in coupling during
543	the active condition occurred between the IPS and a network comprising the SMA, IPL and
544	STG, known to be involved in predictive processing, for example of self-generated auditory
545	and imagery speech (Lima et al., 2016; Tian et al., 2016). Although previous neuroimaging
546	studies have mainly shown attenuated brain activity for self-generated actions (e.g.,
547	Whitford, 2019), increases in functional connectivity such as we describe have been
548	reported in the primary auditory cortex during attenuated speech (van de Ven et al., 2009),
549	or of somatosensory cortex during attenuated touch (Kilteni and Ehrsson, 2020). Thus,
550	increased functional connectivity in a network centred on the key numerosity region, IPS,
551	and that has been associated with speech-related processing further supports that
552	numerosity underestimation stems from a process related to attenuation when participants
553	self-generate words.
EE /	

555 Besides numerosity underestimation, we observed that participants formed more accurate 556 numerosity judgments for self- vs. externally-generated words: while participants' word 557 estimations were lower in the active condition than in the passive condition, the relation

558	between their estimated number of words and the actual number of words was better in
559	the active condition vs. passive condition, suggesting a sharper representation of the
560	number of self-generated words. This result corroborates recent findings showing better
561	monitoring for decisions that are committed rather than observed (Pereira et al., 2020). This
562	improved monitoring of self-generated words could be related to the sharpening of
563	expected representations known in the sensory domain (Kok et al., 2012) or to a self-
564	generation effect underlying the facilitation of information encoding and enhanced recall for
565	self-generated stimuli (Bertsch et al., 2007; Slamecka and Graf, 1978). We note that this
566	effect was not replicated during the mock pilot experiment, which included a smaller
567	sample of participants with a globally higher absolute accuracy. It is possible that this subtle
568	effect could not be observed in such conditions, which warrants future investigations and
569	cautious interpretation.
570	Performance monitoring is modulated at the neural but not behavioral level
571	Previous research has shown that both humans and non-human primates (Beran et al.,
572	2006; Duyan and Balcı, 2019, 2018) can monitor the quality of their numerosity estimations.
573	
	Thus, in addition to asking participants to estimate the number of words they generated or
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574 575 576	Thus, in addition to asking participants to estimate the number of words they generated or heard, we also asked them to estimate their own error during this process (performance monitoring). Although our behavioral results showed similar performance monitoring between conditions, we observed that performance monitoring was associated with

region is not typically associated with performance monitoring such as the prefrontal cortex

- or the insula/inferior frontal gyrus (Vaccaro and Fleming, 2018). Since activity in the left IPS
- is related to numerosity estimation (Cappelletti et al., 2007; Dormal et al., 2012), this

581	parametric modulation could therefore represent a substrate for monitoring specific to
582	numerosity estimations. By investigating global fMRI activity during error estimations, we
583	also observed decreased activation in the insula and putamen and increased activity in the
584	caudate nucleus when comparing the active vs. passive conditions. To note, the anterior
585	insula and putamen were activated during both conditions but were attenuated in the
586	active compared to the passive conditions. While the anterior insula activations are
587	consistent with previous literature on performance monitoring (Ullsperger et al., 2010;
588	Bastin et al., 2017), the findings of modulated activity in the striatum were unexpected.
589	Both areas are known as essential for the control of goal-directed decision-making (Balleine
590	et al., 2007; Kim and Im, 2019). Further links between performance monitoring and activity
591	modulation between conditions in the striatum regions should be explored in future studies.
592	Methodological considerations
593	As generating vs. listening to words inherently involves different behavioral and neural
594	processes, several aspects of our design should be considered when interpreting the current
595	findings as reflecting attenuation per se rather than experimental confounds. At the
596	behavioral level, the larger underestimation during the active condition was not due to
597	difficulty differences between conditions as task difficulty was matched by design, and
598	absolute accuracy (correct numerosity estimations of words generated/heard) was similar in

599 both conditions. Of note, a steeper slope during numerosity estimations and number of

600 words generated in the active condition suggests that participants better tracked their

601 performance even when underestimating more compared to the passive condition.

- 602 Although we could not explicitly control whether participants counted the number of words
- 603 they generated or heard, instructions were given not to do so. Yet, counting seems unlikely

604	as absolute accuracy reached only 19.5% of all trials, which is comparable to a recent study
605	with a similar setup (Serino et al., 2021), and much lower than what is typically observed
606	when participants are instructed to count (e.g, Kansaku et al., 2007). Furthermore, a similar
607	level of absolute accuracy was obtained on simulated data with numerosity estimations
608	drawn from a normal distribution with SD = 2, suggesting that behavior in this task is
609	approximated by a noisy sampling process rather than counting. At the neural level, to
610	ensure that the inherent differences between conditions did not contaminate our results,
611	we focused analyses on the numerosity and error estimation phases which were identical
612	between conditions, instead of the word generation/listening phases. In addition, we did
613	not base our conclusions on a direct contrast between the two conditions, but on
614	correlations between neural activity and numerosity or error estimates.
615	Conclusion
616	Based on behavioral and neuroimaging data, we propose that higher-level cognitive
617	functions such as numerosity estimations about the number of self-generated words are
618	attenuated. Such attenuation involves a functional network including a key-numerosity
619	region (IPS) and speech-related regions including the SMA, IPL and STG. While attenuating
620	the sensory consequences of one's actions is of crucial importance for aspects of the self,
621	such as the sense of agency, attenuating the products of one's mental activities may also be
622	relevant to distinguish them from external sources of information. Our paradigm offers a
623	
	promising tool to investigate attenuation processes related to the self in cognition and to

625 to the study of clinical cases in which attenuation in sensory and cognitive domains may be

- 626 is altered, including patients with psychotic symptoms like thought insertion whereby
- 627 thoughts are not considered as one's own, but of somebody else.

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638

639 Author Contributions

- GS, NF, GR, OB developed the study concept and contributed to the study design. Testing,
- 641 data collection and data analysis were performed by GS. GS, MP, JP and NF provided
- 642 methodological support. GS, NF, MP, and OB drafted the paper; all authors provided critical

revisions and approved the final version of the paper for submission.

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849 LEGENDS OF FIGURES AND TABLES

850 Figures

Figure 1. Schematic representation of the general task flow: active (top) and passive
(bottom) conditions consisting of instruction, word generation/listening, numerosity and
error estimation. Each condition was repeated 4 times per block. Auditory and visual
instructions were provided in French. Simulated distribution of derived behavioral
performance measures using numerosity and error estimation values are depicted in Figure
1-1.

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Figure 2. Behavioral results. (A) Individual numerosity performance in the active (red) and 858 859 passive (blue) conditions. A value of zero represents ideal performance, where the reported 860 and actual number of words match. Each dot represents a participant mean numerosity performance. Grey lines connect performance from the same participant across conditions. 861 (B) Mixed-effects linear regression between numerosity estimation (reported number of 862 863 words) and an actual number of words. Reference dashed line with a slope equal to 1 represents ideal performance. Thick lines represent the global model fit, while thin lines 864 865 depict individual estimates. Individual plots are depicted in Figure 2-1. (C) Mean slope coefficient estimates with 2.5% and 97.5% confidence intervals. 866

Figure 3. Percentage of simulated accurate numerosity estimations (occurrences of value 10) in normal distribution centred on 10 with varying standard deviation. Simulation was iterated 10000 times. Reference dashed line of 19.5% absolute numerosity estimations accuracy (as observed in the experiment empirical data) occurs with the standard deviation of 2. Each dot represents a single iteration of the data simulation (overlapping dots are
depicted in higher color intensity).

Figure 4. Neural correlates of numerosity performance. (A) Main effect (active+passive 873 conditions) of the parametric modulation of numerosity performance during numerosity 874 estimation in the right intraparietal sulcus (IPS, depicted in green). (B) Box plot of the 875 corresponding individual beta estimates in the right IPS. Each dot represents a participant 876 877 mean beta estimates. Grey lines connect beta estimates from the same participant across 878 conditions. (C) Overlap between the parametric modulation of numerosity performance during numerosity estimation (depicted in green) main effect (active + passive conditions) at 879 the lower statistical threshold of peak level uncorrected p<0.005 (exploratory analyses) and 880 881 parametric modulation of performance monitoring during the error estimation (active vs. passive condition) (depicted in purple); peak level uncorrected p<0.001. 882

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Figure 5. PPI analysis: numerosity estimation. (A) Increased functional connectivity in the active vs. passive condition between the right intraparietal sulcus seed (IPS, depicted in green) and bilateral supplementary motor area (SMA), left inferior parietal lobule (IPL) and superior temporal gyri (STG), depicted in red. (C) Box plots of the corresponding beta estimates for each significant PPI cluster. Each dot represents a participant mean beta estimates. Grey lines connect beta estimates from the same participant across conditions.

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Figure 6. Neural correlates of performance monitoring. (A) Decreased neural activity during
the active vs. passive condition in the right putamen and insula bilaterally (depicted in blue).

Increased activity in the active vs. passive condition in the left caudate nucleus (depicted in
red). (B) Box plots of the corresponding beta estimates in the active (red) and passive (blue)
conditions for each significant cluster observed. Each dot represents a participant mean
beta estimates. Grey lines connect beta estimates from the same participant across
conditions.

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Figure 7. Parametric modulation of performance monitoring. (A) Positive association
between the trial-wise performance monitoring and BOLD signal during performance
monitoring in the active vs. passive condition in the left intraparietal sulcus (IPS, depicted in
purple). (B) Box plot of corresponding beta estimates in the left IPS in the active (blue) and
passive (red) conditions. Each dot represents a participant mean beta estimates. Grey lines
connect beta estimates from the same participant across conditions.

905 Tables

Table 1. Numerosity estimation: difference between active and passive conditions. Brain areas showing a difference in activity between the active and passive condition during the numerosity estimation phase, independent of parametric modulation. The activation clusters of numerosity estimation main effect are detailed in Table 1-1. Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere, R – right hemisphere</p>

912

913 **Table 2.** Parametric modulation of numerosity performance (exploratory analyses at lower
914 statistical threshold). Brain areas in which the BOLD signal correlates with the trial-by-trial

915	behavioral measures of numerosity performance during the numerosity estimation phase.
916	Voxel level p<0.005 uncorrected, cluster threshold at p<0.05 FWE corrected. BA $-$
917	Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere
918	
919	Table 3. PPI analysis: numerosity estimation. Brain areas identified through PPI analysis
920	seeding from the right intraparietal sulcus during numerosity estimation. Voxel level
921	p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k –
922	cluster size, R – right hemisphere, L – left hemisphere
923	
924	Table 4. Error estimation: difference between active and passive conditions. Brain areas
925	showing a difference in activity between the active and passive condition during the error
926	estimation phase, independent of parametric modulation. The activation clusters of error
927	estimation main effect are detailed in Table 4-1. Voxel level p<0.001 uncorrected, cluster
928	threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right
929	hemisphere, L – left hemisphere
930	
931	Extended data legends

Figure 1-1. Data simulation of behavioral performance measures. Data was simulated with pseudorandom generation of an actual number of words and numerosity estimations ranging between 5 and 20. Error estimation varied between 0 and 5 as set during the task design. (A) Simulated numerosity performance. Increasing intensity of red represent linear increase of overestimation (positive values of numerosity performance), while increasing 45 intensity in blue represent linear increase of underestimation (negative values of
numerosity performance). (B) Simulated performance monitoring when the number of
words is constant (10 or 15 words). The performance monitoring value is depicted in the
heatmap changing from blue (being correct) to red (worse performance monitoring).

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Figure 2-1. Mixed-effects linear regression between numerosity estimation (reported number of words) and an actual number of words depicted for each participant. Reference dashed line with a slope equal to 1 represents ideal performance. Thick lines represent the individual model fit per condition (active: red and passive: blue). Each dot represents a participant's single trial performance (overlapping dots are depicted in higher color intensity).

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Table 1-1. Numerosity estimation: main effect (active + passive conditions). Brain areas
activated during the numerosity estimation phase independent of parametric modulation.
Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA –
Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere, R – right
hemisphere

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Table 4-1. Error estimation: main effect (active + passive conditions). Brain areas with activations during the error estimation phase, independent of parametric modulation. Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere, R – right hemisphere















		Peak voxel MNI coordinate						
BA	Anatomical Label		k	х	У	z	p_{FWE}	Т
	Active < passive							
7 6 40 31 13 24 21 4 32 39 3 5 9 23 27 8 18 44	Middle temporal g. Precuneus Superior temporal g. Postcentral Middle cingulum Cerebellum SMA Insula Precentral Supramarginal g. Angular g. Superior parietal Putamen Middle frontal g. Caudate Superior fontal g. Caudate Superior parietal g. Calcarine Rolandic percular Supramarginal g. Thalamus Hippocampus Fusiform g. Inferior temporal g. Lingual g. Cuneus Occipital g.	L/R	113587	20	8	-12	<0.001	9.75
	Thalamus	L	314	-11	-23	15	<0.001	6.84
10	Middle frontal g.	L	442	-36	50	27	0.004	4.97
10	Middle frontal g.	R	399	29	53	32	0.005	4.69

Table 1. Numerosity estimation: difference between active and passive conditions. Brain areas showing a difference in activity between the active and passive condition during the numerosity estimation phase, independent of parametric modulation. The activation clusters of numerosity estimation main effect are detailed in Table 1-1. Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere, R – right hemisphere

			Peak voxel MNI coordinate					
BA	Anatomical Label		k	х	У	Z	p_{FWE}	Т
	Main effect (active + passive)							
7	Intraparietal sulcus (superior parietal g., angular g.)	R	466	29	-65	50	0.004	20
7	Intraparietal sulcus (superior/inferior parietal g., middle occipital g.)	L	758	-30	-63	42	0.000	15.9

Table 2. Parametric modulation of numerosity performance (exploratory analyses at lower statistical threshold). Brain areas in which the BOLD signal correlates with the trial-by-trial behavioral measures of numerosity performance during the numerosity estimation phase. Voxel level p<0.005 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere

			Peak voxel MNI coordinate						
BA	Anatomical Label		k	х	У	z	p_{FWE}	Т	
	Active > passive								
41 42	Superior temporal g.	L	177	-54	-20	6	0.038	5.14	
40	Inferior parietal lobule (supramarginal g., parietal inferior g.)	L	291	-44	-42	29	0.003	5.14	
6	Supplementary motor area	L/R	167	-3	-30	63	0.049	4.59	

Table 3. PPI analysis: numerosity estimation. Brain areas identified through PPI analysis seeding from the right intraparietal sulcus during numerosity estimation. Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere

			Peak voxel MNI coordinate						
BA	Anatomical Label		k	х	У	Z	p_{FWE}	Т	
	Active > passive								
	Caudate nucleus	L	336	-15	30	-6	0.004	5.76	
	Active < passive								
45 47 13	Insula, inferior frontal g. triangular part	L	392	-33	24	-6	0.002	5.3	
	Putamen	R	209	20	12	-6	0.043	5.2	
13 47 45	Insula, inferior frontal g. triangular part	R	482	32	27	0	0.000	4.3	

Table 4. Error estimation: difference between active and passive conditions. Brain areas showing a difference in activity between the active and passive condition during the error estimation phase, independent of parametric modulation. The activation clusters of error estimation main effect are detailed in Table 4-1. Voxel level p<0.001 uncorrected, cluster threshold at p<0.05 FWE corrected. BA – Broadmann area, k – cluster size, R – right hemisphere, L – left hemisphere