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2 **An inability to exclude visual noise in migraine.**

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5

**Running title:** Visual noise in migraine.

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## 1. Abstract:

**Purpose:** People with migraine are relatively poor at judging the direction of motion of coherently-moving signal-dots when interspersed with noise-dots drifting in random directions, a task known as motion coherence. Although this has been taken as evidence of impoverished *global* pooling of motion signals, it could also arise from unreliable coding of *local* direction (of each dot), or an inability to segment signal from noise (*noise-exclusion*). The aim of this study was to determine how these putative limits contribute to impoverished motion processing in migraine.

**Methods:** Twenty-two participants with migraine (mean age: 34.7±8.3 years; 16 female) and 22 age and sex matched controls (mean age: 34.4±6.2 years) performed a motion coherence task and a motion equivalent noise task, the latter quantifying *local* and *global* limits on motion processing. In addition, participants were tested on analogous equivalent noise paradigms involving judgements of orientation and size, so that the specificity of any findings (to visual dimension) could be ascertained.

**Results:** Participants with migraine exhibited higher motion coherence thresholds than controls ( $p=0.01$ , independent t-test). However, this difference could not be attributed to deficits in either local or global processing since they performed normally on all equivalent noise tasks ( $p>0.05$ , multivariate analyses of variance).

**Conclusions:** These findings indicate that motion perception in the participants with migraine was limited by an inability to exclude visual noise. We suggest that this is a defining characteristic of visual dysfunction in migraine, a theory that has the potential to integrate a wide range of findings in the literature.

42 **2. Introduction:**

43

44 Migraine is an episodic disorder characterised by throbbing (commonly unilateral)  
45 head pain, which may be accompanied by nausea, vomiting and an aversion to sound  
46 or light<sup>1</sup>. In approximately 30% of cases, a transient sensory and/or motor disturbance  
47 known as an aura is also experienced<sup>2</sup>. Certain visual stimuli can also trigger a  
48 migraine attack<sup>3</sup> and numerous studies have shown that individuals with migraine  
49 exhibit subtle differences in visual psychophysical performance, both ictally and  
50 interictally (see reviews<sup>4, 5</sup>). This is particularly the case for tasks involving  
51 judgements of visual motion<sup>6</sup>.

52

53 Processing of visual motion relies on at least two hierarchical processing stages. In the  
54 primary visual cortex (area V1), motion is processed *locally*, i.e. cells are sensitive to  
55 the direction of motion within a small region of space<sup>7</sup>. This information is then  
56 relayed to the medial temporal (MT) and medial superior temporal (MST) areas,  
57 where it is integrated to form a global motion percept<sup>8</sup>. People with migraine  
58 seemingly process *local* motion normally, since they perform as well as a control  
59 group when asked to discriminate or classify the direction of a stimulus containing a  
60 single direction of motion<sup>6, 9-11</sup>. However, people with migraine perform relatively  
61 poorly on motion coherence tasks where the participant must classify the direction of  
62 motion of a set of signal-dots moving coherently (in one direction) but interspersed  
63 with noise-dots drifting in random directions (Fig. 1A)<sup>6, 9, 10, 12-14</sup>.

64

65 Since the signal-direction in a coherence task cannot be determined from a single  
66 dot's trajectory, the participant must make a judgement of *global* motion direction. As  
67 a result, high motion coherence thresholds are often taken as evidence of a selective  
68 deficit in global motion pooling. However, motion coherence judgements can be  
69 limited not only by global integration, but also, by unreliable *local* processing<sup>15</sup>. This  
70 could be the case, for example, if higher cortical areas inherit input from V1 cells  
71 prone to high levels of random firing, i.e. elevated internal noise. A further limit on  
72 motion coherence performance is defined by an observer's ability to segregate *signal*  
73 from *noise* dot directions. Thus, computational models show that human observers  
74 perform much better on coherence tasks than would be expected if they used a pure  
75 pooling strategy<sup>15, 16</sup>, suggesting that they are capable of selectively monitoring  
76 directions of interest.

77

78 To try and disentangle these putative limits to motion processing we used a technique  
79 known as equivalent noise (EN) analysis. This psychophysical paradigm allows  
80 performance to be parcellated into *independent* estimates of local and global  
81 processing<sup>17</sup>. Similar to the motion coherence paradigm, EN analysis requires  
82 participants to classify the direction of motion of signal dots that are corrupted by  
83 noise<sup>15</sup>. However, in EN analysis, noise is added by manipulating the standard  
84 deviation of the distribution of directions presented, rather than adding noise dots that  
85 drift in random directions (Fig. 1B). As a result, every dot contributes to the signal,  
86 and the optimum strategy is to integrate *all* directions of motion in the stimulus.  
87 Consequently, an estimate of global processing is obtained that does not rely on the  
88 participants' ability to exclude noise. Further, by measuring performance in the

89 absence (as well as in the presence) of noise, an independent estimate of a  
90 participant's ability to process information locally is also available.

91

92 We sought to determine if motion processing in migraine is (a) limited by local  
93 processing, global processing and/or noise exclusion, and (b) part of a more general  
94 integration deficit. To this end, participants with and without migraine were tested on  
95 a series of matched psychophysical tasks. A motion coherence paradigm was used to  
96 assess each participant's ability to classify the direction of signal motion whilst  
97 excluding random noise. Independent estimates of local and global motion processing  
98 performance were obtained using a motion EN paradigm. Finally, to assess the  
99 specificity of any findings to motion processing participants undertook analagous EN  
100 tasks that probed local and global processing for judgements of orientation and size.

101

### 102 **3. Materials and Methods:**

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104 Ethics approval was granted by the University of East London Psychology Research  
105 Ethics Committee and the Department of Psychological Sciences Ethics Committee at  
106 Birkbeck College. Informed written consent was obtained from each participant in  
107 accordance with the declaration of Helsinki.

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#### 109 **Participants**

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111 Data were gathered from 22 participants with migraine (MG) and 22 migraine-free  
112 control participants (CON) (Table 1). The two groups were matched for sex (16

113 female) and did not differ significantly with respect to age [mean age: 34.7±8.3 (MG)  
114 and 34.4±6.2 years (CON);  $t_{(42)}=0.04, p=0.97$ ]. All participants with migraine fulfilled  
115 the International Headache Society (2004) diagnostic criteria for migraine without  
116 aura (MO) or migraine with visual aura (VA), and had been diagnosed previously by a  
117 general practitioner or neurologist. All participants had a minimum visual acuity of  
118 20/20 binocularly (with or without optometric correction). No participant had a  
119 history of mental illness and none were taking daily medication at the time of testing.

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### 121 **General procedure**

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123 The experiment lasted 60-75 minutes and consisted of: (i) a brief test of visual acuity  
124 (assessed using a hand-held LogMar near visual acuity chart); (ii) a customised  
125 questionnaire about basic demographics and migraine history; (iii) a motion  
126 coherence paradigm; (iv) three EN paradigms, which probed local and global  
127 processing for judgements of visual orientation, motion and size (separately).  
128 Individual EN and coherence tasks were blocked and presented in a random order to  
129 avoid sequence effects. All responses were given verbally and relayed to the computer  
130 by the experimenter.

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### 132 **Motion Coherence procedure**

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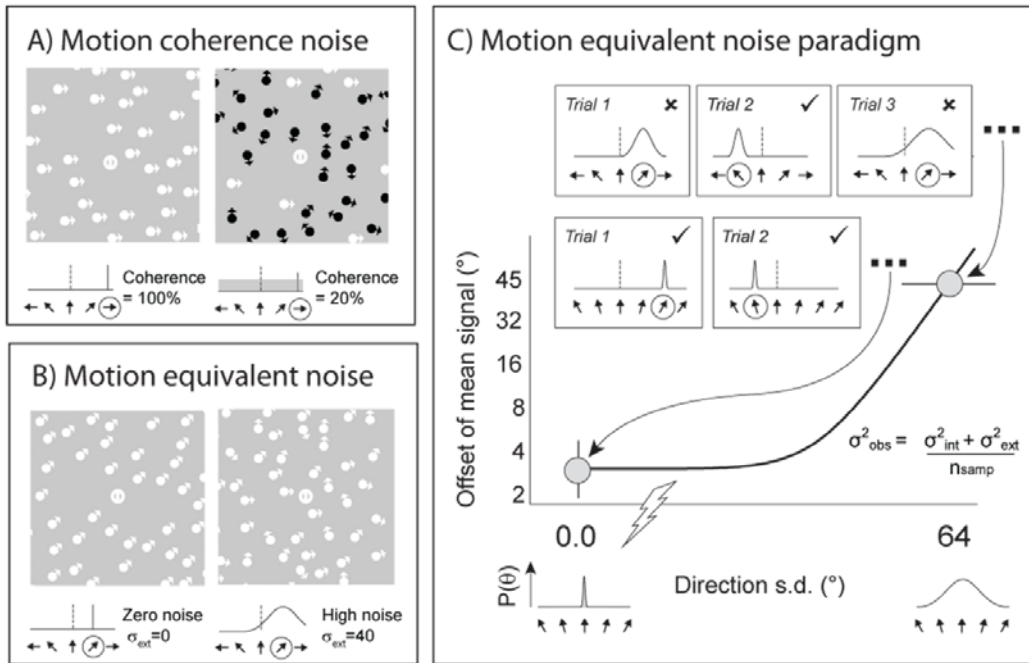
134 Participants classified the direction of motion of a number of coherently moving dots  
135 (the signal) embedded in noise. All signal dots were restricted to motion in the  
136 horizontal plane (all left or all right on any given trial). Noise was added to the

137 stimulus by assigning a subset of dots directions of motion that were randomly  
138 sampled from a flat distribution (Fig. 1A). Under the control of QUEST<sup>18</sup>, an adaptive  
139 staircase procedure manipulated the level of coherence on each trial, where coherence  
140 was defined as the percentage of dots that constituted the signal. The staircase  
141 converged on the level of coherence necessary for each participant to correctly  
142 ascertain the direction of motion on 82% of trials: the motion coherence threshold (see  
143 Supplementary Fig. 1A for further details). Lower coherence thresholds therefore  
144 reflected superior performance, indicating that the participant needed fewer signal  
145 dots to correctly identify the direction of signal motion. The staircase terminated after  
146 75 trials and was preceded by 15 practice trials.



147 **Table 1. Migraine group demographics and details of migraine history.** Details are provided for:  
 148 (1) Type (MO: migraine without aura; VA: migraine with visual aura); (2) Sex (F: female; M: male);  
 149 (3) Age; (4) Onset (age of migraine onset); (5) Freq 1 (number of migraine attacks experienced within  
 150 the last three months); (6) Freq 2 (number of migraine attacks experienced within the last year); (7)  
 151 Last (time, in weeks, since last migraine attack); (8) Duration (average duration, in hours, of a migraine  
 152 attack when painkillers are administered); (9) Severity (index of migraine severity, derived from the  
 153 multiplication of average migraine duration by the number of years migraine has been experienced).

Type	Sex	Age	Onset	Freq 1	Freq 2	Last	Duration	Severity
MO	F	21	13.5	1	3.5	8	60	144
MO	F	25	23	4	16	2	6.5	192
MO	F	38	16	4	20	1	24	384
MO	F	39	30	3.5	12	1	24	144
MO	F	40	5	6	24	2	48	517.5
MO	F	43	32	3	10	4	60	108
MO	M	23	16	2	6.5	4	24	32
MO	M	34	11.5	2	3	5	96	26.25
MO	M	38	28	3	10	3	4	22.5
MO	M	40	5.5	3	15	2.5	60	80
VA	F	21	10	3	12	2	6.5	100
VA	F	24	19	12	182	0.29	4.5	1536
VA	F	29	22	1	7.5	1.5	36	132
VA	F	30	14	3	12	3	6.5	440
VA	F	32	28	5	20	2	24	52.5
VA	F	33	10.5	0	1	30	24	840
VA	F	36	18	1.5	8	2	60	1575
VA	F	40	32	8	18	1	72	67.5
VA	F	44	28	5	24	1	10	45.5
VA	F	51	25	2	6.5	3	48	169
VA	M	38	6	12	48	0.29	12	110
VA	M	44	12.5	0	50	16	24	910
<b>Mean</b>		34.68	18.43	3.82	23.14	4.30	33.36	346.72
<b>Stdev</b>		8.25	8.81	3.26	37.65	6.66	25.89	463.62



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**Figure 1. Psychophysical procedures.** (A) Example high (100%) and low (20%) coherence motion stimuli. Signal dots are shown in white and noise dots in black. Directions of motion are indicated by the orientation of the arrow-heads. (Note: in the actual experiment all dots were white). Below each example stimulus is shown the corresponding distribution of signal values (solid black line) and noise values (dark grey shaded region). In the coherence task, noise was increased by changing the proportion of signal to noise dots. (B) Zero and high noise motion stimuli, with corresponding distributions of motion directions. In the equivalent noise task, noise was added by increasing the standard deviation of motion directions in the stimuli. In the plots of signal and noise distributions, the reference direction is denoted by a vertical black dotted line; the (average) direction of signal motion is circled. (C) The equivalent noise function (solid black line) is constrained by 2 data-points: the ‘zero noise’ threshold, which represents the minimum directional offset that can be reliably discriminated, and the ‘high noise’ threshold, which represents the maximum level of noise that can be tolerated for a large directional offset. The function has two parameters (inset in C), providing estimates of internal noise and global sampling (see Supplementary Material).

170 **Equivalent noise procedure**

171

172 A fast, efficient version of the EN paradigm, adapted for use with clinical populations,  
173 was used to assess local and global processing limits. In the EN tasks, participants  
174 judged whether a number of signal elements, presented for a brief duration were, on  
175 average, drifting clockwise or anti-clockwise of vertical-upward motion (motion task;  
176 Fig. 1B), tilted to the left or right of vertical (orientation task; Supplementary Fig.  
177 2A), or smaller or larger than a reference (size task; Supplementary Fig. 2B). The  
178 reference direction, orientation and size were defined by the fixation guide itself,  
179 which was comprised of a small white circle bisected by a vertical line (identical in all  
180 tasks).

181

182 Two independent staircases were randomly interleaved: a ‘zero noise’ and a ‘high  
183 noise’ condition (Fig. 1C). In the zero noise condition, external noise was set to zero  
184 and the staircase tracked the minimum orientation offset from vertical (orientation  
185 task), directional offset from vertical (motion task) or size offset from reference (size  
186 task) that could be reliably classified (Supplementary Fig. 1B). In the high noise  
187 condition, the staircase tracked the maximum level of external noise that could be  
188 tolerated for a large (fixed) signal offset (Supplementary Fig. 1C). In this condition,  
189 the signal level was fixed at  $\pm 22.5^\circ$  for the orientation,  $\pm 45^\circ$  for the motion and  $\pm 0.5$   
190 octaves for the size task. These values were selected on the basis of previous studies  
191 and pilot data<sup>15, 19, 20</sup>. Both staircases terminated after 75 trials each. As *per* the  
192 coherence task, the staircases were under the control of QUEST and converged on  
193 82% correct thresholds. For each participant and task a two-parameter EN function  
194 was fit to their data, providing estimates of internal noise (a measure of local

195 processing) and sampling (global processing). (See Fig. 1C and Supplementary  
196 Materials). To accustom participants to the nature of the task, all test blocks were  
197 preceded by 15 practice trials. In addition, for a subset of observers (10 participants  
198 with migraine and 8 without), 15 catch trials were randomly interleaved into each EN  
199 paradigm. On each catch trial the stimulus was presented at a large signal level in the  
200 absence of external noise ( $\pm 22.5^\circ$ ,  $\pm 45^\circ$  and  $\pm 0.5$  octaves for orientation, motion and  
201 size tasks).

202

### 203 **Stimulus parameters**

204

205 All stimuli were generated in Matlab (MathWorks, Cambridge, MA) using the  
206 Psychophysics Toolbox extensions<sup>21, 22</sup> and were presented on a MacBook Pro laptop  
207 computer that was connected to a luminance-calibrated LCD monitor at a spatial and  
208 temporal resolution of 1920x1080 pixels and 60Hz, respectively.

209

210 Test images were generated by randomly dropping 100 elements (disks) within a  
211 circular region with a diameter of  $15^\circ$ . For motion and size judgements, individual  
212 elements could overlap. In the motion task, overlapping elements led to occlusion. In  
213 the size task, the contrasts of overlapping elements were summed. For the orientation  
214 task, element overlap was avoided by ensuring that adjacent elements were separated  
215 by a minimum distance equal to twice their diameter. The resulting images were  
216 presented in the centre of the screen for 400 milliseconds against a background grey  
217 display. Stimuli were viewed in a dark room from a distance of 51 cm. The fixation  
218 guide had a diameter of  $0.44^\circ$ .

219

220 For the orientation task, individual disks were comprised of random phase sine-wave  
221 gratings with a spatial frequency of 3.4 cycles per degree presented at 50% contrast in  
222 a circular hard-edged mask with a diameter of  $0.44^\circ$  (Supplementary Fig. 1A). For the  
223 size task individual disks had the same characteristics as for orientation, but varied in  
224 size and were randomly oriented (Supplementary Fig. 1B). The spatial frequency of  
225 the grating was scaled to the diameter of the disk such that the number of cycles  
226 presented remained constant across changes in size. In addition, for the size task, the  
227 contrast of individual disks was randomly jittered in the range of 25-75% (sampled  
228 from a flat distribution) in order to minimise the availability of contrast cues. For the  
229 motion tasks, white dots with a diameter of  $0.44^\circ$  were used instead of windowed  
230 gratings (Fig. 1B). Individual dots had a lifetime of 300ms, were spatially updated  
231 every 50ms, moved at  $3^\circ/\text{sec}$  and were presented at 50% contrast.

232

### 233 **Data transformation and filtration**

234

235 All variables, with the exception of age and age of migraine onset, were log  
236 transformed as this typically reduced skew and kurtosis. Following this  
237 transformation, the distribution of variables did not differ significantly from normal  
238 ( $p_s > 0.05$ ; one-sample Kolmogorov-Smirnoff tests). Data were then filtered  
239 (separately for CON, MO and VA groups) so that extreme outliers with respect to  
240 parameter estimates and associated confidence intervals ( $> 2.58$  Z-scores from the  
241 group mean) were excluded from analysis. This led to the exclusion of 5.42% of the  
242 data, which represented outliers that were seemingly randomly distributed across the  
243 different groups [migraine (1.75%); control (3.67%)], tasks [motion coherence

244 (0.87%); motion EN (1.05%); orientation EN (1.22%); size EN (2.27%)] and  
245 individual participants.

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## 247 **4. Results**

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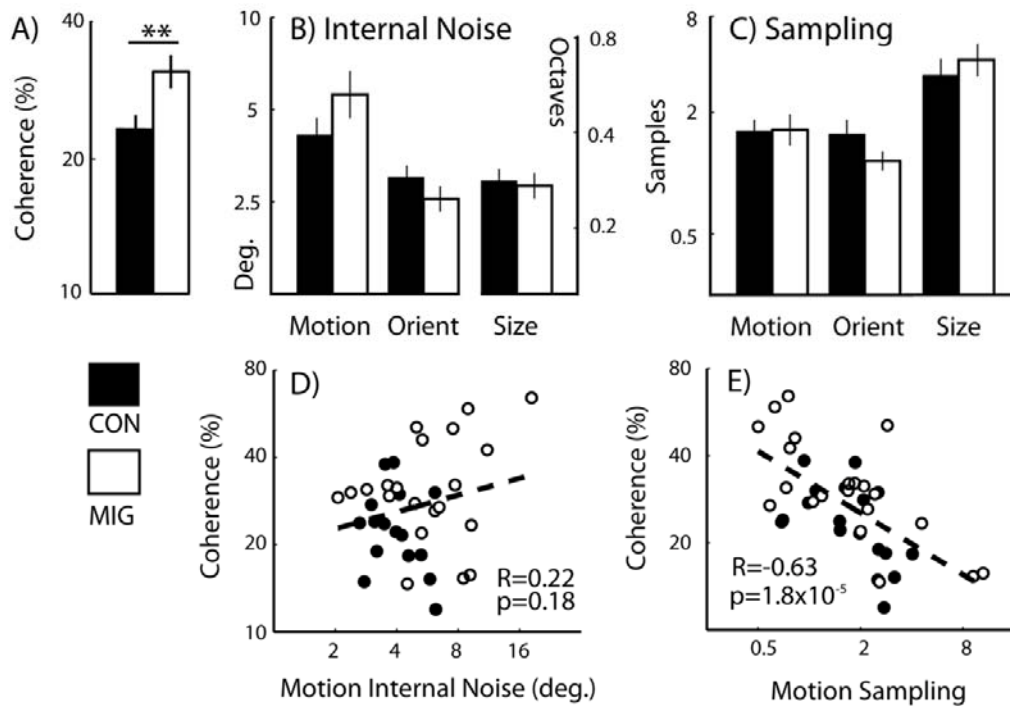
249 None of the variables of interest differed significantly between migraine sub-groups  
250 (MO and VA) (independent t-tests,  $p>0.05$ ); consequently, MO and VA data were  
251 pooled for all subsequent analyses. The percentage of catch trials answered correctly  
252 was at ceiling, and did not differ between groups or across tasks (ANOVA,  $p>0.05$ ).

253

### 254 **Motion coherence thresholds**

255

256 To determine whether performance on the motion coherence task differed between  
257 migraine and control groups (Fig. 2A), coherence thresholds were analysed using an  
258 independent t-test (Table 2). A one-tailed test was employed since there are multiple  
259 reports of elevated coherence thresholds in migraine (see Introduction). Motion  
260 coherence thresholds were elevated in the migraine group ( $32\pm 3.3\%$ ) relative to the  
261 control group ( $24\pm 1.8\%$ ) ( $t_{(37)}=-2.37$ ,  $p=0.01$ , Cohen's  $d=0.78$ ), requiring a higher  
262 proportion of signal to noise dots to reliably classify the direction of signal motion.



264

265 **Figure 2. Coherence and equivalent noise plots.** Group mean (A) coherence thresholds, (B) levels of  
 266 internal noise and (C) sampling are shown for control and migraine participants. Scatter-plots show  
 267 correlations between motion coherence thresholds and (D) motion internal noise and (E) motion  
 268 sampling. Error bars denote the standard error of the mean. Deg. = degrees. Note: data have been log-  
 269 transformed; however, for ease of interpretation, axis tick-marks denote equivalent untransformed  
 270 values.

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**Table 2. Comparing group performance on motion coherence and equivalent noise tasks.** Migraine and control group performance were compared using independent t-tests. Appropriate corrections were made to the degrees of freedom (d.f.) where equal variances could not be assumed. *P* values reported are for two-tailed tests, with the exception of the analysis of motion coherence thresholds, for which a single-tailed test was used (corrected alpha=0.1) (see text for further details). Bonferroni corrections were made for three multiple comparisons in the analysis of equivalent noise measures, reflecting the three different visual dimensions tested (corrected alpha=0.0167). *t*=t-statistic; d.f.=degrees of freedom; *p*=significance level; Cohen's *d*=effect size; *Th*=motion coherence threshold;  $\sigma_{int}$ =internal noise;  $n_{samp}$ =sampling. \*significant effect at the stated alpha level.

		<b>t</b>	<b>d.f.</b>	<b><i>p</i></b>	<b>Cohen's <i>d</i></b>
<b>Coherence</b>	<b>Th</b>	-2.37	37	*0.01	0.78
<b>Motion</b>	$\sigma_{int}$	-2.33	33.02	0.03	0.71
	$n_{samp}$	-0.04	41	0.97	0.02
<b>Orientation</b>	$\sigma_{int}$	1.21	41	0.23	0.38
	$n_{samp}$	1.82	32.56	0.08	0.59
<b>Size</b>	$\sigma_{int}$	0.22	39	0.83	0.07
	$n_{samp}$	-0.67	38	0.51	0.22

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**Table 3. Predicting motion coherence thresholds.** A regression analysis showing the prediction of motion coherence thresholds from variance in three predictor variables [motion internal noise, motion sampling and group (migraine or control)]. All variables were added to the model simultaneously (i.e. non-hierarchically). *Beta*=beta coefficient; *Beta<sub>st</sub>*=standardized beta coefficient; *t*=t-statistic; *p*=significance level;  $\sigma_{int}$ =internal noise;  $n_{samp}$ =sampling. \*predicts a significant proportion of unique variance in the outcome variable.

<b>Predictor</b>	<b>Beta</b>	<b>Beta<sub>st</sub></b>	<b>t</b>	<b><i>p</i></b>
Motion $\sigma_{int}$	0.15	0.17	1.34	0.19
Motion $n_{samp}$	-0.36	-0.63	-5.40	*5.2x10 <sup>-6</sup>
Group	0.1	0.28	2.20	*0.03

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292 **Internal noise and sampling**

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294 To determine whether there was a general trend for group differences in internal  
295 noise, a multivariate analyses of variance (MANOVA) was undertaken with one  
296 between-participants factor (group at 2 levels: migraine and control) and three  
297 dependent variables (orientation, motion and size internal noise) (Fig. 2B). This  
298 revealed no main effect of group for internal noise (Wilks'  $\lambda=0.85$ ,  $F_{(3,34)}=2$ ,  $p=0.14$ ,  
299 partial- $\eta^2=0.15$ ). A similar analysis revealed no effect of group on sampling (Wilks'  
300  $\lambda=0.86$ ,  $F_{(3,33)}=1.83$ ,  $p=0.16$ , partial- $\eta^2=0.14$ ; Fig. 2C).

301

302 To determine whether group differences existed on a subset of EN tasks, levels of  
303 internal noise and sampling were exposed to a series of *post hoc* independent t-tests  
304 comparing migraine and control group performances (Table 2). Since analyses were  
305 undertaken for all visual dimensions tested (orientation, motion and size), *Bonferroni*  
306 corrections were made for three multiple comparisons (corrected alpha level=0.0167).  
307 The analyses revealed no significant differences in levels of internal noise or sampling  
308 between migraine and control groups for any of the EN tasks.

## 309 **Predicting coherence thresholds from internal noise and sampling**

310

311 To determine how motion coherence thresholds related to EN performance, bi-variate  
312 correlations were undertaken (Fig. 2D&E). Motion sampling was found to be highly  
313 negatively correlated with motion coherence thresholds ( $R=-0.63$ ,  $p=1.8 \times 10^{-5}$ ).

314 Participants who were good at global pooling of information in the EN task needed  
315 fewer signals dots in the coherence task to correctly classify the direction of signal  
316 motion (Fig. 2E). In contrast, motion internal noise did not correlate with motion  
317 coherence thresholds ( $R=0.22$ ,  $p=0.18$ ; Fig. 2D).

318

319 Next, a regression analysis was undertaken. This tested the extent to which the three  
320 predictor variables [group (migraine or control), motion internal noise, motion  
321 sampling] predicted variance in motion coherence thresholds (the outcome variable)  
322 (Table 3). The resulting model was highly significant ( $F_{(3,34)}=13.3$ ,  $p=7 \times 10^{-6}$ ) and  
323 accounted for 54% of the variance in coherence thresholds ( $R=0.74$ ). Both group  
324 (6.6%) and motion sampling (39.44%) variables were found to predict a significant  
325 proportion of unique variance in coherence thresholds, whereas internal noise did not  
326 (2.4%). These findings indicate that even when differences in levels of internal noise  
327 and sampling were factored out, group membership (migraine vs. control) accounted  
328 for a significant proportion of variance in coherence thresholds.

329

330 Finally, none of the psychophysical measures recorded (coherence thresholds, internal  
331 noise or sampling) correlated with migraine characteristics (Supplementary Table 1).  
332 However, we note that the migraine characteristics included were based on self-report  
333 (e.g. migraine frequency, duration and severity), and hence, were highly subjective

334 and prone to recall bias. Nor do they capture the fact that the nature of participants'  
335 migraines may have changed with time.

336

## 337 **5. Discussion:**

338

339 In support of previous findings, motion coherence thresholds were elevated in the  
340 migraine group relative to the control group. However, this difference could not be  
341 attributed to deficits in either local or global processing. EN analysis generated  
342 statistically indistinguishable estimates of internal noise (local processing) and  
343 sampling (global processing) for migraine and control groups across all three  
344 judgements types (orientation, motion and size). Further, regression analysis indicated  
345 that group membership (migraine or control) predicted a significant proportion of the  
346 variance in coherence thresholds, even once levels of internal noise and sampling  
347 were controlled for. As discussed below, these findings are consistent with a relative  
348 inability to exclude visual noise in migraine.

349

350 The finding of elevated motion coherence thresholds in the migraine group is  
351 consistent with a number of previous reports. Whilst basic judgements of local  
352 position<sup>14</sup> and motion<sup>11</sup> do not differ between migraine and control groups, repeated  
353 studies have shown impaired performance on global form and global motion  
354 coherence tasks in which participants must detect global structure embedded in noise<sup>6,</sup>  
355 <sup>9, 10, 12-14</sup>. However, it has been argued that so-called 'global' coherence paradigms of  
356 this kind do not rely exclusively on global integration processes; instead, performance  
357 may also be limited by local processing, i.e. internal noise<sup>15</sup>, or the ability to exclude

358 external noise<sup>16</sup>. Consequently, EN analysis was undertaken so that independent  
359 estimates of local and global processing limits could be obtained.

360

361 The EN analysis undertaken here showed that levels of internal noise did not differ  
362 between migraine and control groups across any of the dimensions tested (orientation,  
363 motion or size). This is consistent with a number of previous studies. For example, a  
364 technique known as the N-pass method<sup>23-25</sup>, which measures the consistency in a  
365 participant's responses to sequential presentations of identical signal plus noise  
366 stimuli, has been used to estimate levels of internal noise in migraine<sup>26-28</sup>. The  
367 principle underlying the technique is that internal noise reflects the level of random  
368 firing in a cell population that is sensitive to the dimension of interest, e.g. the  
369 direction of motion. As a result, a participant that is characterised by high internal  
370 noise will show poor consistency in responses across sequential presentations, since  
371 intrinsic variability in cellular responses, which is independent of the stimulus, will  
372 limit performance and drive random responses. Studies using this technique have  
373 shown that for global motion<sup>28</sup> and two out of three global form tasks tested<sup>26-28</sup>,  
374 levels of internal noise in participants with migraine are indistinguishable from those  
375 of control participants.

376

377 The EN analyses undertaken here also indicated normal global integration in  
378 migraine: levels of sampling were indistinguishable from control participants' for  
379 judgements of orientation, motion and size. Although EN analysis has been applied to  
380 the study of migraine previously, it has not been used to characterise *visuospatial*  
381 performance; instead, previous studies have incorporated judgements of visual  
382 *contrast*. Thus, the findings are not directly comparable to our own: contrast EN

383 analysis is different from spatial and motion versions of the task, most pertinently,  
384 with respect to the nature of the external noise added to the stimulus<sup>29</sup>. Consequently,  
385 performance is captured by a more complex model that includes additional free  
386 parameters including a multiplicative noise term<sup>30,31</sup>. Nonetheless, two independent  
387 studies using contrast EN analysis have reported indistinguishable levels of sampling  
388 in participants with and without migraine<sup>27,32</sup>. Further, they showed that levels of  
389 additive internal noise (equivalent to the local noise parameter in the EN model used  
390 here) also did not differ between groups. This suggests that the findings we report (i.e.  
391 normal local and global processing in migraine) may extend to other (non-spatial)  
392 visual dimensions.

393

394 Taken together with previous studies, the data reported here can be reconciled with a  
395 simple model of visual processing in migraine that posits normal local and global  
396 processing, coupled with a low tolerance to external noise. Thus, performance is  
397 seemingly unaffected on tasks that only require integration of the signal (e.g. spatial  
398 and motion EN tasks), but is impaired on judgements that first require segregation of  
399 the signal from noise (e.g. form and motion coherence tasks). It is noteworthy that a  
400 selective deficit in the mechanisms of external noise exclusion has previously been  
401 demonstrated in another clinical group characterised by visuo-cortical dysfunction<sup>16</sup>.  
402 Thus, in amblyopia, performance is reportedly normal on *EN* tasks that involve  
403 judgements of global form<sup>33,34</sup> and motion<sup>35</sup>, but impaired on related form  
404 coherence<sup>36</sup> and motion coherence tasks<sup>37-40</sup>. Although speculative, the similarity in  
405 the pattern of these findings in migraine and amblyopia, coupled with their widely  
406 differing aetiologies, raises the possibility that the mechanisms involved in external

407 noise exclusion are particularly vulnerable following cortical damage or cortical  
408 reorganisation.

409

410 A number of cortical models of migraine have already been suggested in the  
411 literature. The majority of these are based on the notion of abnormal levels of cortical  
412 excitation<sup>4,41</sup>, i.e. *hypo*-excitability (reduced neural activity), or more commonly,  
413 *hyper*-excitability (elevated neural activity) relative to healthy controls (see review<sup>5</sup>).  
414 Thus, strengthened excitatory connections<sup>42,43</sup>, impaired mechanisms of inhibition<sup>44</sup>,  
415 <sup>45</sup> and abnormal pre-activation levels<sup>46</sup> have all been posited in migraine. However,  
416 these models are often poorly specified, such that precise behavioural predictions  
417 cannot be made on their basis. For example, hyper-excitability could imply elevated  
418 levels of stimulus-driven (i.e. spiking) activity, a specific elevation in base-line firing  
419 rates, or else a *generalised* increase in activity, all of which would lead to different  
420 predicted effects on the signal-to-noise ratio, and hence, visual psychophysical  
421 performance<sup>5</sup>.

422

423 With respect to the current study, the data reported are clearly inconsistent with  
424 versions of both the *hyper*- and *hypo*-excitability models that posit an abnormal level  
425 of base-line firing rates, since these would predict an elevation or reduction  
426 (respectively) in internal noise. Instead, we report normal levels of internal noise in  
427 migraine across all three visual dimensions tested (coupled with a selective elevation  
428 in motion coherence thresholds). An alternative version of the *hyper*-excitability  
429 model, which *is* broadly consistent with these data, is one in which stimulus-driven  
430 (spiking) activity is elevated, whilst base-line firing-rates are unaffected. Let us  
431 assume that a predominant direction of motion is selected by the observer once a

432 threshold firing-rate is exceeded within a population of appropriately-tuned direction-  
433 sensitive neurones: if a single direction of motion is presented, hyper-excitability will  
434 increase the likelihood that activity associated with the target direction will reach  
435 threshold, and hence be reported. However, for a noisy (e.g. motion coherence)  
436 stimulus, a state of hyper-excitability will *also* increase the probability that activity  
437 driven by the noise will reach threshold, and hence compete with representations of  
438 the signal.

439

440 Consistent with this model of (stimulus-driven) cortical *hyper*-excitability, Antal et  
441 al.<sup>9</sup> demonstrated *superior* motion discrimination performance in migraine (relative to  
442 controls) for a stimulus comprised of a single direction of motion (100% coherence),  
443 coupled with impoverished (relative) performance once the coherence of the stimulus  
444 was decreased (i.e. noise was increased). In an earlier study, Antal et al.<sup>47</sup> showed that  
445 a similar dissociation could also be induced in healthy control participants: following  
446 an experimental reduction in the excitability of cortical area MT, the discrimination of  
447 intermediate coherence motion was enhanced, whilst the discrimination of 100%  
448 coherent motion was impaired. Although we did not find *superior* classification  
449 performance in migraine for a stimulus comprised of a single direction of motion  
450 (remember that these trials were interleaved with a high noise staircase in the EN task,  
451 potentially making the task harder), we *did* find a *selective* impairment in the  
452 processing of a noisy (motion coherence) stimulus. Taken together, these data suggest  
453 that a dissociation in the processing of motion coherence stimuli and stimuli  
454 comprised of a single direction of motion (as reported) *may* be a signature of cortical  
455 (stimulus-driven) hyper-excitability.

456

457 In conclusion, the findings reported here are inconsistent with local or global  
458 processing deficits in migraine, but instead, implicate impaired mechanisms of visual  
459 noise exclusion. This hypothesis has the potential to integrate a wide range of findings  
460 from the existing literature and open up novel avenues for investigation. Specifically,  
461 it predicts that relative to control participants, people with migraine will be impaired  
462 on any visual discrimination or detection task for which signal and external noise  
463 must be segregated prior to an integration stage, provided that sufficient external  
464 noise is added to the stimulus. Future studies should focus on the mechanisms  
465 involved in visual noise exclusion, since little is known about this process. One  
466 possibility that has been raised is that impaired noise exclusion reflects a state of  
467 (stimulus-driven) cortical hyper-excitability, which increases competition between  
468 representations of the signal and the noise. An alternative possibility, which is equally  
469 speculative however, is that representations of the noise compete with the signal to a  
470 greater extent in migraine because of a failure in endogenous attentional control, i.e.  
471 an inability to selectively monitor channels of interest that are most likely to carry the  
472 signal<sup>48,49</sup>. To begin to tease these possibilities apart, it is clear that sophisticated  
473 psychophysical techniques must be employed in conjunction with clearly specified  
474 models of cortical function, so that highly specific predictions can be tested. We  
475 believe that the efficient version of the EN paradigm, which can be adapted to test  
476 across multiple sensory dimensions *and modalities*, represents an invaluable tool in  
477 this approach.

478

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- 605

## Supplementary Material

606

607

608 *Equivalent noise analysis*

609

610 The standard equivalent noise (EN) function is of the form:

611

$$\sigma_{obs} = \frac{\sigma_{int} + \sigma_{ext}}{n_{samp}} \quad (1)$$

613

614 where (for motion)  $\sigma_{obs}$  is the participant's offset threshold (i.e. the smallest  
615 directional offset from vertical that can be reliably classified),  $\sigma_{int}$  is the participant's  
616 additive internal noise,  $\sigma_{ext}$  the external noise in the stimulus, and  $n_{samp}$  the effective  
617 number of samples that the participant pools to determine the average direction of  
618 motion.

619

620 The traditional method of EN analysis constrains (1) by measuring offset thresholds at  
621 multiple levels of external noise, typically 6 or more, thereby requiring several  
622 thousand trials. However, the novel, rapid method use here, provides reliable  
623 estimates of internal noise and sampling in fewer than 100 trials. This rapid EN  
624 approach constrains the EN function with just two data-points / staircases (Fig. 1C).  
625 The first ('zero noise' condition) involves a manipulation of the signal direction  
626 across trials in the absence of noise, such that a basic offset threshold is estimated;  
627 this constrains the fit along the ordinate axis. The second ('high noise') condition  
628 relies on an inverse manipulation: the mean of the signal is fixed at a high level whilst

629 the level of external noise is manipulated across trials, such that the maximum level of  
630 noise that can be tolerated for a given performance level is estimated. This constrains  
631 the fit of the model in the orthogonal dimension (along the abscissa), and avoids  
632 sampling uninformative regions of the curve.

633

#### 634 *Correction for stimulus wrapping*

635

636 For circular dimensions, i.e. orientation and motion, the stimulus wraps (at  $\pi$  for  
637 orientation and  $2\pi$  for motion). Thus, an orientation of  $0^\circ$  is the same as an orientation  
638 of  $180^\circ$ , whilst a direction of  $0^\circ$  is equivalent to one of  $360^\circ$ . Consequently, the  
639 standard deviation of a distribution that is sampled to generate noise underestimates  
640 the actual variance presented at high noise levels, such that the equivalent noise model  
641 predicts lower thresholds in this area of the curve than are actually recorded<sup>15</sup>. To  
642 overcome this issue we ran Monte Carlo simulations of a model observer's  
643 performance across a range of internal noise and sampling levels. These indicated that  
644 an observer's sampling level ( $n_{\text{samp}}$ ) is a function of their high noise threshold [i.e. the  
645 maximum level of noise that can be tolerated (MTN)] and can be captured by the  
646 following equation:

$$647 \quad n_{\text{samp}} = \exp (A\text{MTN}^2 + B\text{MTN} + C) \quad (2)$$

648

649 where best fits are obtained with values for A, B and C of 0.0001, 0.0329 and -1.903  
650 for motion, 0.0006, 0.0681 and -1.95 for orientation, and -0.4228, 2.797 and -1.241  
651 for size judgements, respectively. Note that these values are specific to a defined  
652 threshold performance level (82% here). This simple association between MTN and

653 sampling holds true because at high levels of external noise the effect of internal noise  
654 is negligible.

655

656 Once an estimate of sampling has been derived from the MTN, internal noise can be  
657 calculated from the 'zero noise' threshold. Thus, when  $\sigma_{\text{ext}}=0$ , by re-arranging  
658 equation (1):

659

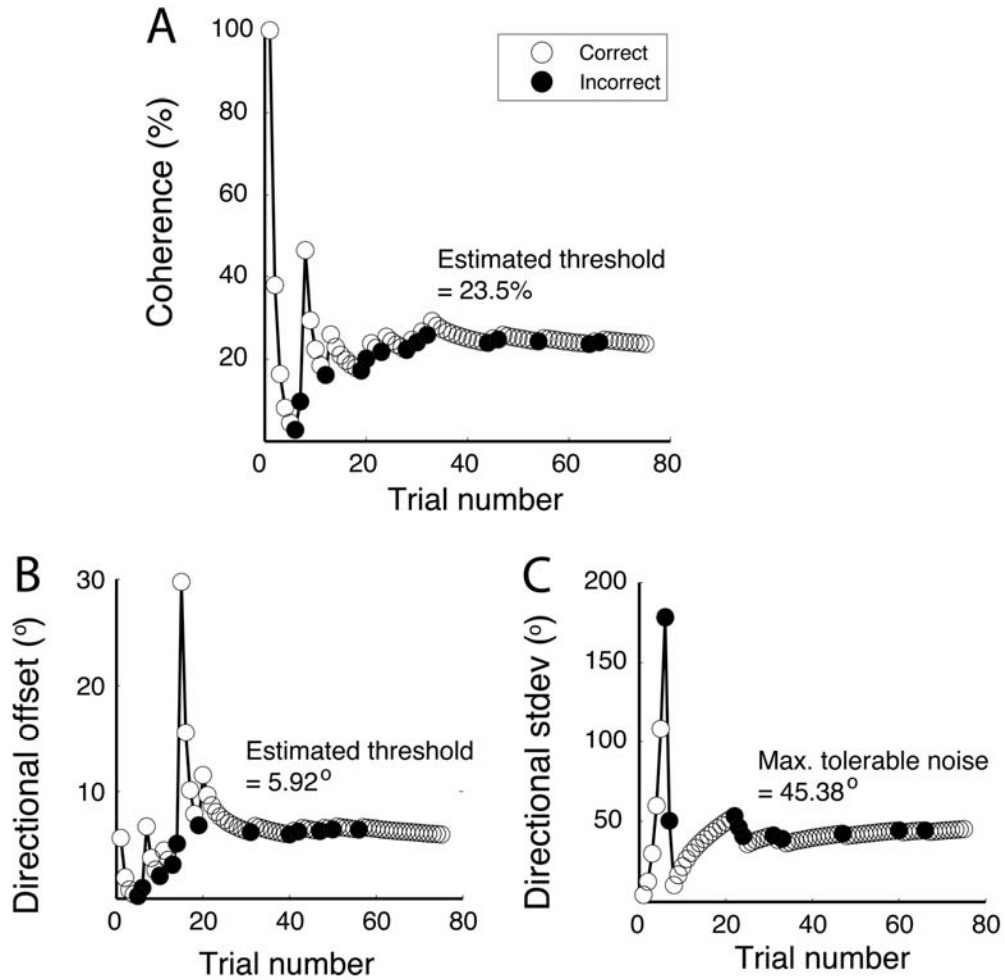
660 
$$\sigma_{\text{int}}^2 = \sigma_{\text{obs}}^2 n_{\text{samp}} \quad (3)$$

661

662

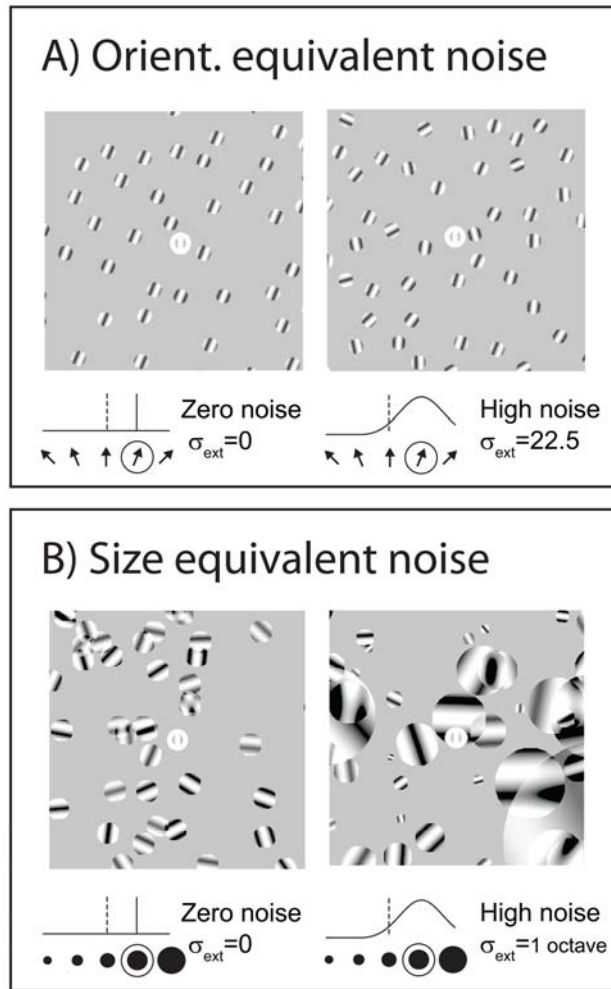
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**Supplementary Figure 1.** Example staircases. Example staircases are shown for one participant's data for the (A) motion coherence task, (B) motion equivalent noise task (zero noise condition) and (C) motion equivalent noise task (high noise condition). Under the control of QUEST, the stimulus level was set (on each trial) to the most probable Bayesian estimate of the underlying threshold - in this case, the 82% correct threshold.



672

673 **Supplementary Figure 2.** Orientation and size equivalent noise tasks. Example stimuli are shown for  
 674 (A) orientation and (B) size equivalent noise tasks with zero noise conditions and high noise conditions  
 675 on the left and right, respectively. Underneath each is shown the corresponding distribution of  
 676 directions or sizes present in the stimulus. The reference orientation / size is denoted by a vertical black  
 677 dotted line; the average signal orientation / size is circled.  
 678

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**Supplementary Table 1. Correlations between psychophysical measures and migraine characteristics.** Pearson's correlation coefficients (R) and associated significance levels (*p*) are reported. Th=motion coherence threshold;  $\sigma_{\text{int}}$ =internal noise;  $n_{\text{samp}}$ =sampling.

			Age	Onset	Freq1	Freq2	Last	Duration	Severity
<b>Coherence</b>	<b>Th</b>	<b>R</b>	-0.06	0.36	-0.19	-0.17	-0.02	-0.13	-0.31
		<b><i>p</i></b>	0.74	0.11	0.45	0.46	0.93	0.57	0.18
<b>Orientation</b>	$\sigma_{\text{int}}$	<b>R</b>	-0.19	0.37	-0.11	-0.14	0.17	-0.09	-0.28
		<b><i>p</i></b>	0.23	0.09	0.63	0.54	0.45	0.67	0.20
	$n_{\text{samp}}$	<b>R</b>	-0.07	-0.04	-0.28	-0.14	0.13	-0.06	0.01
		<b><i>p</i></b>	0.66	0.86	0.25	0.56	0.56	0.78	0.96
<b>Motion</b>	$\sigma_{\text{int}}$	<b>R</b>	0.08	0.00	0.12	0.15	-0.08	0.33	0.24
		<b><i>p</i></b>	0.63	0.99	0.60	0.49	0.71	0.13	0.29
	$n_{\text{samp}}$	<b>R</b>	0.09	-0.30	0.28	0.21	0.04	-0.12	0.32
		<b><i>p</i></b>	0.57	0.18	0.24	0.35	0.87	0.58	0.15
<b>Size</b>	$\sigma_{\text{int}}$	<b>R</b>	-0.17	-0.06	-0.17	-0.20	0.37	-0.37	-0.12
		<b><i>p</i></b>	0.30	0.79	0.49	0.38	0.09	0.10	0.60
	$n_{\text{samp}}$	<b>R</b>	-0.14	-0.03	-0.05	-0.11	0.22	-0.18	-0.05
		<b><i>p</i></b>	0.40	0.91	0.84	0.65	0.36	0.46	0.84