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# 1 Variance-dependent neural activity in an unvoluntary

# 2 averaging task

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# 13 Abstract

14 Ensemble statistics of a visual scene can be estimated to provide a gist of the scene without

15 detailed analysis of all individual items. The simplest and most widely studied ensemble

16 statistic is mean estimation, which requires averaging an ensemble of elements. Averaging is

17 useful to estimate the mean of an ensemble and discard the variance. The source of variance

18 can be external, i.e., variance across the physical elements, or internal, i.e., imprecisions in the

19 estimates of the elements by the visual system. The equivalent noise paradigm is often used to

20 measure the impact of the internal variance (i.e., the equivalent input noise). This paradigm

21 relies on the assumption that the averaging process is equally effective independently of the

22　main source of variance, internal or external, so any difference between the processing when

23　the main source of variance is internal and external must be assumed not to affect the averaging

24　efficiency. The current fMRI study compared the neural activity when the main variance is

25　caused by the stimulus (i.e., high variance) and when it is caused by imprecisions in the

26　estimates of the elements by the visual system (i.e., low variance). The results showed that the

27　right superior frontal and left middle frontal gyri can be significantly more activated when the

28　variance in the orientation of the Gabors was high than when it was low. Consequently, the use

29　of the equivalent noise paradigm requires the assumption that such additional neural activity in

30　high variance does not affect the averaging efficiency.

## Keywords
31

# Introduction

We have the subjective impression that we can perceive the entire visual scene at a glance, but the visual system has limited resources and the entire visual scene cannot be simultaneously processed with optimal efficiency. For instance, some processing requires the focus of attention to be optimal, but attention can only be divided among few items (Pylyshyn & Storm, 1988; Treisman & Gelade, 1980). Nevertheless, the visual system does not completely discard the unattended information of the visual scene as some global information can be perceived even in the absence of focal attention (for a review, see Whitney & Yamanashi Leib, 2018). Ensemble statistics of a visual scene can be estimated to provide a gist of the visual scene without detailed analysis of all individual items. The process of extracting ensemble statistics is often described as "obligatory" or "compulsory" (Fischer & Whitney, 2011; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) as attention may not necessarily be required (Alvarez & Oliva, 2008, 2009; Bronfman, Brezis, Jacobson, & Usher, 2014; Chong & Treisman, 2005).

The simplest and most widely studied ensemble statistic is mean estimation, which requires averaging an ensemble of elements. Averaging is useful to estimate the mean of an ensemble and discard the variance. When the variance across elements is high, the ability to estimate the mean of the a priori distribution (e.g., orientation discrimination threshold) depends on the averaging efficiency (also referred to as calculation efficiency or sampling efficiency), which quantifies the observer's performance relative to the ideal performance (e.g., Beaudot & Mullen, 2006). Since the correctness of the answer is defined relative to the mean of the a priori distribution, the ideal performance is limited by the variance of the a priori distribution.

When the variance is low (e.g., all identical elements), the performance of a human observer cannot solely depend on the averaging efficiency as performance is also limited by imprecisions in the estimates of the elements (i.e., internal noise) by the visual system. Consequently, in

absence of external variance, the ability to estimate the mean of the a priori distribution is typically presumed to depend on two factors (Beaudot & Mullen, 2006; Dakin, 2001, 2015; Dakin, Bex, Cass, & Watt, 2009; Dakin, Mareschal, & Bex, 2005; Mansouri, Allen, Hess, Dakin, & Ehrt, 2004; Mareschal, Bex, & Dakin, 2008; Tibber et al., 2015): the variance introduced by the visual system (typically referred to as internal noise) and the averaging efficiency of the effective stimulus (i.e., the stimulus + orientation-jitter due to imprecisions in samples estimates). The equivalent noise paradigm is often used to evaluate the impact of these imprecisions. Knowing the performance in absence of noise and the effective averaging efficiency in absence of noise enables to derive the internal variance due to imprecisions in samples estimates. However, the effective averaging efficiency in absence of noise cannot be directly measured. Nevertheless, by assuming (usually implicitly) that the effective averaging efficiency in absence of noise is the same as the averaging efficiency measured in high noise (i.e., the noise-invariant processing assumption, Allard & Cavanagh, 2011; or the contrast-invariant calculation assumption Pelli, 1990), it is possible to derive the internal variance based on the performance in absence of noise and in high noise. Consequently, this assumption is critical for evaluating the internal noise using the equivalent noise paradigm.

The equivalent noise paradigm is more commonly used for contrast thresholds and white pixel noise, and relies on the noise-invariant processing assumption (Allard & Cavanagh, 2011, 2012; or the contrast-invaraint processing assumption, Pelli, 1990): the calculation efficiency measured in high noise is assumed to be the same as the effective calculation efficiency in low noise. The presence of high white pixel noise obviously increases neural activity, so to use the equivalent noise paradigm, one must assume that this additional neural activity in high noise does not affect the calculation efficiency. This assumption has been criticized by Baker and colleagues (Baker & Meese, 2012; Baker & Vilidaite, 2014; Baldwin, Baker, & Hess, 2016), who argue that white noise may compromise the use of the equivalent because it introduces

82  neural activity that can interfere with the processing of the target (but see Allard & Faubert,

83  2013, 2014). Although it is obvious that some neural activity is greater in the presence of white

84  pixel noise than the absence of noise due to the greater contrast, it is not obvious if adding

85  increasing the variance across elements would increase neural activity. For instance, we would

86  not necessarily expect additional neural activity when adding an orientation jitter to each

87  element of an ensemble.

88  An important distinction that is not always explicitly stated is that the averaging process can be

89  voluntary or involuntary (Dakin et al., 2009). For voluntary averaging, only a small number of

90  elements is presented (e.g., 4, Allard & Cavanagh, 2012; or 6, Dakin et al., 2009), each element

91  is perceptually distinct (e.g., top row in Figure 1), and the observer voluntarily decides to

92  estimate the mean of an attribute (e.g., orientation) or not. The triggering of this averaging

93  process therefore depends on the volition of the observer so it is not compulsory or obligatory.

94  For involuntary averaging, however, computing the mean is compulsory or obligatory, that is,

95  beyond the volition of the observer (Dakin et al., 2009; Fischer & Whitney, 2011; Parkes et al.,

96  2001). Involuntary averaging typically occurs when a large amount of elements are presented

97  in the periphery (e.g., bottom row in Figure 1) and is particularly relevant for scene perception

98  as it provides a gist of the ensemble statistics and has been studied for many attributes such as

99  orientation (e.g., Alvarez & Oliva, 2009), size (Im & Halberda, 2013), motion (Mareschal et

100  al., 2008) and color (Bronfman et al., 2014).
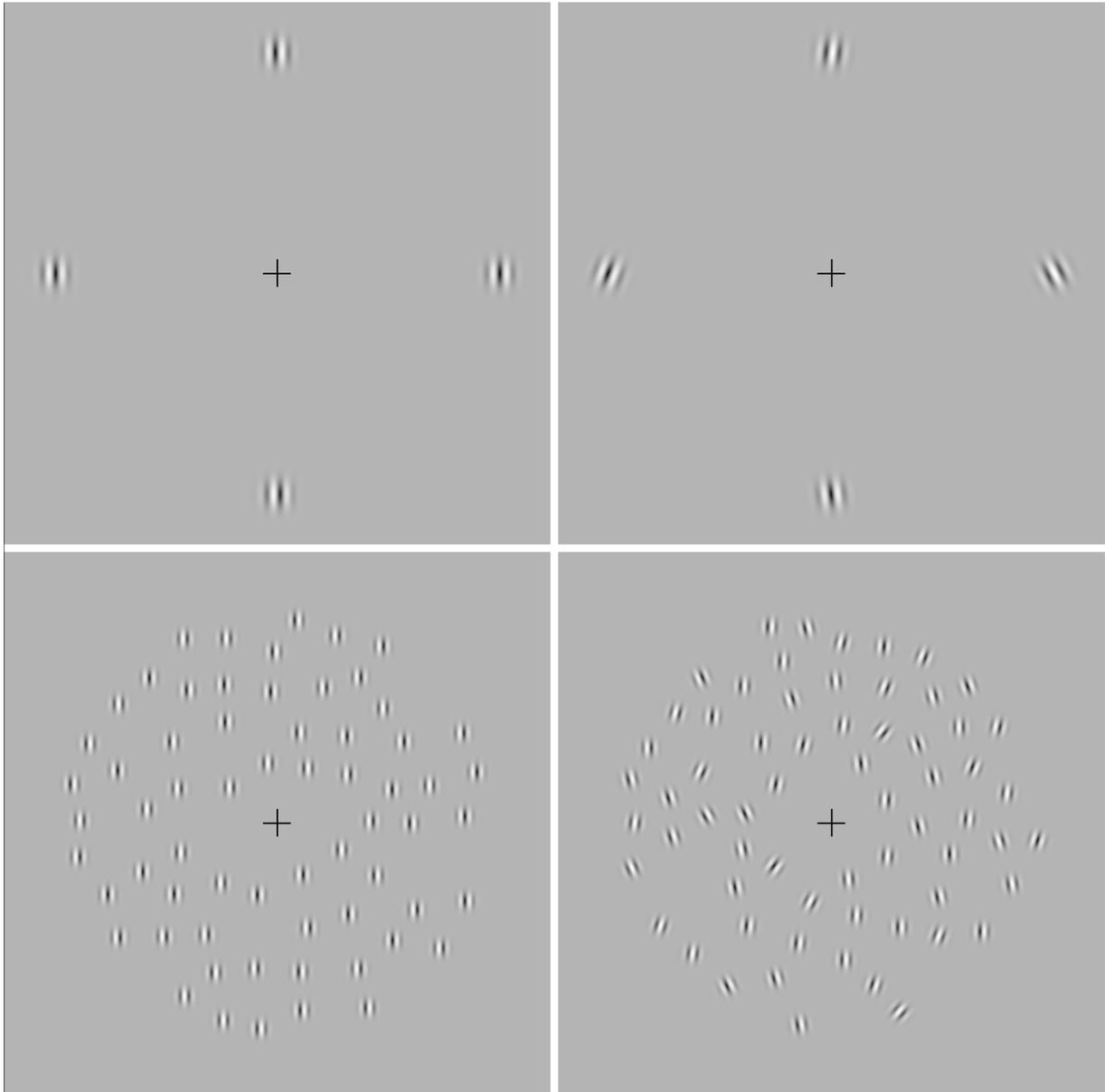
**Figure 1. Examples of stimuli for the voluntary (top) and involuntary (bottom) for low (left) or high (right) variance across samples. The task consisted in judging the mean orientation of the ensemble relative to vertical (clockwise or counterclockwise).**

For voluntary averaging (e.g., top row in Figure 1), Allard and Cavanagh (2012) concluded that observers averaged the physical (i.e., external) variance across elements, but not the internal variance resulting from imprecision estimates of individual elements by the visual system. In other words, they voluntarily and effectively averaged dissimilar elements, but not apparently identical elements. This claim was based on the psychophysical finding that performance at

110 discriminating the mean of the a priori distribution improved with the number of samples in

111 high variance (i.e., high jitter added to every elements), but not in low variance (i.e., identical,

112 or nearly identical, elements and variance in sample estimates is mainly due to the sample

113 estimates by the observers). They concluded that some voluntary averaging processing

114 operating in high variance was not effective in low variance, which contradicts the noise-

115 invariant processing assumption (Allard & Cavanagh, 2011; in the current context, it could also

116 be referred to as the "variance-invariant processing assumption") that the same processing

117 operates in low and high variance. However, it has been argued that the result of this

118 psychophysical study does not necessarily imply different averaging efficiencies in low and

119 high variance as the apparent absence of averaging efficiency in low variance could be

120 explained by greater imprecision estimates with more samples (Dakin, 2015) or by

121 multiplicative noise (i.e., internal variance proportional to the external variance, Bocheva,

122 Stefanov, Stefanova, & Genova, 2015). Thus, despite the observable voluntary averaging

123 efficiency in high variance and the absence of observable efficiency in low variance, the claim

124 that different averaging processes operate in both conditions (i.e., the variance-invariant

125 processing assumption underlying the equivalent noise paradigm) remains debated.

126 Given that voluntary averaging depends on the volition of the observer, a variance-dependent

127 averaging process would not be surprising; why bother voluntarily averaging elements that

128 appear identical? On the other hand, we may intuitively expect involuntary averaging

129 processing to be independent of the variance across the elements to average. Indeed, a

130 compulsory or obligatory averaging process would be expected to operate whether the

131 perceived variance across elements is mainly due to the stimulus variance across elements when

132 the variance is high or to imprecisions in the estimates of the samples when the variance is low

133 (e.g., identical samples).

134 The aim of the current study was to investigate if the processing differs whether the main source

135 of the sample imprecision is coming from the stimulus (i.e., high variance) or from the

136 imprecision estimates of the observer (i.e., low variance). For this purpose, we recorded the

137 neural activity when the main variance was coming from the stimulus and from the observer

138 for a voluntary (i.e., 4 sparse elements; top images in Figure 1) and an involuntary (64 elements

139 presented in the periphery; bottom images in Figure 1) orientation-averaging task.

# Method

## *Participants*

142 Seventeen young adults were included in the study (9 females; mean age ± SD: 26.6 ± 4.4

143 years; age range: 21-38 years), but 3 subjects were excluded for in-scanner motion

144 (movements > 3 mm across trials). The participants were part of the French cohort population

145 SilverSight (~350 subjects) established and followed-up ever since 2015 at Vision Institute –

146 Quinze-Vingts National Ophtalmology Hospital, Paris, France (Lagrené et al., 2019). All

147 participants were right-handed, had normal or corrected-to-normal vision, and they had no

148 history of neurological or psychiatric disorders, or ocular disorders, or sensorimotor

149 dysfunctions. All participants gave their informed written consent before participating in the

150 study in accordance with the tenets of the Declaration of Helsinki and they were approved by

151 the Ethical Committee "CPP Ile de France V" (ID_RCB 2015-A01094-45, CPP N°: 16122).

## *Apparatus*

153 Stimuli were displayed using nordicAktiva software (https://www.nordicneurolab.com/) on an

154 MRI-compatible liquid crystal display monitor (NordicNeuroLab, Bergen, Norway) positioned

155 at the head of the scanner bore. Participants viewed the screen (size: 69.84 cm (H) x 39.26 cm

156 (V); pixels: 1920 x 1080; refresh rate: 120 Hz, mean luminance intensity: 203 cd/m$^2$) at a

157 distance of 115 cm via a mirror fixed above the head-coil. The visible part of the screen

158 subtended approximately 34 x 19 degrees of visual angle (dva).

### *Stimuli and Procedure*

160 Observers were asked to report the mean orientation of an ensemble of Gabors relative to

161 vertical and respond as soon as possible, while answering as accurately as possible. For

162 voluntary averaging, the stimuli were similar to the ones of a previous study on voluntary

163 averaging (Allard & Cavanagh, 2012): 4 Gabors displayed 8 dva to the left, right, above, and

164 below fixation (top row in Figure 1) so that each element was perceptually distinct (Dakin et

165 al., 2009). The spatial frequency of the Gabors was 2 cpd; their spatial envelope was a Gaussian

166 with a SD of 0.33 dva; their contrast was maximized and their phases were randomized.

167 For involuntary averaging, 64 Gabors were presented in the periphery in which case computing

168 their mean orientation is expected to be compulsory or obligatory, that is, beyond the volition

169 of the observer (Dakin et al., 2009; Fischer & Whitney, 2011; Parkes et al., 2001). The Gabors

170 were randomly positioned between 2 and 8 dva of eccentricity with the constraint that center-

171 to-center distance between Gabors had to be at least 1.5 dva (bottom row in Figure 1). In order

172 to increase the gap between Gabors, their Gaussian spatial envelope was smaller (SD of 0.17

173 dva) and their spatial frequency was 3 cpd.; their contrast was maximized and their phases were

174 randomized.

175 In the low variance condition, the Gabors were all vertically orientated. In the high variance

176 condition, the orientations of the Gabors were selected from a Gaussian distribution centered

177 vertically with a SD of the distribution of 16 degrees. The stimuli were presented for 200 ms,

178 which was too brief for the observer to saccade to the target (Hallett, 1986).

179 We used a block-design paradigm with 4 different conditions: low-variance with 4 elements

180 (LV-4; top-left in Figure 1), low-variance with 64 elements (LV-64; bottom-left in Figure 1),

181 high-variance with 4 elements (HV-4; top-right in Figure 1) and high-variance with 64

182 elements (HV-64; bottom-right in Figure 1). 120 trials were performed per condition for a

183 total of 480 trials. These trials were separated among six functional runs presented in a

184 random order: 3 runs for voluntary averaging (LV-4 and HV-4), and 3 runs for involuntary

185 averaging (LV-64 and HV-64). Each functional scan lasted 5 minutes and was composed of

186 sixteen 5-trial blocks alternating between LV and HV with the first block randomly selected

187 (LV or HV). Each 5-trial block lasted 15 seconds. The sixteen blocks were interspersed with

188 four 15-second blocks with a fixation cross at the center of the screen (Fixation condition)

189 displayed against a gray background.

190 Each stimulus was displayed for 200 ms followed by a fixation cross in the center of the

191 screen displayed against a gray background. The interval between the onset of two successive

192 stimuli was 2.8 s. Participants had to give a categorical answer after each image by pressing

193 the corresponding handheld grips response device (NordicNeurolab) to indicate whether the

194 mean orientation of the Gabors was tilted clockwise or counterclockwise from vertical. They

195 were instructed to fixate on the center of the screen (fixation cross) during the entire

196 experiment and to respond as accurately and as quickly as possible. Response accuracy and

197 reaction times were recorded.

198 A practice session in a psychophysical laboratory was conducted a few days before the

199 experiment for participants to be familiarized with the psychophysical task and the four types

200 of stimuli prior to the data acquisition.

### fMRI acquisition

202 Images were acquired using a 3T Siemens Magnetom Skyra whole-body MRI system

203 (Siemens Medical Solutions, Erlangen, Germany) with a 64-channel head-coil at the Quinze-

204 Vingts National Ophthalmology Hospital in Paris, France. Task-based fMRI and an

10

205   anatomical image were acquired for all participants. The anatomical volume consisted of a

206   T1-weighted, high-resolution, three-dimensional MPRAGE sequence (TR/TE/IT/flip angle =

207   2300 ms/ 2.9 ms/ 900 ms/ 9°; matrix size = 256 x 240 x 176; voxel size = 1 x 1 x 1.2 mm).

208   For functional scan, 304 volumes of 64 slices were acquired using a T2*-weighted SMS-EPI

209   sequence (TR/TE/flip angle = 1000 ms/ 30 ms/ 90°; matrix size = 100 x 100; SMS = 2;

210   GRAPPA = 2; voxel size = 2.5 x 2.5 x 2.4 mm).

211   ### *Data analysis*

212   Data analysis was performed using SPM12 release 7487 (Wellcome Department of Imaging

213   Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 2018a

214   (Mathworks Inc., Natick, MA, USA).

215   For each participant, the first 4 functional volumes of each runs were discarded to allow for

216   equilibration effects. The remaining volumes were realigned to correct for head movements to

217   the mean functional images using a rigid body transformation. The T1-weighted anatomical

218   volume was then realigned (affine transformation) to match the mean functional image of

219   each participant, and was then normalized (non-rigid, non-linear transformation) into the MNI

220   space. A 4th degree B-Spline interpolation was applied. The anatomical normalization

221   parameters were subsequently used for the normalization of functional volumes. Finally, each

222   functional scan was smoothed by an 8 mm FWHM (Full Width at Half Maximum) Gaussian

223   kernel. Slice-timing correction was not applied in line with the recommendations of the

224   Human Connectome Project functional preprocessing pipeline for multi-slice sequences

225   (Glasser et al., 2013).

226   Statistical analysis was performed using general linear model (Friston et al., 1994) for block

227   designs at single participant level. For each participant, five conditions of interest (LV-4, LV-

228   64, HV-4, HV-64 and Fixation) were modelled as five regressors, constructed as box-car

functions and convolved with a canonical hemodynamic response function. Reaction-time for

each trial and movement parameters derived from realignment corrections (three translations

and three rotations) were also considered in the model as an additional factor of no interest to

account for related variance. Time-series for each voxel were high-pass-filtered (1/128 Hz

cutoff) to remove low-frequency noise and signal drift. On an individual level (first level

analysis), we identified the brain regions involved in the processing of each level of variance

content relative to the fixation ([LV-ALL > Fixation], and [HV-ALL > Fixation]) irrespective

to the number of elements. Then, we identified the cerebral regions involved in the processing

of low-variance stimuli related to the high-variance stimuli, as well as the inverse fMRI

contrast ([LV-ALL > HV-ALL] and, [HV-ALL > LV-ALL]. We also, tested the effect of

number of elements ([ALL-4 > ALL-64], and [ALL-64 > ALL-4]) irrespective to the variance

content, and we identified brain regions involved in the processing of variance related to the

number of elements ([LV-4 > HV-4], [HV-4 > LV-4], [LV-64 > HV-64], and [HV-64 > LV-

64]. Finally, we tested the effect of level of variance for both number of elements conditions

relative to the fixation (([LV-4 > Fixation], [HV-4 > Fixation], [LV-64 > Fixation], and [HV-

64 > Fixation]).

To allow population inference, we performed a second level-random analysis using a one-

sample t-test. Areas of activation were considered significant if they exceed a significant

threshold fixed at $p<0.05$ FWE-corrected for multiple comparisons at cluster level, with a

minimum cluster extend k=20.

# Results

## *Behavior*

The percentage of trials on which participants did not give an answer within 2.8 seconds was

lower than 1% for each of the four conditions (LV-4=0.6%; HV-4=0.8%; LV-64=0.5% and

253 HV-64=0.5%). These results confirm that participants followed the instructions to respond as

254 fast as possible. No-response trials were removed from behavioral analyses.

255 Figure 2 shows the number of participants who answered clockwise for each stimulus as a

256 function of the mean of the ensemble for conditions in high variance. With 4 Gabors (left

257 graph in Figure 2), the mean orientation of the stimulus varied considerably across stimuli and

258 the participants' answers were highly correlated with the stimulus' mean orientation as

259 confirmed by a linear regression analysis ($b$=0.38, $t(11)$=16.7, $p$<0.001). Indeed, when the

260 mean orientation was highly tilted clockwise, almost all of participants answered "clockwise"

261 and when the mean orientation was highly tilted counterclockwise, almost all of them

262 answered "counterclockwise" (i.e., just a few answered "clockwise"). As a result, the

263 participants' answers were stimulus driven, not random (Figure 3). With 64 Gabors (right

264 graph in Figure 2), the stimulus' mean orientation was much closer to vertical due to the

265 greater number of elements. Although the participants' answers were less correlated with the

266 actual stimulus mean (Figure 3), the participants' answers also significantly depended on the

267 mean orientation ($b$=0.40, $t(11)$=2.93, $p$<0.01). These results confirm that participants

268 effectively performed the task of reporting the mean orientation relative to vertical (i.e., they

269 did not answer randomly).

270
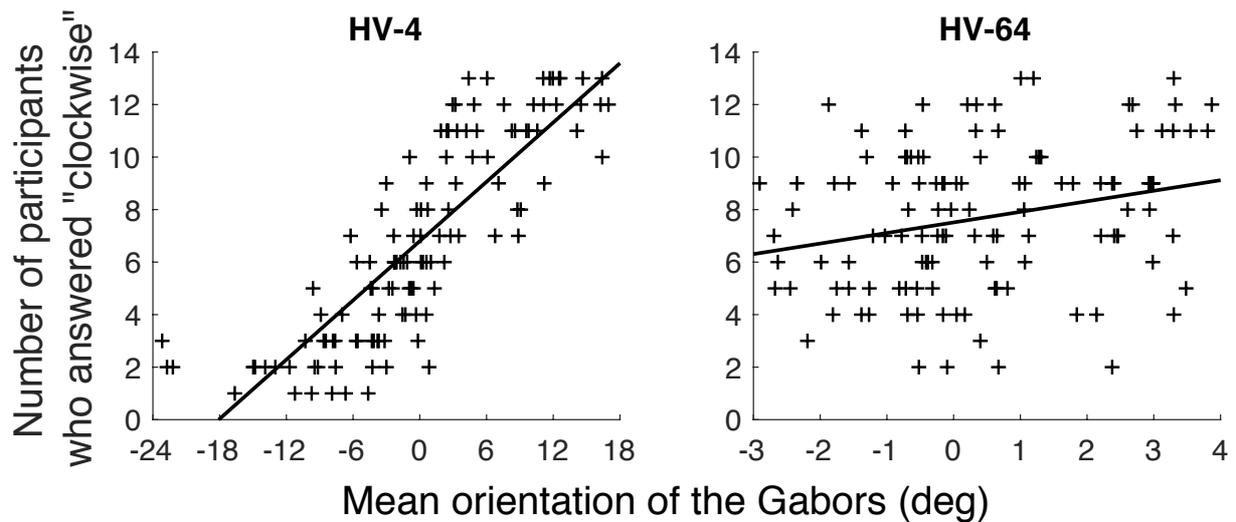
**Figure 2. Number of participants who answered "clockwise" as a function of the mean of the ensemble for each of the 120 stimuli in high variance with 4 Gabors (HV-4, left) and with 64 Gabors (HV-64, right). The solid lines represent the linear regressions.**
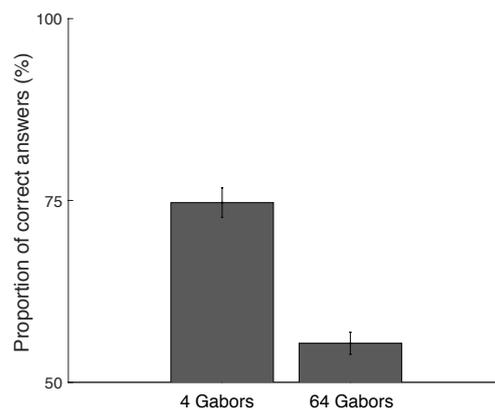


**Figure 3. Proportion of correct answers for both tasks in high variance. Error bars represent standard error from the mean.**

The distributions for the reaction times and the median reaction times (Figure 4) were highly similar for the 4 conditions. The reaction times for the 4 conditions were analyzed with an inverse Gaussian generalized linear mixed model with an identity link and no significant effect was found for the two fixed factors, which were the variance (estimate=12.15 , t= 1.25, $p$=0.21) and the number of elements (estimate=-0.26 , t= -1.58, $p$=0.11). The fact that similar reaction times were observed in low and high variance is compatible with the hypothesis that the processing was independent of the variance across elements (i.e., the variance-invariant

285  processing assumption). Consequently, from the behavioral data alone, there was no evidence

286  of different processing involved in low and high variance (but see fMRI results below).

287
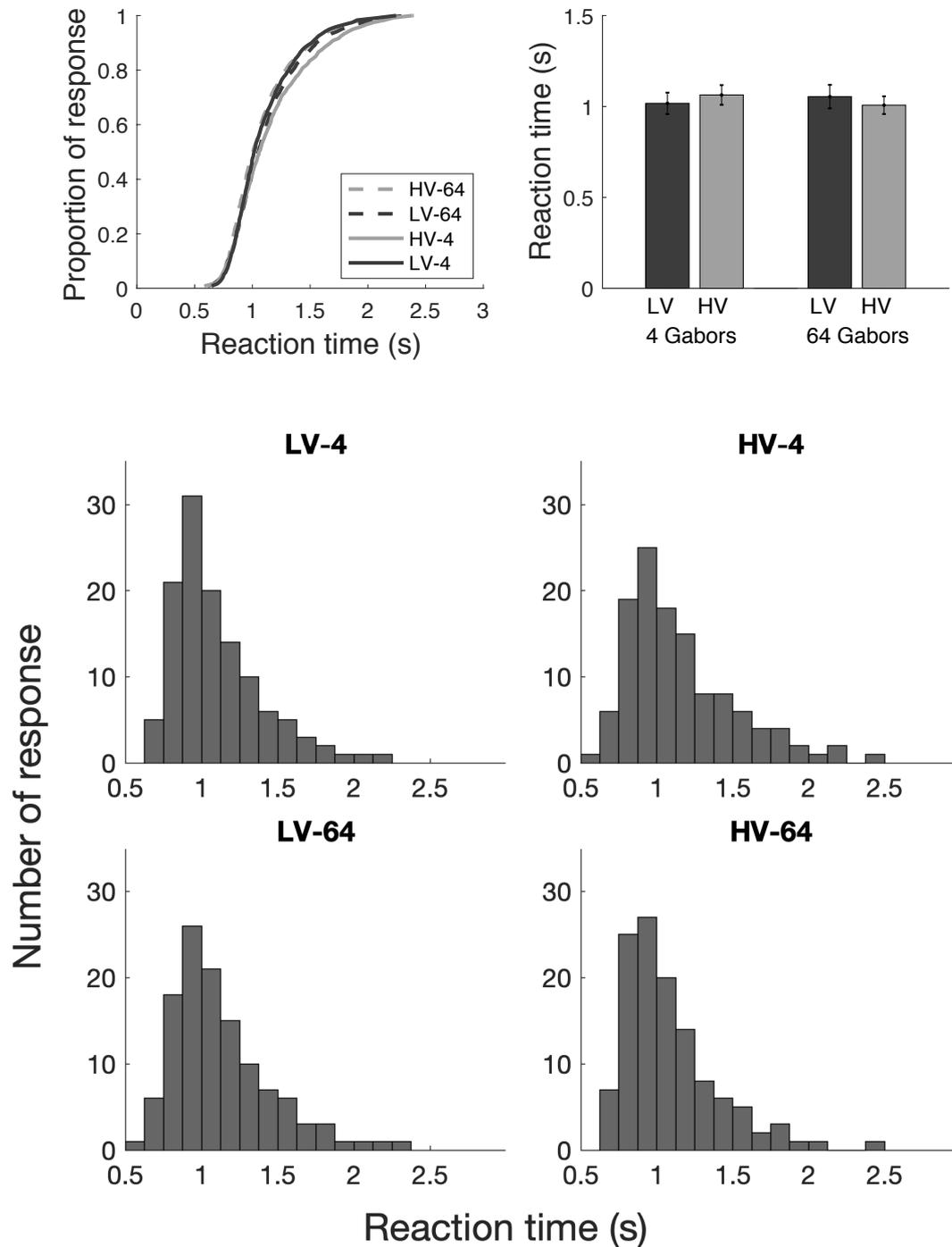


288

289  **Figure 4. Proportion of response given as a function of the reaction time for the four conditions with all**

290  **the participants (top left). Mean median reaction times for the four conditions averaged across observers**

291  **(top right). LV = low variance condition and HV = high variance condition. Error bars represent standard**

292  **error from the mean. Histograms of the reaction times for the 4 conditions (bottom).**

293    *fMRI*

294    *Effect of variance content*. Results for the effect of variance content relative to the fixation,

295    irrespective to the number of elements are shown in Table 1 and Figure 5. Results for direct

296    comparisons of variance conditions are presented in Table 2 and Figure 6.

| | | H | BA | k | x | y | z | t |
|---|---|---|---|---|---|---|---|---|
| fMRI contrasts | | | | | | | | |
| **[LV-ALL > Fix]** | Superior Parietal Gyrus | L | 7 | 94 | -35 | -42 | 53 | 9.16 |
| | [Postcentral Gyrus] | | 1 | | -40 | -35 | 48 | 7.10 |
| | Superior Frontal Gyrus | L | 6 | 49 | -17 | 1 | 50 | 6.81 |
| **[HV-ALL > Fix]** | Superior Parietal Gyrus | L | 7 | 141 | -35 | -42 | 53 | 11.22 |
| | | | | | -40 | -35 | 48 | 8.40 |
| | | | | | -42 | -40 | 58 | 6.65 |
| | Superior Frontal Gyrus | L | 6 | 191 | -17 | 3 | 53 | 7.54 |
| | [Middle Frontal Gyrus] | | | | -30 | 1 | 60 | 7.54 |
| | [Middle Frontal Gyrus] | | | | -25 | -5 | 50 | 6.85 |
| | Middle Frontal Gyrus | R | 6 | 36 | 26 | -2 | 53 | 6.40 |

297    **Table 1. Cerebral regions exhibiting an effect of the level of variance (low-variance stimuli: LV-ALL and**

298    **high-variance stimuli: HV-ALL) related to fixation (Fix). The statistical threshold for cluster was defined**

299    **as *p*<0.05 FWE corrected for multiple comparisons with an extent voxel threshold defined as 20 voxels.**

300    **Only regions revealing significant differences between conditions were included. For each cluster, the**

301    **region showing the maximum t-value was listed first, followed by the other regions in the cluster [in**

302    **square brackets]. Montreal Neurological Institute (MNI) coordinates (x, y, z) of the peak and number of**

303    **voxels (k) of clusters are also shown. H = hemisphere; R = right hemisphere; L = left hemisphere; BA =**

304    **Brodmann area.**
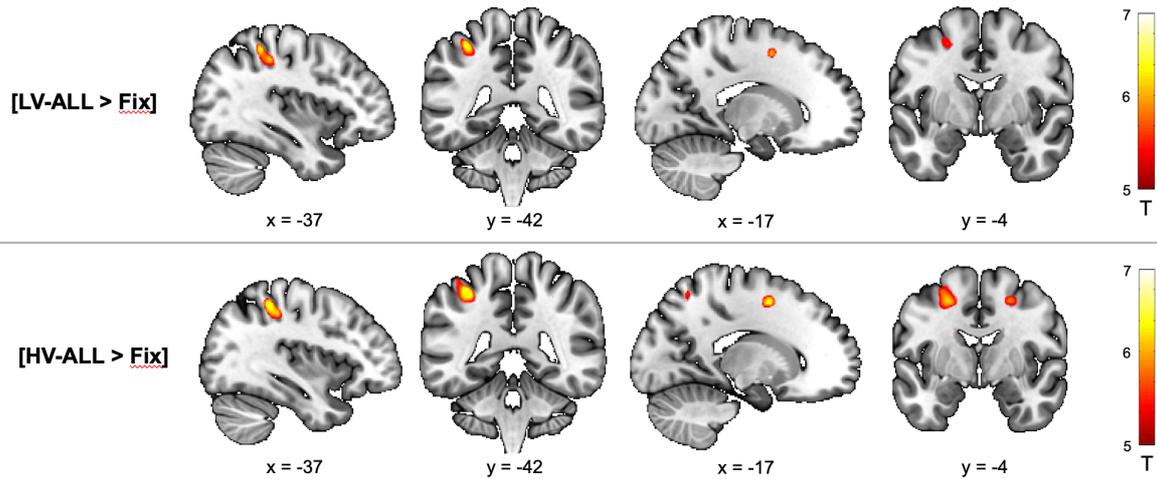
**Figure 5. Cerebral regions whose activity was elicited by the fMRI contrasts [LV-ALL > Fix] and [HV-ALL > Fix] projected onto 2D slices (*p*<0.05 FWE-corrected at cluster level, k=20; LV = low-variance; HV = high-variance; Fix = fixation).**

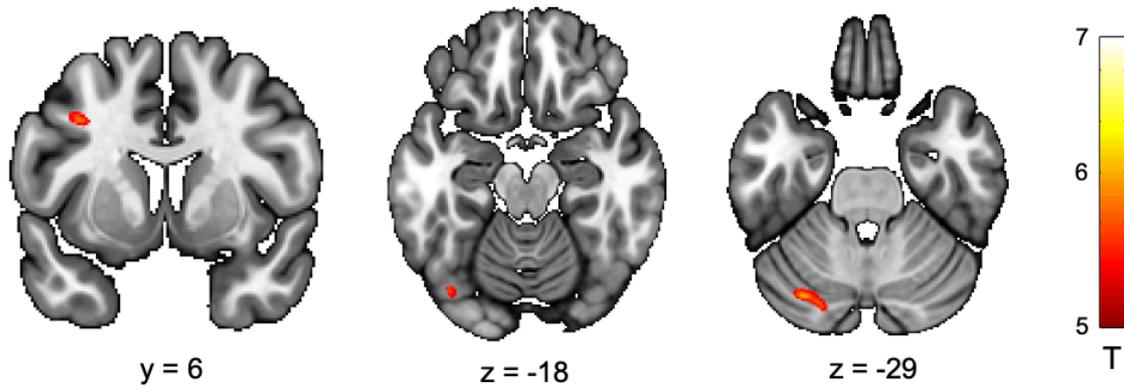| | | H | BA | k | x | y | z | t |
|---|---|---|---|---|---|---|---|---|
| fMRI contrasts | | | | | | | | |
| **[LV-ALL > HV-ALL]** | *No significant activation* | | | | | | | |
| **[HV-ALL > LV-ALL]** | Cerebellum | L | - | 59 | -30 | -75 | -30 | 6.22 |
| | [Inferior Occipital Gyrus] | | 19 | | -40 | -77 | -18 | 6.07 |
| | Middle Frontal Gyrus | L | 6 | 37 | -35 | 6 | 38 | 6.33 |
| | [Middle Frontal Gyrus] | | | | -30 | -16 | 38 | 5.79 |

**Table 2. Cerebral regions exhibiting an effect for direct comparison of variance contents between low-variance (LV-ALL) and high-variance (HV-ALL) stimuli. The statistical threshold for cluster was defined as *p*<0.05 FWE corrected for multiple comparisons with an extent voxel threshold defined as 20 voxels. Only regions revealing significant differences between conditions were included. For each cluster, the region showing the maximum t-value was listed first, followed by the other regions in the cluster [in square brackets]. Montreal Neurological Institute (MNI) coordinates (x, y, z) of the peak and number of voxels (k) of clusters are also shown. H = hemisphere; R = right hemisphere; L = left hemisphere; BA = Brodmann area.**

**[HV-ALL > LV-ALL]**

y = 6          z = -18          z = -29

317

321   We began by contrasting the processing of Gabor orientation in low-variance to fixation

322   ([(LV-ALL > Fix] contrast), and observed recruitment of the superior parietal and the superior

323   frontal gyri in the left hemisphere. Similarly, the processing of Gabor orientation in high-

324   variance condition ([HV-ALL > Fix]) showed activation of the superior parts of the parietal

325   and frontal gyri in the left hemisphere, and supplementary involvement of the middle frontal

326   gyrus bilaterally. Direct comparisons of variance contents showed no significant results for

327   low-variance to high-variance ([LV-ALL > HV-ALL]). The opposite contrast ([HV-ALL >

328   LV-ALL]) elicited activations in the cerebellum, the inferior occipital gyrus and the middle

329   frontal gyrus in the left hemisphere.

330   Critically, the direct comparison of variance conditions related to the number of elements

331   showed significant results only for the contrast [HV-64 > LV-64] involving the recruitment of

332   the left middle frontal gyrus and the superior frontal gyrus bilaterally (mainly in the right

333   hemisphere; see Table 3 and Figure 7).

|  | | H | BA | k | x | y | z | t |
|---|---|---|---|---|---|---|---|---|
| fMRI contrasts | | | | | | | | |
| **[LV-4 > HV-4]** | *No significant activation* | | | | | | | |
| **[HV-4 > LV-4]** | *No significant activation* | | | | | | | |
| **[LV-64 > HV-64]** | *No significant activation* | | | | | | | |
| **[HV-64 > LV-64]** | Middle Frontal Gyrus | L | 8 | 93 | -37 | 11 | 40 | 7.43 |
| | Superior Frontal Gyrus | R | 8 | 33 | 6 | 31 | 50 | 6.89 |
| **[LV-4 > HV-64]** | *No significant activation* | | | | | | | |
| **[HV-64 > LV-4]** | *No significant activation* | | | | | | | |
| **[LV-64 > HV-4]** | *No significant activation* | | | | | | | |
| **[HV-4 > LV-64]** | *No significant activation* | | | | | | | |

334 **Table 3. Cerebral regions exhibiting an effect for direct comparisons between variances conditions related**

335 **to the number of elements (low-variance with 4 elements: LV-4, high-variance with 4 elements: HV-4,**

336 **low-variance with 64 elements: LV-64 and high-variance with 64 elements: HV-64) related to fixation**

337 **(Fix). The statistical threshold for cluster was defined as *p*<0.05 FWE corrected for multiple comparisons**

338 **with an extent voxel threshold defined as 20 voxels. Only regions revealing significant differences between**

339 **conditions were included. Montreal Neurological Institute (MNI) coordinates (x, y, z) of the peak and**

340 **number of voxels (k) of clusters are also shown. H = hemisphere; R = right hemisphere; L = left**

341 **hemisphere; BA = Brodmann area.**

**[HV-64 > LV-64]**

x = -37          x = 6
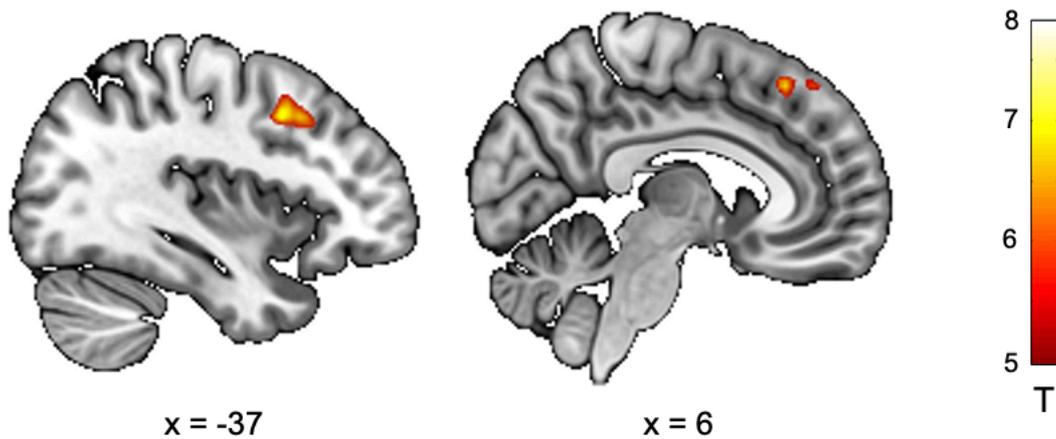
342

343 **Figure 7. Cerebral regions whose activity was elicited by the fMRI contrast [HV-64 > LV-64] projected**

344 **onto 2D slices (*p*<0.05 FWE-corrected at cluster level, k=20; LV = low-variance, HV = high-variance).**

345 *Effect of number of elements*. Direct comparisons of the number of elements irrespective to

346 the variance contents for Gabor orientations ([ALL-4 > ALL-64], and [ALL-64 > ALL-4]

347 showed no significant results. Results for the effect of the number of elements related to the

348 variance contents compared to the fixation condition are shown in supplementary information

349 section (SI-Table 1 and SI-Figure 1).

350 Results for the processing of variance contents related to the number of elements relative to

351 the fixation showed activation for high variance only for 4 Gabors and for both low- and high-

352 variances conditions for 64 Gabors. Precisely, these three contrasts ([HV-4 > Fix], [LV-64 >

353 Fix], and [HV-64 > Fixation], involved common cerebral structures with the left superior

354 parietal gyrus, the left middle and superior frontal gyri. In addition, the contrast [HV-4 > Fix]

355 elicited specific activation of the middle and superior frontal gyri in the right hemisphere

356 whereas the contrast [LV-64 > Fix] elicited activation located in the left supramarginal gyrus.

357 Finally, the contrast [HV-64 > Fix] showed significant results also on the left supramarginal

358 gyrus and the right middle occipital gyrus.

20

# Discussion

The reaction times around 1 second are consistent with a previous study (Bocheva et al., 2015) in which participants were also asked to respond as fast as possible (while being accurate). The fact that the reaction times in the current study did not vary with the variance across samples (i.e., between LV and HV) is consistent with the variance-invariant processing assumption: in low variance, imprecisions in sample estimates introduces variance across samples and the observer averages these estimates as they do in high variance. These results diverge from the ones of Bocheva and colleagues, who found reaction times longer with higher variance stimuli, but can be explained by the task difficulty. In Bocheva's study, the same signal strengths (i.e., mean of the a priori distribution) were used at all variances, but mean orientation discrimination thresholds were higher with higher variance, so the task was, on average, more difficult at higher variance (lower signal strength relative to the participants' thresholds). In the current study, all conditions were below thresholds as the mean of the a priori distribution was 0 (note that according to the equivalent noise paradigm, the correctness must be defined relative to the mean of the a priori distribution, not the actual mean of the stimulus). Thus, without a signal strength greater relative to threshold, we did not observe in the behavioral data a violation of the variance-invariant processing assumption, that is, that the same averaging processing operates independently of the source of the main variance (imprecisions in sample estimates or the stimulus). Conversely, the results regarding the response time suggests that the different reaction times observed at different levels of variance in a previous study was due to a confounding factor (i.e., task difficulty), not variance level per se.

The fMRI data showed that low- and high-variance elicited neural activations within common brain regions including the superior parietal and frontal gyri in the left hemisphere. These cortical regions are known to be involved in calculation tasks (Fehr, Code, & Herrmann, 2007; Rickard et al., 2000; Rosenberg-Lee, Chang, Young, Wu, & Menon, 2011) and particularly in

384   the left hemisphere (Arsalidou & Taylor, 2011). Critically, our parietal cluster in the left

385   hemisphere (x = -35, y = -42, z = 53) appeared to be very close to the brain coordinate located

386   in the horizontal segment of the intraparietal sulcus (x = -37, y = -48, z = 49) reported by Andres

387   and colleagues (2011) and mainly involved on number magnitude processing (Dehaene, Piazza,

388   Pinel, & Cohen, 2003) or division operations (Andres et al., 2011). The similar activation of

389   brain areas typically related to arithmetic calculation and orientation averaging begs the

390   speculation of a calculation that is not specific to arithmetic. Further investigations are required

391   to investigate this speculative link.

392   Although no behavioral differences were observed between averaging in low and high variance,

393   and similar brain areas were activated, some differences in neural activity amplitude were

394   observed. The right superior frontal and left middle frontal gyri were significantly more

395   activated when the variance in the orientation of the Gabors was high than when it was low.

396   The direct comparison between high and low variance conditions also elicited an unexpected

397   cerebral activity overlapping the cerebellum (Crus I) and the inferior occipital gyrus in the left

398   hemisphere. Andres and colleagues (2011) reported a similar cluster for arithmetic operation

399   (multiplication and subtraction), but in the right hemisphere. Conversely, no cortical area

400   showed significantly more neural activation in the low variance conditions compared with the

401   high variance conditions. Thus, more neural activity was observed when estimating the mean

402   orientation of a high-variance ensemble compared to estimating the mean orientation of a low-

403   variance ensemble.

404   The additional activation that occurred in high variance relative to low variance appears to be

405   mainly driven by the 64-Gabor condition and not by the 4-Gabor condition. These results are

406   surprising to us. As mentioned in the introduction, based on a previous psychophysical study

407   (Allard & Cavanagh, 2011), we could expect voluntary averaging (i.e., 4-Gabor) to occur when

408   the elements are dissimilar (i.e., high variance), but not when they appear identical (i.e., low

409 variance) because observers may not bother averaging samples that appear identical.

410 Interestingly, however, additional activation in the right superior frontal and left middle frontal

411 gyri was observed in high variance relative to low variance for involuntary averaging (i.e., 64-

412 Gabor condition). This result was less expected, but has more impact given that most studies

413 on ensemble statistics focus on large ensembles (e.g., 64) rather than small ensembles as in

414 voluntary averaging.

415 The current finding showing additional activation in the left middle frontal gyrus with 64

416 samples in high variance relative to low variance is consistent with the hypothesis that some

417 of this additional processing is related to averaging calculation. Indeed, the middle frontal

418 gyrus from both hemispheres has been found to be involved in mental calculations involving

419 working memory, especially for complex tasks (Arsalidou & Taylor, 2011). Similarly,

420 bilateral involvement of the frontal regions in both hemispheres for the fMRI contrast [HV-64

421 > LV-64] suggested that supplementary processing were needed during high variance

422 condition (Fehr et al., 2007). Consequently, the current findings with 64 elements to average,

423 are consistent with the hypothesis that more processing relevant to the averaging calculation

424 occurs when the main source of variance was due to physical variance across elements (i.e.,

425 high variance) than when the source of variance was due to imprecision estimates by the

426 visual system (i.e., low variance). Further studies are required to test this hypothesis.

427 It is also possible that the different activation is caused by different efforts by the observer

428 due to the apparent task difficult as the stimuli in low and high variance appear very different.

429 Some observers have reported that the task seemed more difficult when all the orientations

430 were close to vertical and others actually reported that the task was more difficult when the

431 orientations of the Gabors were dissimilar because it was more difficult to average. Thus, it is

432 possible that observers reduced their effort in low variance because they gave up more in low

433 variance (task appeared too difficult) or because they put more efforts in high variance as the

434    tasked appeared more difficult. If the observers modulated their effort based on the apparent

435    task difficulty and the effort level affects the averaging efficiency, then this would obviously

436    violate the variance-invariant processing assumption as different effective averaging

437    efficiencies would occur in low and high variance. In other words, using the equivalent noise

438    paradigm for an averaging task requires the assumption that the observer's averaging efforts

439    are not modulated by the apparent task difficulty that may differ between low and high

440    variance.

441    Note that we are not assuming that the task difficulty is the same in low and high variance; it

442    is the typical equivalent noise paradigm that relies on the assumption that the task difficulty is

443    the same in these two conditions. In high variance, the samples are all vertically oriented

444    (mean of the a priori distribution) and some orientation noise-jitter (variance of the a priori

445    distribution) is added to each sample. In absence of stimulus variance, the samples are all

446    vertically oriented and some orientation noise-jitter (due to imprecision in sample estimates

447    by the visual system, i.e., internal noise) is added to each sample. Thus, the effective stimulus

448    (i.e., samples after the internal noise is added) is supposed to be equivalent according to the

449    assumption underlying the equivalent noise paradigm (see the noise-invariant processing

450    assumption, Allard & Cavanagh, 2011, 2012; and the contrast-invariant calculation

451    assumption Pelli, 1990): samples are vertically oriented and some orientation noise-jitter is

452    added. Consequently, according to the equivalent noise paradigm, the task difficulty is

453    assumed *not* to differ between low and high variance when the a priori distribution is centered

454    on vertical. If the task difficulty differed between low and high variance conditions, then this

455    would undermine the use of the equivalent noise paradigm. In sum, the equivalent noise

456    paradigm requires to assume that the task difficult in low and high variance did not differ and

457    that observers put the same level of effort in low and high variance.

Nevertheless, it is possible that the effective averaging efficiency was the same in low and high variance despite the fact that there was more neural activity in high variance. The additional neural activity in brains areas related to arithmetic calculation may not be related to the averaging process. For instance, orientation uniformity in low variance could lead to greater suppression/inhibition in early visual areas and thus reduced activity is fed forward to later visual areas, or higher variance could lead to richer accidental contour structure activating later form-selective areas more effectively, or higher variance may produce more attentionally engaging accidental stimuli solicitating more task-unrelated attention. If the additional neural activity in high noise is not caused by the averaging calculation per se and it does not affect indirectly the averaging process (e.g., through lateral inhibition between processes or competing attentional resources), then it would be justified to assume that the same effective averaging efficiency operates in low and high variance. On the other hand, if the additional neural activity reflects more processing related to the involuntary averaging computation, or if it reflects different efforts do to apparent task difficulty, or if it causes some other process to indirectly affect the averaging computation, then it would undermine the assumption that the effective averaging efficiency is the same in low and high variance. Further studies are required to determine if this additional neural activity affects directly or indirectly the effective averaging efficiency.

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## Open Practices Statement

The datasets generated during and/or analysed during the current study are available from the

corresponding author on reasonable request. The experiment was not preregistered.

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582

583 # Supplementary information

| | | H | BA | k | x | y | z | t |
|---|---|---|---|---|---|---|---|---|
| fMRI contrasts | | | | | | | | |
| **[LV-4 > Fix]** | *No significant activation* | | | | | | | |
| **[HV-4 > Fix]** | Superior Parietal Gyrus | L | 7 | 59 | -35 | -42 | 53 | 9.51 |
| | [Postcentral Gyrus] | | 1 | | -40 | -35 | 50 | 5.53 |
| | Middle Frontal Gyrus | L | 6 | 103 | -27 | 1 | 63 | 6.96 |
| | [Middle Frontal Gyrus] | | | | -25 | -5 | 53 | 6.36 |
| | [Superior Frontal Gyrus] | | | | -17 | -2 | 50 | 6.27 |
| **[LV-64 > Fix]** | Supramarginal Gyrus | L | 1 | 160 | -42 | -35 | 48 | 11.54 |
| | [Superior Parietal Gyrus] | | 7 | | -35 | -42 | 53 | 8.18 |
| | [Superior Parietal Gyrus] | | | | -20 | -60 | 58 | 5.85 |
| | Middle Frontal Gyrus | L | 6 | 52 | -32 | -2 | 58 | 6.28 |
| | | | | | -22 | -2 | 48 | 6.12 |
| **[HV-64 > Fix]** | Supramarginal Gyrus | L | 1 | 231 | -40 | -35 | 45 | 9.53 |
| | [Superior Parietal Gyrus] | | 7 | | -35 | -42 | 53 | 8.88 |
| | [Superior Parietal Gyrus] | | | | -22 | -55 | 48 | 7.08 |
| | Superior Frontal Gyrus | L | 6 | 145 | -20 | 1 | 50 | 8.04 |
| | [Middle Frontal Gyrus] | | | | -30 | -2 | 58 | 7.00 |
| | Middle Occipital Gyrus | R | 18 | 50 | 13 | -95 | 13 | 6.32 |
| | [Lingual Gyrus] | | 17 | | 16 | -87 | 0 | 5.58 |

584 **Table S1. Cerebral regions exhibiting an effect for the number of elements related to the variance contents**

585 **(low-variance with 4 elements: LV-4, high-variance with 4 elements: HV-4, low-variance with 64**

586 **elements: LV-64 and high-variance with 64 elements: HV-64) related to fixation (Fix). The statistical**

587 **threshold for cluster was defined as $p<0.05$ FWE corrected for multiple comparisons with an extent voxel**

588 **threshold defined as 20 voxels. Only regions revealing significant differences between conditions were**

589 **included. For each cluster, the region showing the maximum t-value was listed first, followed by the other**

590 **regions in the cluster [in square brackets]. Montreal Neurological Institute (MNI) coordinates (x, y, z) of**

591 the peak and number of voxels (k) of clusters are also shown. H = hemisphere; R = right hemisphere; L =

592 left hemisphere; BA = Brodmann area.

593
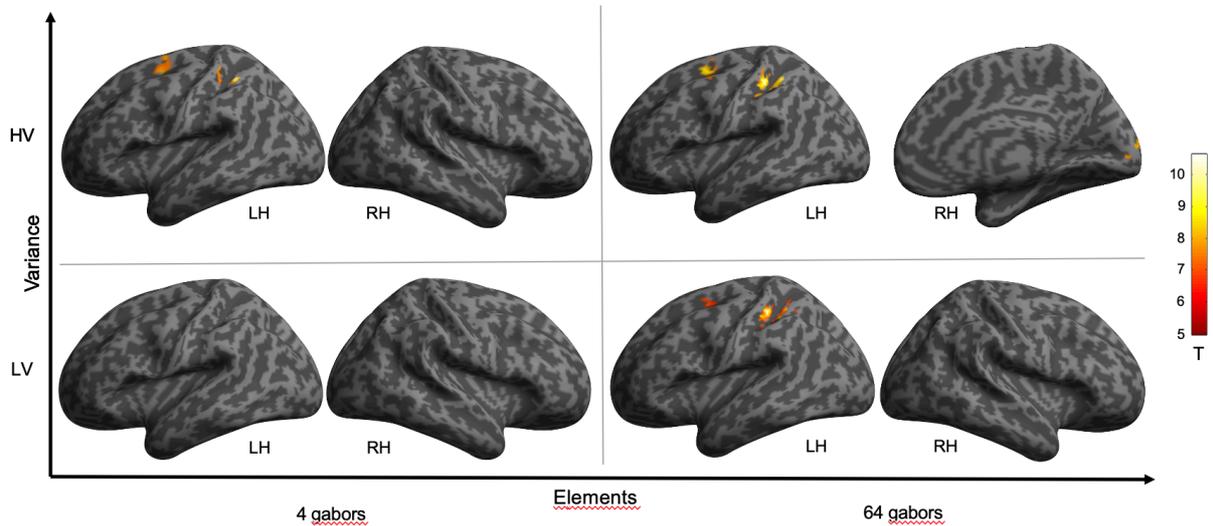


594

595 **Figure S1. Cerebral regions whose activity was elicited by the fMRI contrasts [LV-4 > Fix], [HV-4 > Fix],**

596 **[LV-64 > Fix] and [HV-64 > Fix] projected onto 3D anatomical templates (*p*<0.05 FWE-corrected at**

597 **cluster level, k=20 ; LV = low-variance, HV = high-variance, Fix = fixation LH = left hemisphere, RH =**

598 **right hemisphere).**