Increased functional connectivity of the intraparietal sulcus underlies the attenuation of numerosity estimations for self-generated words

Giedre Stripeikyte, Michael Pereira, Giulio Rognini, Jevita Potheegadoo, Olaf Blanke, Nathan Faivre

JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Behavioral/Cognitive

Increased functional connectivity of the intraparietal sulcus underlies the attenuation of numerosity estimations for self-generated words

https://doi.org/10.1523/JNEUROSCI.3164-20.2021

Cite as: J. Neurosci 2021; 10.1523/JNEUROSCI.3164-20.2021

Received: 18 December 2020
Revised: 29 June 2021
Accepted: 1 July 2021

Increased functional connectivity of the intraparietal sulcus underlies the attenuation of numerosity estimations for self-generated words

Abbreviated title: Attenuation of numerosity estimations

Authors
Giedre Stripeikyte[1,2], Michael Pereira[1,2,3], Giulio Rognini[1,2], Jevita Potheegadoo[1,2], Olaf Blanke[1,2,4]*, Nathan Faivre[1,2,3]*

Affiliations
1. Center for Neuroprosthetics, Swiss Federal Institute of Technology (EPFL), CH-1202 Geneva, Switzerland
2. Brain Mind Institute, Faculty of Life Sciences, Swiss Federal Institute of Technology (EPFL), CH-1015 Lausanne, Switzerland
3. Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LPNC, 38000 Grenoble, France
4. Department of Neurology, University of Geneva, CH-1211 Geneva, Switzerland

* These authors contributed equally to this study

Corresponding authors
Olaf Blanke
Bertarelli Chair in Cognitive Neuroprosthetics
Center for Neuroprosthetics & Brain Mind Institute
School of Life Sciences
Campus Biotech
Swiss Federal Institute of Technology
Ecole Polytechnique Fédérale de Lausanne (EPFL)
CH – 1202 Geneva
E-mail: olaf.blanke@epfl.ch

Nathan Faivre
Laboratoire de Psychologie et Neurocognition
CNRS UMR 5105, UGA BSHM
1251 Avenue Centrale, 38058 Grenoble Cedex 9, France
E-mail: nathan.faivre@univ-grenoble-alpes.fr

Number of pages: 43
Number of figures: 7; **tables:** 4
Number of words abstract: 194; **introduction:** 647; **discussion:** 1498

Conflict of interest statement
The authors declare no competing interests.

ABSTRACT

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

SIGNIFICANCE STATEMENT

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 sensory events from self and external origins. Here, we designed a novel fMRI paradigm to assess whether cognitive processes such as numerosity estimations are also subject to attenuation. When asking participants to estimate the number of words they had generated or passively heard, we found bigger underestimation in the former case, providing behavioral evidence of attenuation. Attenuation was associated with increased functional 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 sensory consequences but also impact cognitive processes such as numerosity estimations.

INTRODUCTION

The ability to distinguish self- versus externally-generated stimuli is crucial for self-representation (Kircher and David, 2003; Legrand, 2006). A typical mechanism by which stimuli generated by oneself and those caused by external sources are distinguished is sensory attenuation, whereby self-generated stimuli are perceived as less intense. Indeed, previous studies have shown that self-produced stimuli in the auditory (Baess et al., 2011; Timm et al., 2014), visual (Hughes and Waszak, 2011; Benazet et al., 2016) and somatosensory domains (Shergill et al., 2013; Kilteni and Ehrsson, 2020), are perceived as less intense compared to the same stimuli when they are externally generated. Such attenuation was shown at the behavioral level and at the neural level in sensory cortical regions (e.g., auditory cortex (Rummell et al., 2016; Whitford, 2019)) as well as the thalamus, cerebellum, supplementary motor area and inferior parietal cortex (Hickok, 2012; Lima et al., 2016; Bansal et al., 2018; Brooks and Cullen, 2019).

Previous studies have shown that attenuation not only applies to stimuli that are generated by overt actions, but also extends to covert processes such as motor imagery (Kilteni et al., 2018) or inner speech (Scott et al., 2013; Whitford et al., 2017). In the latter case, attenuation of the electrophysiological (Whitford et al., 2017; Jack et al., 2019) and behavioral (Scott et al., 2013) responses corresponding to the test stimulus (phoneme) was observed when it matched the imagined cued phoneme. These studies used phonemes that are integrated into the early stages of hierarchical speech processing implying primary sensory cortices (Liebenthal et al., 2005; DeWitt and Rauschecker, 2012), where attenuation 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 percept) or whether it can also impact cognitive processes that are non-perceptual in nature such as abstract judgments or performance monitoring.

To answer this question, we investigated the cognitive function of numerosity estimations, defined as approximate judgments when counting is not involved (Dehaene, 1997). Properties of numerosity estimations such as innateness, amodality, or precision that linearly decreases with increasing numerosity have been described (Anobile et al., 2016; 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 Arsalidou & Taylor, 2011). If attenuation for self-related functions extends to higher-level 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 relation to modulation of IPS activity. Thus, this study aimed at investigating whether numerosity estimations of self-generated words were attenuated compared to numerosity estimations of passively heard words, thereby demonstrating that self-attenuation applies to cognitive processes beyond sensory processing.

To investigate which brain regions and networks showed activity related to attenuation processes, we designed a functional magnetic resonance imaging (fMRI) paradigm allowing the controlled comparison of numerosity estimations of either self-generated words (active condition) during a phonetic verbal fluency task or externally-generated words (passive 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). Assuming that attenuation occurs during numerosity estimations (active condition), we

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

METHODS

Participants

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

Experimental task

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

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

Stimuli

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). Twenty different cue letters were used for active and passive conditions. The same cue 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 list of 420 French words (Ferrand and Alario, 1998). The audio stimuli presented during the 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 pronouncing words in the passive condition was matched to the participants' gender. During the experiment, participants were equipped with MRI compatible earphones and report buttons for the right hand.

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,
216 cue letter 'p') test (Lezak, 1995) was performed overtly to verify that subjects understood
217 the task correctly. Overall, the experiment lasted approximately 1h 30 min (MRI session)
218 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 the runs 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).

Control order experiment

An additional control experiment in the mock scanner was performed to rule out the possibility that repetition effects occurred between consecutive blocks. It consisted only of 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 played (mean of 10 words/block ranging from 6 to 20 words per trial) and their playing pace (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 and word playing pace as in the preceding random block but with a shuffled order. This control experiment consisted of 2 'random' and 2 'repeated' blocks, with 4 trials/block, and lasted approximately 30 min.

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

241 below, these indices were defined at the single-trial level so they could serve as parametric
242 regressors of interest in the fMRI analysis.

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)

259

260 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.

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

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

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.

Behavioral data analysis

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

condition ("active", "passive" or "random", "repeat" for the control order experiment) as a fixed effect and a random intercept by participant and condition. The inclusion of additional random effects was guided by model comparison and selection based on Bayesian Information Criteria. Analyzes were performed using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages in R (R-project.org). The significance of fixed effects was estimated using Satterthwaite's approximation for degrees of freedom of F statistics (Luke, 2017).

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 in the control experiment. Namely, we conducted a Bayesian linear model of numerosity 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 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 on the difference between numerosity performance during the active and passive conditions observed in the main fMRI experiment.

Data simulation of absolute accuracy during numerosity estimations

To examine weather absolute accuracy (correct numerosity estimations of words generated/heard) of numerosity estimations observed in the experimental data may be approximated by a noisy sampling process rather than counting, we performed data simulations. More specifically, we simulated 1000 numerosity estimations (as the main experiment contained 40 trials/subject * 25 subjects) from a normal distribution centred on 10 and standard deviation (SD) varying from 0.5 to 6 with 0.1 steps. We rounded each item

307 to the nearest integer and counted how many times the number 10 was obtained. The
308 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
311 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
317 varied according to the experiment duration (2278 ± 61 volumes).

318 **fMRI data preprocessing**

319 Anatomical and functional images were processed and analyzed using SPM-12 (Welcome
320 Centre for Human Neuroimaging, London, UK). Pre-processing steps included slice time
321 correction, field-map distortion correction, realignment and unwarping to spatially correct
322 for head motions and distortions, co-registration of structural and functional images,
323 normalization of all images to common Montreal Neurological Institute (MNI) space, and
324 spatial smoothing with a Gaussian kernel with a full-width at half maximum (FWHM) of 4
325 mm. Quality assurance of all EPI images was performed with the criteria of maximum 2 mm
326 translation and 2° rotation between volumes. In addition, an excessive movement was
327 estimated with the mean framewise displacement (FD) (Power et al., 2012) with the
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.

fMRI data analysis

We used a two-level random-effects analysis. In the first-level analysis, condition-specific effects were estimated according to a general linear model (GLM) fitted for each subject. An average mask of grey matter from all subjects was built using FSL (fsl.fmrib.ox.ac.uk/fsl) and used to mask out white matter and non-brain tissues. The GLM was built using six boxcar regressors corresponding to the duration of the word generation/listening phase, numerosity estimation and error estimation in the active and passive conditions. Parametric modulators of numerosity performance and performance monitoring were included in the numerosity estimation and error estimation regressors, respectively. Further, we added regressors of no interest corresponding to audio instructions, button presses and excluded trials, plus six regressors for head motion (translation and rotation).

At the second-level (group level), we performed a one-way analysis of variance (ANOVA) with F-tests to assess main effects common to active and passive conditions and t-tests to analyze the difference between conditions (active vs. passive) for each regressor of interest: numerosity estimation and error estimation. We used a voxel-level statistical threshold of $p<0.001$ and corrected for multiple comparisons at the cluster level using family-wise error (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).

Functional connectivity analysis

Psychophysiological Interaction (PPI) analysis was employed to identify modulations of 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

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.

Data and code availability

The MRI data that support the findings of this study is available on a public repository on zenodo.org (https://doi.org/10.5281/zenodo.4925909). Behavioral data, analysis and task codes are available here: https://gitlab.epfl.ch/lnco-public/cognitive-attenuation.

RESULTS

Behavioral results

By design, the number of generated and heard words was matched between conditions (active: M = 10.7, SD = 3.6, CI(95%) = [10.4, 11.1]; passive: M = 10.7, SD = 3.5, CI(95%) = [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: M = 28.4, SD = 7.0, CI(95%) = [27.7, 29.0], $F_{(1,26)} = 2.04$, p = 0.16). Having shown that conditions were similar in terms of difficulty, we turned to the analysis of numerosity performance and performance monitoring.

Numerosity performance indices revealed that globally, participants underestimated the number of words (M = -0.05, SD = 0.11, CI(95%) = [-0.06, -0.05]). This underestimation was

significantly larger ($F_{(1,24)}$ = 5.85, p = 0.023, 18 subjects out of 25 showed the effect) in the active condition (M = -0.07, SD = 0.11, CI(95%) = [-0.08, -0.06]) compared to the passive condition (M = -0.04, SD = 0.12, CI(95%) = [-0.05, -0.03]) (Figure 2 A). Comparable results were obtained during the pilot experiment in the mock scanner in an independent group of subjects (active: M = -0.05, SD = 0.01, CI(95%) = [-0.06, -0.03]); passive: M = -0.03, SD = 0.10, CI(95%) = [-0.04, -0.02]; $F_{(1,16)}$ = 5.80 p = 0.016). These two experiments suggest that numerosity estimations for self-generated words are attenuated.

We further show that the larger underestimation in the active compared to the passive condition was also found when considering the measures of accuracy (active: M = -1.48, SD = 2.38, CI(95%) = [-1.69, -1.26]); passive: M = -0.94, SD = 2.59, CI(95%) = [-1.17, -0.71]; F(1,24) = 4.43 p = 0.045) and accuracy ratio as dependent variables (active: M = 0.89, SD = 0.20, CI(95%) = [0.87, 0.91]); passive: M = 0.95, SD = 0.23, CI(95%) = [0.93, 0.97]; F(1,24) = 7.44 p = 0.011).

We then assessed the linear relationship between the reported (numerosity estimation) and actual number of words (Figure 2 B). Besides a main effect of words ($F_{(1,908)}$ = 1042, p < 0.001) and of condition ($F_{(1,198)}$ = 8.25, p = 0.0045), we found an interaction between condition and generated/heard words ($F_{(1,802)}$ = 4.3, p = 0.038). This interaction was driven by a steeper slope in the active condition (M = 0.62, CI(95%) = [0.57, 0.67]) compared to the passive condition (M = 0.55, CI(95%) = [0.50, 0.60]) (Figure 2 C), which indicates better numerosity tracking for self-generated words during the main fMRI experiment (a slope of value 1 reflecting ideal performance). We note that this interaction did not reach significance in our pilot experiment ($F_{(1,350)}$ = 1.10, p = 0.66), which calls for interpreting this result with caution.

Next, we investigated whether performance monitoring varied between conditions, by quantifying how well participants were able to track the error made when estimating the number of generated/heard words. We found no differences in performance monitoring ($F_{(1,24)}$ = 1.09, p = 0.3) between the active (M = 0.07, SD = 0.06, CI(95%) = [0.07, 0.08]) and passive (M = 0.08 , SD = 0.06, CI(95%) = [0.07, 0.09]) conditions during the main fMRI experiment, nor during the mock scanner pilot experiment ($F_{(1,16)}$ = 0.78, p = 0.39; active: M = 0.07, SD =0.06, CI(95%) = [0.06, 0.08]; passive: M = 0.06, SD =0.06, CI(95%) = [0.06, 0.07]). This confirms the absence of evidence supporting an effect of attenuation on performance 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, CI(95%) = [10.9, 14.1]) and covertly (M = 12.3, SD = 3.96, CI(95%) = [10.6, 13.9]; paired t-test; $t_{(24)}$ = -0.4; p=0.69). This control task confirms that subjects did generate words covertly and comparably to overt fluency, as instructed.

Control order experiment. The global underestimation (M = -0.06, SD = 0.11, CI(95%) = [-0.08, -0.05]) was replicated as in the main experiment. This underestimation was not different (F(1,117) = 0.03, p = 0.87) between 'random' (M = -0.06, SD = 0.12, CI(95%) = [-0.09, -0.04]) and 'repeated' (M = -0.07, SD = 0.12, CI(95%) = [-0.09, -0.04]) blocks, with a 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.

fMRI results

Numerosity performance

Brain activity during the numerosity estimation phase was widespread, irrespective of the experimental condition (Table 1-1). Differences between conditions revealed widespread relative deactivations in the active compared to the passive condition in the bilateral parietal cortex including IPS, middle-superior temporal gyri, precuneus, cerebellum, middle cingulate gyri, SMA, insula, middle-superior frontal gyri, hippocampus, caudate nucleus, putamen (for the detailed list of all areas see Table 1).

To avoid contaminating the results with inherent differences between the active and passive 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 such a pattern of activity, namely the right IPS, whose activity was negatively correlated with numerosity performance (main effect F = 20.0, p_{FWE} = 0.042, k_{vox} = 148, x = 29, y = -65, z = 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 activation did not differ between the active and passive conditions ($p_{FWE} > 0.05$), suggesting that this effect was independent of whether words were heard or actively generated.

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

Performance monitoring

Besides numerosity performance, we also quantified brain activity during the error estimation phase. We found widespread cortical and subcortical activations during this phase compared to baseline, irrespective of the experimental condition (Table 4-1). Moreover, bilateral insula and right putamen were significantly less active during the active compared to the passive condition (Figure 6, Table 4). The left caudate nucleus showed the opposite pattern, with higher activity in the passive than in the active condition.

To avoid confounding factors between the active and passive condition, we looked more specifically at parametric modulations of error monitoring. We observed that BOLD signal in the left IPS was more related to performance monitoring in the active compared to the passive condition ($t = 4.02$, $p_{FWE} = 0.041$, $k_{vox} = 198$, $x = -27$, $y = -66$, $z = 47$; Figure 7). Interestingly, this activation cluster spatially overlapped with the observed activation cluster related to the main effect of numerosity performance when applying a lower statistical threshold (exploratory analysis, $p<0.005$ peak level uncorrected, $pFWE < 0.05$ cluster level) (see Figure 4 C).

462 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

466

DISCUSSION

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

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

496 Attenuation of self-generated stimuli has been mostly investigated for sensory processes
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
500 absence of overt actions (e.g., Kilteni et al., 2018; Jack et al., 2019;). For example, imagined
501 self-touch was felt as less intense compared to externally applied touch (Kilteni et al., 2018).
502 Similarly, imagined speech elicited reduced electrophysiological signals related to auditory
503 processing (Whitford et al., 2017). These studies, however, investigated cognitive processes
504 intimately linked to sensorimotor systems (e.g., imagined movement and touch), yet, to the
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
507 no or less obviously implicated sensorimotor processes (e.g., Dehaene, 1997). Here we show
508 that differential attenuation can be observed for cognitive processes such as numerosity
509 estimations that depend on whether they are self-generated or not. As of today, there is no
510 consensus to explain how the brain attenuates expected (e.g., self-generated) stimuli while
511 remaining sensitive to unexpected ones (for a recent review and unifying theoretical
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.

554

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

between their estimated number of words and the actual number of words was better in the active condition vs. passive condition, suggesting a sharper representation of the number of self-generated words. This result corroborates recent findings showing better monitoring for decisions that are committed rather than observed (Pereira et al., 2020). This improved monitoring of self-generated words could be related to the sharpening of expected representations known in the sensory domain (Kok et al., 2012) or to a self-generation effect underlying the facilitation of information encoding and enhanced recall for self-generated stimuli (Bertsch et al., 2007; Slamecka and Graf, 1978). We note that this effect was not replicated during the mock pilot experiment, which included a smaller sample of participants with a globally higher absolute accuracy. It is possible that this subtle effect could not be observed in such conditions, which warrants future investigations and cautious interpretation.

Performance monitoring is modulated at the neural but not behavioral level

Previous research has shown that both humans and non-human primates (Beran et al., 2006; Duyan and Balcı, 2019, 2018) can monitor the quality of their numerosity estimations. 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 hemodynamic activity in the left IPS predominantly in the active condition. Interestingly, this 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

parametric modulation could therefore represent a substrate for monitoring specific to numerosity estimations. By investigating global fMRI activity during error estimations, we also observed decreased activation in the insula and putamen and increased activity in the caudate nucleus when comparing the active vs. passive conditions. To note, the anterior insula and putamen were activated during both conditions but were attenuated in the active compared to the passive conditions. While the anterior insula activations are consistent with previous literature on performance monitoring (Ullsperger et al., 2010; Bastin et al., 2017), the findings of modulated activity in the striatum were unexpected. Both areas are known as essential for the control of goal-directed decision-making (Balleine et al., 2007; Kim and Im, 2019). Further links between performance monitoring and activity modulation between conditions in the striatum regions should be explored in future studies.

Methodological considerations

As generating vs. listening to words inherently involves different behavioral and neural processes, several aspects of our design should be considered when interpreting the current findings as reflecting attenuation per se rather than experimental confounds. At the behavioral level, the larger underestimation during the active condition was not due to difficulty differences between conditions as task difficulty was matched by design, and absolute accuracy (correct numerosity estimations of words generated/heard) was similar in both conditions. Of note, a steeper slope during numerosity estimations and number of words generated in the active condition suggests that participants better tracked their performance even when underestimating more compared to the passive condition. Although we could not explicitly control whether participants counted the number of words they generated or heard, instructions were given not to do so. Yet, counting seems unlikely

as absolute accuracy reached only 19.5% of all trials, which is comparable to a recent study with a similar setup (Serino et al., 2021), and much lower than what is typically observed when participants are instructed to count (e.g, Kansaku et al., 2007). Furthermore, a similar level of absolute accuracy was obtained on simulated data with numerosity estimations drawn from a normal distribution with SD = 2, suggesting that behavior in this task is approximated by a noisy sampling process rather than counting. At the neural level, to ensure that the inherent differences between conditions did not contaminate our results, we focused analyses on the numerosity and error estimation phases which were identical between conditions, instead of the word generation/listening phases. In addition, we did not base our conclusions on a direct contrast between the two conditions, but on correlations between neural activity and numerosity or error estimates.

Conclusion

Based on behavioral and neuroimaging data, we propose that higher-level cognitive functions such as numerosity estimations about the number of self-generated words are attenuated. Such attenuation involves a functional network including a key-numerosity region (IPS) and speech-related regions including the SMA, IPL and STG. While attenuating the sensory consequences of one's actions is of crucial importance for aspects of the self, such as the sense of agency, attenuating the products of one's mental activities may also be relevant to distinguish them from external sources of information. Our paradigm offers a promising tool to investigate attenuation processes related to the self in cognition and to compare and distinguish them from sensory attenuation processes. It may be of relevance 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.

628

Acknowledgments

The authors are grateful for the technical support during data acquisition to the Foundation Campus Biotech Geneva (FCBG) Human Neuroscience Platform of the Campus Biotech. This work was supported by the Bertarelli Foundation (grant number 532024), the Swiss National Science Foundation (grant number 3100A0-112493), National Center of Competence in Research (NCCR) "Synapsy - The Synaptic Bases of Mental Diseases" (grant number 51NF40 – 185897), and two generous donors advised by Carigest SA. Nathan Faivre has received funding from the European Research Council (ERC) under the European Union Horizon 2020 research and innovation programme (grant number 803122).

Author Contributions

GS, NF, GR, OB developed the study concept and contributed to the study design. Testing, data collection and data analysis were performed by GS. GS, MP, JP and NF provided 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.

646 **REFERENCES**

647 Anobile, G., Cicchini, G.M., Burr, D.C., 2016. Number As a Primary Perceptual Attribute: A
648 Review. Perception 45, 5–31. https://doi.org/10.1177/0301006615602599

649 Arsalidou, M., Taylor, M.J., 2011. Is 2+2=4? Meta-analyses of brain areas needed for
650 numbers and calculations. Neuroimage 54, 2382–2393.
651 https://doi.org/10.1016/j.neuroimage.2010.10.009

652 Baess, P., Horváth, J., Jacobsen, T., Schröger, E., 2011. Selective suppression of self-initiated
653 sounds in an auditory stream: An ERP study. Psychophysiology 48, 1276–1283.
654 https://doi.org/10.1111/j.1469-8986.2011.01196.x

655 Balleine, B.W., Delgado, M.R., Hikosaka, O., 2007. The role of the dorsal striatum in reward
656 and decision-making. J. Neurosci. 27, 8161–8165.
657 https://doi.org/10.1523/JNEUROSCI.1554-07.2007

658 Bansal, S., Ford, J.M., Spering, M., 2018. The function and failure of sensory predictions.
659 Ann. N. Y. Acad. Sci. 1426, 199–220. https://doi.org/10.1111/nyas.13686

660 Bastin, J., Deman, P., David, O., Gueguen, M., Benis, D., Minotti, L., Hoffman, D.,
661 Combrisson, E., Kujala, J., Perrone-Bertolotti, M., Kahane, P., Lachaux, J.P., Jerbi, K.,
662 2017. Direct Recordings from Human Anterior Insula Reveal its Leading Role within the
663 Error-Monitoring Network. Cereb. Cortex 27, 1545–1557.
664 https://doi.org/10.1093/cercor/bhv352

665 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models
666 Using lme4 | Bates | Journal of Statistical Software. J. Stat. Softw. 67.

667 Benazet, M., Thénault, F., Whittingstall, K., Bernier, P.M., 2016. Attenuation of visual

668 reafferent signals in the parietal cortex during voluntary movement. J. Neurophysiol.
669 116, 1831–1839. https://doi.org/10.1152/jn.00231.2016

670 Beran, M.J., Smith, J.D., Redford, J.S., Washburn, D.A., 2006. Rhesus macaques (Macaca
671 mulatto) monitor uncertainty during numerosity judgments. J. Exp. Psychol. Anim.
672 Behav. Process. 32, 111–119. https://doi.org/10.1037/0097-7403.32.2.111

673 Bertsch, S., Pesta, B.J., Wiscott, R., McDaniel, M.A., 2007. The generation effect: A meta-
674 analytic review. Mem. Cogn. 35, 201–210. https://doi.org/10.3758/BF03193441

675 Brainard, D.H., 1997. The Psychophysics Toolbox. Spat. Vis. 10, 433–436.
676 https://doi.org/10.1163/156856897X00357

677 Brooks, J.X., Cullen, K.E., 2019. Predictive Sensing: The Role of Motor Signals in Sensory
678 Processing. Biol. Psychiatry Cogn. Neurosci. Neuroimaging 4, 842–850.
679 https://doi.org/10.1016/j.bpsc.2019.06.003

680 Brown, H., Adams, R.A., Parees, I., Edwards, M., Friston, K., 2013. Active inference, sensory
681 attenuation and illusions. Cogn. Process. 14, 411–427. https://doi.org/10.1007/s10339-
682 013-0571-3

683 Bürkner, P.C., 2017. brms: An R package for Bayesian multilevel models using Stan. J. Stat.
684 Softw. https://doi.org/10.18637/jss.v080.i01

685 Burr, D.C., Anobile, G., Arrighi, R., 2018. Psychophysical evidence for the number sense.
686 Philos. Trans. R. Soc. B Biol. Sci. 373. https://doi.org/10.1098/rstb.2017.0045

687 Cappelletti, M., Barth, H., Fregni, F., Spelke, E.S., Pascual-Leone, A., 2007. rTMS over the
688 intraparietal sulcus disrupts numerosity processing. Exp. Brain Res. 179, 631–642.

https://doi.org/10.1007/s00221-006-0820-0

Castronovo, J., Seron, X., 2007. Numerical Estimation in Blind Subjects: Evidence of the Impact of Blindness and Its Following Experience. J. Exp. Psychol. Hum. Percept. Perform. 33, 1089–1106. https://doi.org/10.1037/0096-1523.33.5.1089

Cohen, L., Dehaene, S., 1996. Cerebral Networks for Number Processing: Evdence from a Case of Posterior Callosal Lesion. Neurocase 2, 155–174. https://doi.org/10.1080/13554799608402394

Cowan, N., 2010. The magical mystery four: How is working memory capacity limited, and why? Curr. Dir. Psychol. Sci. 19, 51–57. https://doi.org/10.1177/0963721409359277

Cromwell, H.C., Mears, R.P., Wan, L., Boutros, N.N., 2008. Sensory gating: A translational effort from basic to clinical science. Clin. EEG Neurosci. 39, 69–72. https://doi.org/10.1177/155005940803900209

Dehaene, S., 1997. The Number Sense. Oxford Univ. Press.

DeWitt, I., Rauschecker, J.P., 2012. Phoneme and word recognition in the auditory ventral stream. Proc. Natl. Acad. Sci. U. S. A. 109, 505–514. https://doi.org/10.1073/pnas.1113427109

Dormal, V., Andres, M., Pesenti, M., 2012. Contribution of the right intraparietal sulcus to numerosity and length processing: An fMRI-guided TMS study. Cortex 48, 623–629. https://doi.org/10.1016/j.cortex.2011.05.019

Duyan, Y.A., Balcı, F., 2019. Metric error monitoring in the numerical estimates. Conscious. Cogn. https://doi.org/10.1016/j.concog.2018.11.011

710 Duyan, Y.A., Balcı, F., 2018. Numerical error monitoring. Psychon. Bull. Rev.
711 https://doi.org/10.3758/s13423-018-1506-x

712 Farrer, C., Frith, C.D., 2002. Experiencing oneself vs another person as being the cause of an
713 action: The neural correlates of the experience of agency. Neuroimage 15, 596–603.
714 https://doi.org/10.1006/nimg.2001.1009

715 Ferrand, L., Alario, F.-X., 1998. Normes d'associations verbales pour 366 noms d'objets
716 concrets. Annee. Psychol. 98, 659–709. https://doi.org/10.3406/psy.1998.28564

717 Fleming, S.M., Lau, H.C., 2014. How to measure metacognition. Front. Hum. Neurosci. 8, 1–
718 9. https://doi.org/10.3389/fnhum.2014.00443

719 Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J., 1997. Psychophysiological
720 and modulatory interactions in neuroimaging. Neuroimage 6, 218–229.
721 https://doi.org/10.1006/nimg.1997.0291

722 Hickok, G., 2012. Computational neuroanatomy of speech production. Nat. Rev. Neurosci.
723 13, 135–145. https://doi.org/10.1038/nrn3158

724 Hughes, G., Waszak, F., 2011. ERP correlates of action effect prediction and visual sensory
725 attenuation in voluntary action. Neuroimage 56, 1632–1640.
726 https://doi.org/10.1016/j.neuroimage.2011.02.057

727 Jack, B.N., Le Pelley, M.E., Han, N., Harris, A.W.F., Spencer, K.M., Whitford, T.J., 2019. Inner
728 speech is accompanied by a temporally-precise and content-specific corollary
729 discharge. Neuroimage 198, 170–180.
730 https://doi.org/10.1016/j.neuroimage.2019.04.038

731 Kansaku, K., Carver, B., Johnson, A., Matsuda, K., Sadato, N., Hallett, M., 2007. The role of
732 the human ventral premotor cortex in counting successive stimuli. Exp. Brain Res. 178,
733 339–350. https://doi.org/10.1007/s00221-006-0736-8

734 Kilteni, K., Andersson, B.J., Houborg, C., Ehrsson, H.H., 2018. Motor imagery involves
735 predicting the sensory consequences of the imagined movement. Nat. Commun. 9, 1–
736 9. https://doi.org/10.1038/s41467-018-03989-0

737 Kilteni, K., Ehrsson, H., 2020. Functional connectivity between the cerebellum and
738 somatosensory areas implements the attenuation of self-generated touch. J. Neurosci.
739 40, 894–906. https://doi.org/10.1523/JNEUROSCI.1732-19.2019

740 Kim, B.S., Im, H.I., 2019. The role of the dorsal striatum in choice impulsivity. Ann. N. Y.
741 Acad. Sci. 1451, 92–111. https://doi.org/10.1111/nyas.13961

742 Kircher, T., David, A., 2003. The Self in Neuroscience and Psychiatry, The self in neuroscience
743 and psychiatry. Cambridge University Press, Cambridge.
744 https://doi.org/10.1017/CBO9780511543708

745 Kleiner, M., Brainard, D.H., Pelli, D.G., Broussard, C., Wolf, T., Niehorster, D., 2007. What's
746 new in Psychtoolbox-3? Perception 36, S14. https://doi.org/10.1068/v070821

747 Kok, P., Jehee, J.F.M., de Lange, F.P., 2012. Less Is More: Expectation Sharpens
748 Representations in the Primary Visual Cortex. Neuron 75, 265–270.
749 https://doi.org/10.1016/j.neuron.2012.04.034

750 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear
751 Mixed Effects Models . J. Stat. Softw. 82. https://doi.org/10.18637/jss.v082.i13

752 Legrand, D., 2006. The bodily self: The sensori-motor roots of pre-reflective self-
753 consciousness. Phenomenol. Cogn. Sci. 5, 89–118. https://doi.org/10.1007/s11097-
754 005-9015-6

755 Lezak, M.D., 1995. Neuropsychological assessment (3rd ed.), Neuropsychological
756 assessment (3rd ed.).

757 Liebenthal, E., Binder, J.R., Spitzer, S.M., Possing, E.T., Medler, D.A., 2005. Neural substrates
758 of phonemic perception. Cereb. Cortex 15, 1621–1631.
759 https://doi.org/10.1093/cercor/bhi040

760 Lima, C.F., Krishnan, S., Scott, S.K., 2016. Roles of Supplementary Motor Areas in Auditory
761 Processing and Auditory Imagery. Trends Neurosci. 39, 527–542.
762 https://doi.org/10.1016/j.tins.2016.06.003

763 Luke, S.G., 2017. Evaluating significance in linear mixed-effects models in R. Behav. Res.
764 Methods 49, 1494–1502. https://doi.org/10.3758/s13428-016-0809-y

765 McLaren, D.G., Ries, M.L., Xu, G., Johnson, S.C., 2012. A generalized form of context-
766 dependent psychophysiological interactions (gPPI): A comparison to standard
767 approaches. Neuroimage 61, 1277–1286.
768 https://doi.org/10.1016/j.neuroimage.2012.03.068

769 Miall, R.C., Wolpert, D.M., 1996. Forward models for physiological motor control. Neural
770 Networks. https://doi.org/10.1016/S0893-6080(96)00035-4

771 Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory.
772 Neuropsychologia 9, 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

773 Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: Transforming
774 numbers into movies. Spat. Vis. 10, 437–442.
775 https://doi.org/10.1163/156856897X00366

776 Pereira, M., Faivre, N., Iturrate, I., Wirthlin, M., Serafini, L., Martin, S., Desvachez, A., Blanke,
777 O., Van De Ville, D., Millán, J. del R., 2020. Disentangling the origins of confidence in
778 speeded perceptual judgments through multimodal imaging. Proc. Natl. Acad. Sci. 117,
779 8382–8390. https://doi.org/10.1073/pnas.1918335117

780 Piazza, M., Izard, V., Pinel, P., Le Bihan, D., Dehaene, S., 2004. Tuning curves for approximate
781 numerosity in the human intraparietal sulcus. Neuron 44, 547–555.
782 https://doi.org/10.1016/j.neuron.2004.10.014

783 Piazza, M., Mechelli, A., Price, C.J., Butterworth, B., 2006. Exact and approximate
784 judgements of visual and auditory numerosity: An fMRI study. Brain Res. 1106, 177–
785 188. https://doi.org/10.1016/j.brainres.2006.05.104

786 Power, J.D., Barnes, K.A., Snyder, A.Z., Schlaggar, B.L., Petersen, S.E., 2012. Spurious but
787 systematic correlations in functional connectivity MRI networks arise from subject
788 motion. Neuroimage 59, 2142–2154.
789 https://doi.org/10.1016/j.neuroimage.2011.10.018

790 Press, C., Kok, P., Yon, D., 2020. The Perceptual Prediction Paradox. Trends Cogn. Sci. 24, 13–
791 24. https://doi.org/10.1016/j.tics.2019.11.003

792 Reinert, R.M., Hartmann, M., Huber, S., Moeller, K., 2019. Unbounded number line
793 estimation as a measure of numerical estimation. PLoS One 14, 1–16.
794 https://doi.org/10.1371/journal.pone.0213102

795 Rummell, B.P., Klee, J.L., Sigurdsson, T., 2016. Attenuation of responses to self-generated
796 sounds in auditory cortical neurons. J. Neurosci. 36, 12010–12026.
797 https://doi.org/10.1523/JNEUROSCI.1564-16.2016

798 Scott, M., Yeung, H.H., Gick, B., Werker, J.F., 2013. Inner speech captures the perception of
799 external speech. J. Acoust. Soc. Am. 133, EL286–EL292.
800 https://doi.org/10.1121/1.4794932

801 Serino, A., Pozeg, P., Bernasconi, F., Solcà, M., Hara, M., Progin, P., Stripeikyte, G., Dhanis,
802 H., Salomon, R., Bleuler, H., Rognini, G., Blanke, O., 2021. Thought consciousness and
803 source monitoring depend on robotically controlled sensorimotor conflicts and illusory
804 states. iScience 24, 101955. https://doi.org/10.1016/j.isci.2020.101955

805 Shergill, S.S., White, T.P., Joyce, D.W., Bays, P.M., Wolpert, D.M., Frith, C.D., 2013.
806 Modulation of somatosensory processing by action. Neuroimage 70, 356–362.
807 https://doi.org/10.1016/j.neuroimage.2012.12.043

808 Slamecka, N.J., Graf, P., 1978. The generation effect: Delineation of a phenomenon. J. Exp.
809 Psychol. Hum. Learn. Mem. 4, 592–604. https://doi.org/10.1037/0278-7393.4.6.592

810 Stripeikyte, G., Pereira, M., Rognini, G., Potheegadoo, J., Blanke, O., & Faivre, N. (2021).
811 Increased functional connectivity of the intraparietal sulcus underlies the attenuation
812 of numerosity estimations for self-generated words [Data set]. Zenodo.
813 http://doi.org/10.5281/zenodo.4925909

814 Thomas, E.R., Yon, D., Lange, F.P. de, Press, C., 2020. Action enhances predicted touch.
815 bioRxiv 2020.03.26.007559. https://doi.org/10.1101/2020.03.26.007559

816 Tian, X., Poeppel, D., 2010. Mental imagery of speech and movement implicates the

817 dynamics of internal forward models. Front. Psychol. 1, 1–23.
818 https://doi.org/10.3389/fpsyg.2010.00166

819 Tian, X., Zarate, J.M., Poeppel, D., 2016. Mental imagery of speech implicates two
820 mechanisms of perceptual reactivation. Cortex 77, 1–12.
821 https://doi.org/10.1016/j.cortex.2016.01.002

822 Timm, J., SanMiguel, I., Keil, J., Schröger, E., Schönwiesner, M., 2014. Motor Intention
823 Determines Sensory Attenuation of Brain Responses to Self-initiated Sounds. J. Cogn.
824 Neurosci. 26, 1481–1489. https://doi.org/10.1162/jocn_a_00552

825 Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N.,
826 Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM
827 using a macroscopic anatomical parcellation of the MNI MRI single-subject brain.
828 Neuroimage 15, 273–289. https://doi.org/10.1006/nimg.2001.0978

829 Ullsperger, M., Harsay, H.A., Wessel, J.R., Ridderinkhof, K.R., 2010. Conscious perception of
830 errors and its relation to the anterior insula. Brain Struct. Funct. 214, 629–643.
831 https://doi.org/10.1007/s00429-010-0261-1

832 Vaccaro, A.G., Fleming, S.M., 2018. Thinking about thinking: A coordinate-based meta-
833 analysis of neuroimaging studies of metacognitive judgements. Brain Neurosci. Adv. 2,
834 239821281881059. https://doi.org/10.1177/2398212818810591

835 van de Ven, V., Esposito, F., Christoffels, I.K., 2009. Neural network of speech monitoring
836 overlaps with overt speech production and comprehension networks: A sequential
837 spatial and temporal ICA study. Neuroimage 47, 1982–1991.
838 https://doi.org/10.1016/j.neuroimage.2009.05.057

839 Whitford, T.J., 2019. Speaking-Induced Suppression of the Auditory Cortex in Humans and
840 Its Relevance to Schizophrenia. Biol. Psychiatry Cogn. Neurosci. Neuroimaging 4, 791–
841 804. https://doi.org/10.1016/j.bpsc.2019.05.011

842 Whitford, T.J., Jack, B.N., Pearson, D., Griffiths, O., Luque, D., Harris, A.W.F., Spencer, K.M.,
843 Le Pelley, M.E., 2017. Neurophysiological evidence of efference copies to inner speech.
844 Elife 6, 1–23. https://doi.org/10.7554/eLife.28197

845 Wolpert, D.M., Flanagan, J.R., 2001. Motor prediction. Curr. Biol. 11, 729–732.
846 https://doi.org/10.1016/s0960-9822(01)00432-8

847

848

LEGENDS OF FIGURES AND TABLES

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.

Figure 2. Behavioral results. (A) Individual numerosity performance in the active (red) and passive (blue) conditions. A value of zero represents ideal performance, where the reported and actual number of words match. Each dot represents a participant mean numerosity performance. Grey lines connect performance from the same participant across conditions. (B) Mixed-effects linear regression between numerosity estimation (reported number of 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 depict individual estimates. Individual plots are depicted in Figure 2-1. (C) Mean slope coefficient estimates with 2.5% and 97.5% confidence intervals.

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 conditions) of the parametric modulation of numerosity performance during numerosity estimation in the right intraparietal sulcus (IPS, depicted in green). (B) Box plot of the corresponding individual beta estimates in the right IPS. Each dot represents a participant mean beta estimates. Grey lines connect beta estimates from the same participant across conditions. (C) Overlap between the parametric modulation of numerosity performance during numerosity estimation (depicted in green) main effect (active + passive conditions) at the lower statistical threshold of peak level uncorrected $p<0.005$ (exploratory analyses) and parametric modulation of performance monitoring during the error estimation (active vs. passive condition) (depicted in purple); peak level uncorrected $p<0.001$.

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.

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.

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.

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

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

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

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

Extended data legends

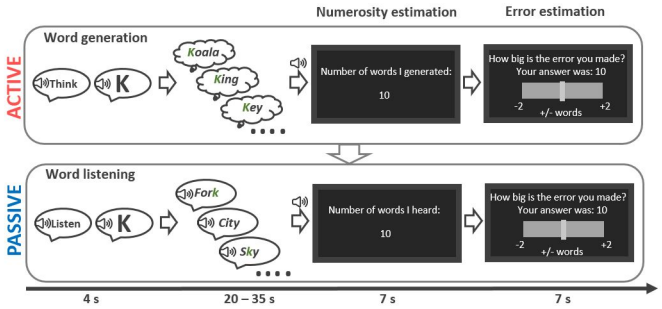
Figure 1-1. Data simulation of behavioral performance measures. Data was simulated with pseudorandom generation of an actual number of words and numerosity estimations ranging between 5 and 20. Error estimation varied between 0 and 5 as set during the task design. (A) Simulated numerosity performance. Increasing intensity of red represent linear increase of overestimation (positive values of numerosity performance), while increasing

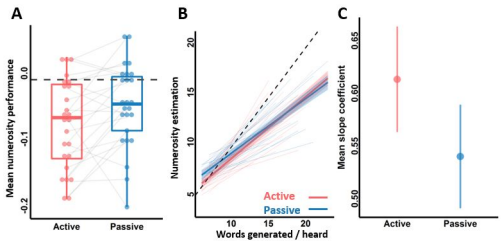
intensity in blue represent linear increase of underestimation (negative values of numerosity performance). (B) Simulated performance monitoring when the number of words is constant (10 or 15 words). The performance monitoring value is depicted in the heatmap changing from blue (being correct) to red (worse performance monitoring).

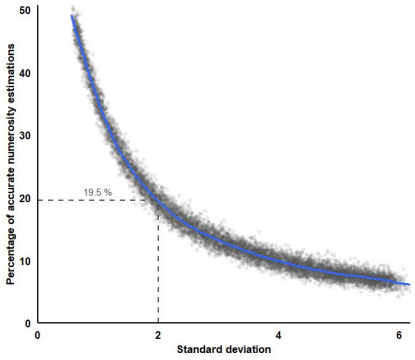
Figure 2-1. Mixed-effects linear regression between numerosity estimation (reported number of words) and an actual number of words depicted for each participant. Reference dashed line with a slope equal to 1 represents ideal performance. Thick lines represent the individual model fit per condition (active: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

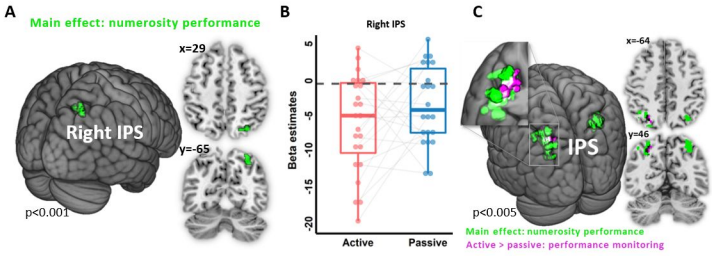
Table 1-1. Numerosity estimation: main effect (active + passive conditions). Brain areas activated during the numerosity estimation phase independent of parametric modulation. Voxel level $p<0.001$ uncorrected, cluster threshold at $p<0.05$ FWE corrected. BA – Broadmann area, k – cluster size, R – right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

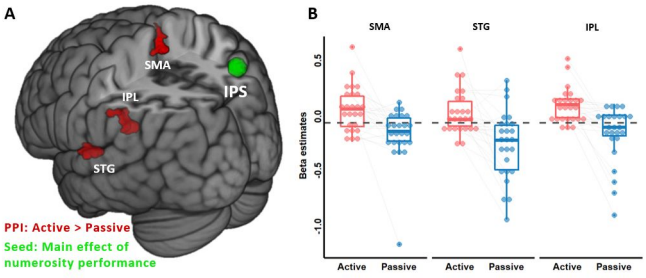
Table 4-1. Error estimation: main effect (active + passive conditions). Brain areas with activations during the error estimation phase, independent of parametric modulation. Voxel level $p<0.001$ uncorrected, cluster threshold at $p<0.05$ FWE corrected. BA – Broadmann area, k – cluster size, R – right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

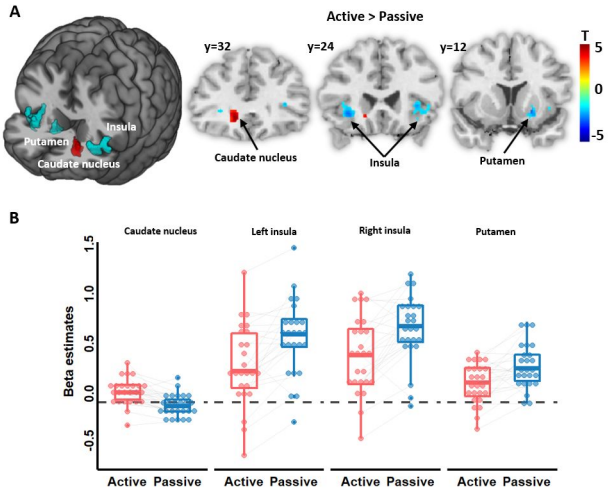


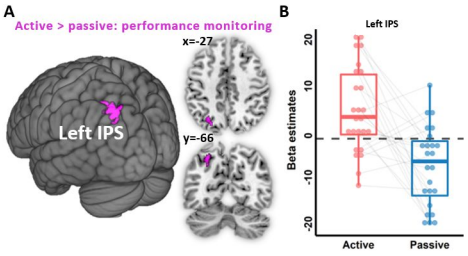












BA	Anatomical Label		k	Peak voxel MNI coordinate x	y	z	p_{FWE}	T
	Active < passive							
	Middle temporal g. Precuneus Superior temporal g. Postcentral 7 Middle cingulum 6 Cerebellum 40 SMA 31 Insula 13 Precentral 24 Supramarginal g. 21 Angular g. 4 Superior parietal 32 Putamen 39 Middle frontal g. 3 Caudate 5 Superior fontal g. 9 Superior parietal g. 23 Calcarine 27 Rolandic percular 8 Supramarginal g. 18 Thalamus 44 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

BA	Anatomical Label		k	Peak voxel MNI coordinate x	y	z	p_{FWE}	T
	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

BA	Anatomical Label		k	Peak voxel MNI coordinate x	y	z	p_{FWE}	T
	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

BA	Anatomical Label		k	Peak voxel MNI coordinate x	y	z	p_{FWE}	T
	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