

1 **Sensorimotor mechanisms selective to numerosity: evidence from** 2 **individual differences**

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14 number system

15

16 **Abstract**

17 We have previously shown that after few seconds of adaptation by finger-tapping, the
18 perceived numerosity of spatial arrays and temporal sequences of visual objects displayed
19 near the tapping region is increased or decreased, implying the existence of a *sensorimotor*
20 *numerosity system* (Anobile et al., 2016). To date, this mechanism has been evidenced only
21 by adaptation. Here we extend our finding by leveraging on a well-established covariance
22 technique, used to unveil and characterize “channels” for basic visual features such as colour,
23 motion, contrast, and spatial frequency. Participants were required to press rapidly a key a
24 specific number of times, without counting. We then correlated the precision of reproduction
25 for various target number presses between participants. The results showed high positive
26 correlations for nearby target numbers, scaling down with numerical distance, implying
27 tuning selectivity. Factor analysis identified two factors, one for low and the other for higher
28 numbers. Principal component analysis revealed two bell-shaped covariance channels,
29 peaking at different numerical values. Two control experiments ruled out the role of non-
30 numerical strategies based on tapping frequency and response duration. These results
31 reinforce our previous reports based on adaptation, and further suggest the existence of at

32 least two sensorimotor number channels responsible for translating symbolic numbers into
33 action sequences.

34

35 **Introduction**

36 Humans share with many animals a primitive non-verbal number system encoding the
37 number of objects in space and events in time (Dehaene, 2011). The capacity to estimate
38 number rapidly but imperfectly is thought to be a primary perceptual attribute, often termed
39 the *number sense* (Burr & Ross, 2008). The past few decades have accumulated much
40 evidence for the existence of the number sense. Many studies show that the sense of number
41 is truly general, transcending space and time, as well as modality and format (Arrighi et al.,
42 2014; Burr et al., 2018; Togoli et al., 2021). More recently, numerosity has been shown to
43 interact strongly with action, leading to the idea of a *sensorimotor number system*,
44 incorporating action, and its interaction with sensory systems (Anobile et al., 2016, 2021).

45 Both physiological and psychophysical studies support the existence of a sensorimotor
46 number system. Adaptation studies provide strong evidence: participants first tap
47 continuously with their index finger for a few seconds, either rapidly or slowly, then estimate
48 the numerosity of a dot array presented near the adapted region: adaptation to fast tapping
49 causes underestimation and slow tapping overestimation (Anobile et al., 2016, 2020;
50 Maldonado Moscoso et al., 2020). Motor adaptation induces similar effects on sequential
51 visual and auditory stimuli (Anobile et al., 2016; Togoli et al., 2020), consistent with the
52 existence of a generalized system linking motor and sensory signals to encode numerosity
53 (Anobile et al., 2021; Burr et al., 2021).

54 Electrophysiological studies in primates also point to the existence of a specific neural
55 substrate for counting a small set of actions. In a seminal paper Sawamura et al. (2002)
56 trained monkeys to repetitively make five identical movements, then switch to a different
57 movement, in a cyclical fashion: neurons in the posterior parietal cortex showed selectivity to
58 the number of self-generated actions, whatever the action. Kirshhock and Nieder (2022)
59 trained crows to peck a specific number of times (1 to 5). Neurons in the telencephalon were
60 shown to be tuned to the impending number of self-generated actions, during the phase
61 between the disappearance of the target to the onset of motor reproduction. The activity of
62 these neurons predicted the behavioural performance and was independent of both stimulus
63 format (dots or digits) and of the temporal characteristics of the motor responses. Each tuning

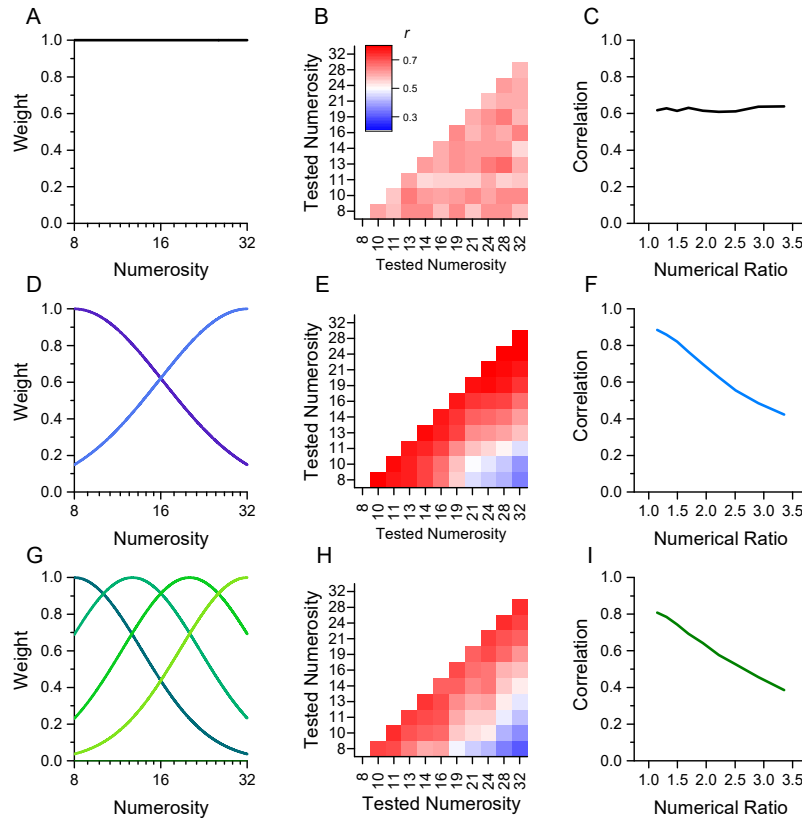
64 function peaked at a given preferred numerosity, with activity scaling down with numerical
65 distance. Overall, these cells in the crow brain could constitute the neural substrate
66 subserving the transformation of sensory inputs into a given quantity of numerical actions,
67 possibly a similar mechanism to that driving the motor number adaptation effects in humans
68 (Anobile et al., 2016).

69 Although motor adaptation has revealed a clear link between action and numerosity
70 perception, this is the only technique used so far to investigate the interaction in humans. The
71 aim of the current study is therefore to expand and generalize our previous findings, using a
72 different psychophysical technique that exploits individual differences in reproduction
73 precision (Peterzell & Kennedy, 2016). This technique has been widely used to reveal visual
74 channels for motion (Morrone et al., 1999), spatial frequency (Reynaud & Hess, 2017;
75 Simpson & McFadden, 2005), contrast sensitivity (Peterzell et al., 1995; Peterzell & Teller,
76 1996), color (Peterzell et al., 2000; Peterzell & Teller, 2000) and duration (Rammsayer &
77 Troche, 2014).

78 The rationale behind this technique is that performance measures of stimuli detected by the
79 same mechanism should correlate more between individuals than stimuli detected by
80 different mechanisms. Figure 1 illustrates the technique by simulation of results in a
81 numerosity reproduction task if the task were mediated for 1, 2 or 4 numerosity-selective
82 channels. It assumes intrinsic variability in reproduction precision across participants,
83 perturbed by additive random noise. The top row simulates results if reproduction of all
84 numerosities were governed by a single mechanism, rather than a range of numerosity-tuned
85 mechanisms. The correlation matrix for all pairs of stimuli (Figure 1B) shows no systematic
86 pattern, only random variations in correlations due to the general noisiness of the channel.
87 Figure 1C plots the average correlation plotted as a function of numerosity ratio, showing no
88 dependence on number ratio. Increasing or decreasing the added noise will change the
89 average correlation, but not create any dependency on numerosity ratio. However, if there
90 exist mechanisms selective for numerosity, the results are quite different. Assuming just two
91 mechanisms tuned to low and high numbers (Figure 1D) yields a correlation matrix with
92 higher correlations between similar numbers (near the diagonal) than dissimilar numbers.
93 This leads to the clear dependency on numerosity ratio shown in Figure 1E. Similarly, for a
94 range of numerosity-selective mechanisms like the four shown in Figure 1G, there will be a
95 strong dependency on numerical distance (Figure 1I). The cases of two and four channels are
96 difficult to distinguish if the amount of added noise is free to vary. Techniques such as cluster

97 analysis and principal component analysis (PCA) can be also applied to study further the
98 tuning of the channels.

99



100

101 **Figure 1.** Simulation of behaviour with 1, 2 or 4 channels mediating numerosity judgments.
102 A: 1-channel model shown as a flat tuning function. (B) Predicted correlation matrix between
103 all pairs of numerosities. There is no systematic variability, only random variations induced
104 by the noise. (C) Average correlation as function of numerical ratio of dot pairs, showing no
105 dependency. (D) 2-channel model centred at numerosities 8 and 32, with full bandwidth of
106 1.45 octaves. (E) Correlation matrix, showing higher correlations near the identity line. (F)
107 Correlation as function of numerical ratio, showing a systematic falloff with numerical ratio.
108 (G-I) Same as D-F for a 4-channel model with channels equally spaced in the range between
109 8 and 32 with full bandwidth of 1.10 octaves.

110

111 Here we applied the interindividual covariance technique to study sensorimotor tuning in
112 humans, using a number matching task similar to that used by Kirschhock & Nieder (2022).
113 We measured the precision with which 30 participants could press a key a given number of
114 times (8-32) without counting, and then correlated performance across all pairs of numbers
115 (like the simulation of Figure 1). The results clearly demonstrate the existence of

116 sensorimotor mechanisms converting symbolic numbers into actions, with correlations
117 decreasing with numerical distance, like Figures 1F & I.

118

119 **Methods**

120 *Participants*

121 An a priori power analysis for a correlation test (r) with a medium effect size of $r^2 = 0.5$, and
122 $\alpha=0.05$ (one tailed, as positive correlations are expected) and power of 0.9 indicated a
123 required sample size of 28 participants. 30 participants took part in the fast-tapping condition
124 (age: average= 25.75, SD=4.5, min=18, max=39) and 29 in the slow tapping condition (age:
125 average= 25.43, SD=4.04, min=18, max=39). Of these, 18 completed both conditions. The
126 experimental procedures were approved by the local ethics committee (*Commissione per*
127 *l'Etica della Ricerca*, University of Florence, July 7, 2020, n. 111). The research was in
128 accordance with the Declaration of Helsinki and informed consent were obtained from all
129 participants prior to the experiment.

130

131 *Stimuli and procedures*

132 Stimuli were generated and presented with PsychToolbox routines for Matlab (ver. R2021a).
133 Stimuli were white visual digit numbers (8, 10, 11, 13, 14, 16, 19, 21, 24, 28, 32) presented in
134 the centre of a grey screen (iMac Retina display 27-inch) for 1 s and subtending 5° of visual
135 angle. Soon after the disappearance of the target digit, participants were asked to repeatedly
136 press a key as many times the target. In separate sessions, participants were asked to tap as
137 fast as they could or at a comfortable rate. Participants were all right-handed and performed
138 the tapping's with their right hand on a spacebar positioned about 30 cm to the right of the
139 monitor, to guarantee a comfortable arm position. Following previous studies (Cordes et al.,
140 2001; Whalen et al., 1999), serial counting was prevented by vocal suppression, repeating
141 aloud the syllable 'ba' (as fast as possible). For each participant, each target number was
142 presented from 25 to 30 times (for a total of 17183 trials: 8259 and 8924 trials in the fast and
143 slow tapping conditions), in separate blocks (usually 5) interspaced by pauses of a few
144 minutes. For those participants who completed both the fast and slow tapping condition, the
145 two were measured on different days (on average within 3-4 days). Each condition took about
146 1.5 hours of testing (3 hours for those who completed both). Before the experiment,

147 participants were familiarized with the task performing one single block of trials with
148 feedback (a digit displaying the number of tappings performed). In this phase 11 trials were
149 presented, one for each tested number (randomly selected trial by trial). No feedback was
150 provided during the rest of the experiment.

151

152 *Control duration task*

153 A randomly selected sub-sample of 9 participants from the slow tapping condition was
154 engaged in a duration control task. On each trial, a tone (500 Hz, ramped on and off with 20
155 ms raised-cosine ramps) was played through headphones, and participants asked to reproduce
156 its duration by repeatedly tapping on a key while pronouncing the syllable 'ba' as fast as
157 possible (to suppress counting). The between average tapping frequency rate in the number
158 task was 3.1 Hz (SD 1.1 Hz) and 3.5 Hz (SD 1.3 Hz) in the duration task ($t_{(8)}=1.03$, $p= 0.33$).
159 Target durations were customised for each participant to perfectly match those previously
160 produced in the number task: for each target number tested in the number matching task, we
161 extracted the average response duration (across trials) and these eleven durations were re-
162 presented as duration targets (Table 1). Before the experiment, participants were familiarized
163 with the task by performing one single block of trials with feedback (2 numbers, one
164 displaying the target duration and the second displaying the reproduced duration, in seconds).
165 In this phase 11 trials were presented, one for each tested duration (randomly selected trial by
166 trial). No feedbacks were provided during the rest of the experiment. As for the number task,
167 for each participant, each duration was presented from 25 to 30 times (for a total of 2455
168 trials), in separate blocks.

169

S1	S2	S3	S4	S5	S6	S7	S8	S9
3	4.1	7.3	3.5	2.2	5	2.4	2.6	2.3
4	6.3	9.2	4.9	3.8	6.3	3.3	2.8	2.9
4.4	7	10.5	5.4	4.2	6.5	3.5	3	3.2
5.1	7.9	11.3	6.2	5	8.3	4.2	3.8	4
5.7	9.3	12.5	7	5.4	8.6	4.3	4	4.4
6.8	10	15.3	8.2	6	9.5	5.4	4.4	5

7.8	11.7	17	9.9	6.9	11.5	6.4	5.3	5.8
8.8	13.7	17.4	10.6	7	13.2	7.4	5.7	6
10.2	15.8	21	12.2	8.6	15.3	8.1	6	7.4
12	17.8	23.3	13.3	9.2	17.7	9.6	7.2	8.8
12.9	21.7	29.2	16	10.8	20.6	11.1	8.2	9.4

170

171

172 *Data analyses*

173 All the analyses were performed with Matlab software (ver. R2021a) with the exception of
174 the repeated measures ANOVA comparing Weber fractions for the number and duration task
175 and the t-test comparing frequency rates for the number and duration task (performed with
176 JASP software, ver. 0.16.3).

177

178 *Data processing*

179 As a first step we detected and eliminated outlier responses. For each experimental condition,
180 and separately for each participant and stimulus intensity, responses were converted into
181 z-scores and eliminated from the analyses if falling above or below 3 STD. In the number
182 matching task, this procedure resulted in the elimination of 0.5% of the trials in the fast-
183 tapping condition and 0.6% in the slow tapping condition. In the control duration task, the
184 same procedure led to the elimination of 0.4% trials in the duration matching condition and
185 0.6% in the number matching condition.

186 As a second step we measured responses accuracy and precision, on non-standardized data.
187 For each task, and separately for each participant and stimulus intensity (numbers or
188 durations), accuracy was indexed as the mean reproduction value across trials and precision
189 as Weber fraction, computed as responses standard deviation divided by the average
190 reproduction.

191

192 *Correlation matrices and numerical distance*

193 As a third step we computed correlation matrices between (non-standardized) Weber
194 fractions using Pearson correlation coefficients and analyses the correlation strength as a
195 function of numerical distance. This last analysis (Figure 2, panels B&D) was performed on

196 binned data. Bins were created to have an approximately equal number of observations for
197 each bin (13, 13, 14, 15). For each target, the numerical distance was calculated as the base
198 ten logarithm ratio between itself and the remaining target numbers. The correlation
199 coefficients between Weber fractions were then averaged within the following numerical
200 distance bins (log10 ratios): <0.08; 0.08–0.14; 0.14–0.21; 0.21–0.29, 0.29–0.39, >0.39).

201 As a sanity check, this analysis was also performed on randomized correlation matrices. For
202 this analysis we applied a bootstrap approach. On each of 10000 iterations, separately for
203 each subject, the Weber fractions were randomized between numerosities and a new
204 correlation matrix computed. Then (as before) the correlation coefficients were averaged
205 within the reported bins. The results of this analysis are reported in Figure 3 (panels B&D) as
206 the “random” curve.

207

208 *Hierarchical clustering and Principal component analysis*

209 The hierarchical clustering was performed on normalised (z-scores) Weber fractions using
210 the linkage method. The distances were calculated with the Euclidean metric and the “ward”
211 algorithm was used to compute the distance between clusters. The number of clusters was
212 determined by the inconsistency index (computed by the build in *inconsistent* function in
213 Matlab 2021a) and results reported as a dendrogram. As for the PCA, to check the validity of
214 this analysis, we tested it with randomized correlation matrices, with a bootstrap approach.
215 On each of 10,000 iterations, separately for each participant, the Weber fractions were
216 randomized between numerosities, and a new clustering was computed. Then at each
217 iteration we looked at the structure of the clusters, counting the time on which the clusters
218 (separately for the fast and slow tapping conditions) contained contiguous numbers (as in
219 Figure 4 A&B).

220 The principal component analysis was performed on normalised (z-scores) and centred
221 Weber fractions and factors rotated with the non-orthogonal promax method (but orthogonal
222 varimax provides similar results). The number of components was determined as those
223 exceeding an eigenvalue of 1 and from visual inspection of the scree plots.

224

225 *Modelling*

226 As a preliminary analysis, we modelled the behaviour of a system with 1, 2 or 4 channels,
227 assuming that each channel would process stimuli with a gaussian tuning (like the illustration
228 of Figure 1). The 1-channel model had infinitely broad tuning, and the tuning of the 2- and 4-
229 channel models was allowed to vary between 0.5 and 2 octaves. The peak of the tuning was
230 equally spaced in log coordinates to be 8 and 32 for the 2-channel model and 8, 12.7, 20.1
231 and 32 for the 4-channel model. The behaviour for numerosities handled by more than one
232 channel was determined by a weighted average of the various channels. The average WF of
233 the channels taken from the actual dataset (i.e. 0.176 for the slow and fast tapping) however
234 the specific values for each observers could vary following a gaussian distribution whose
235 standard deviation was varied to achieve best fit. We then calculated predicted correlations
236 simulating 25 repetitions for each numerosity and observer. Without any noise correlations
237 between the same channel would approximate 1. Hence to achieve reasonable levels of
238 correlation we assumed that the actual measured WF was corrupted by some noise which we
239 manipulated to mimic the average correlation between observed in the actual experiment.
240 Correlation matrices were obtained by simulating 1000 experiments with cohorts of 29-30
241 observers to yield the best fit (R^2).

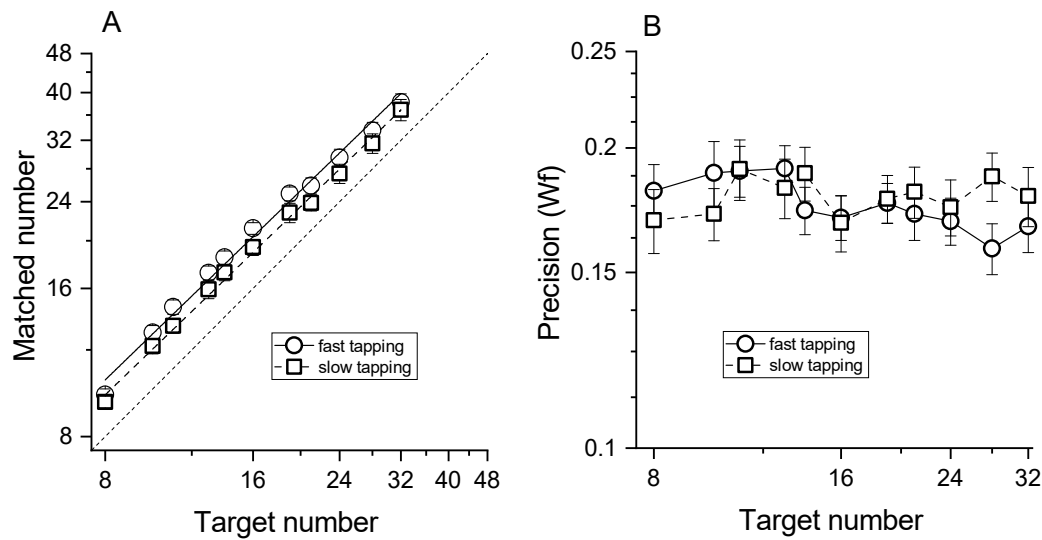
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243 **Results**

244 Participants pressed a key a specific number of times (visually displayed as a digit) while
245 repeatedly pronouncing the syllable 'ba' as fast as possible, to prevent counting. To gauge the
246 generalizability across different motor actions, in separate sessions, participants were
247 required to tap concurrently as fast as they could (fast tapping) or at a comfortable rate (slow
248 tapping).

249 As expected, the rate of tapping was higher in the fast tapping (average= 6.8 Hz, SD = 1)
250 compared with the slow tapping condition (average = 3.3 Hz, SD = 1.6). In both conditions
251 participants were able to correctly perform the numerical matching task, with average number
252 of reproduced actions scaling linearly with visual targets (both $r = 0.99$, Figure 2A). Figure 2
253 B shows precision (Weber fractions, Wfs) in matching target and reproduced numerosity as a
254 function of target number. Average Wfs (across target number) in the fast and slow
255 conditions were virtually identical (average= 0.17, SD= 0.01 and average= 0.17, SD= 0.007
256 for fast and slow tapping respectively) and within each condition, Wfs were roughly constant
257 across targets, following Weber's Law.

258



259

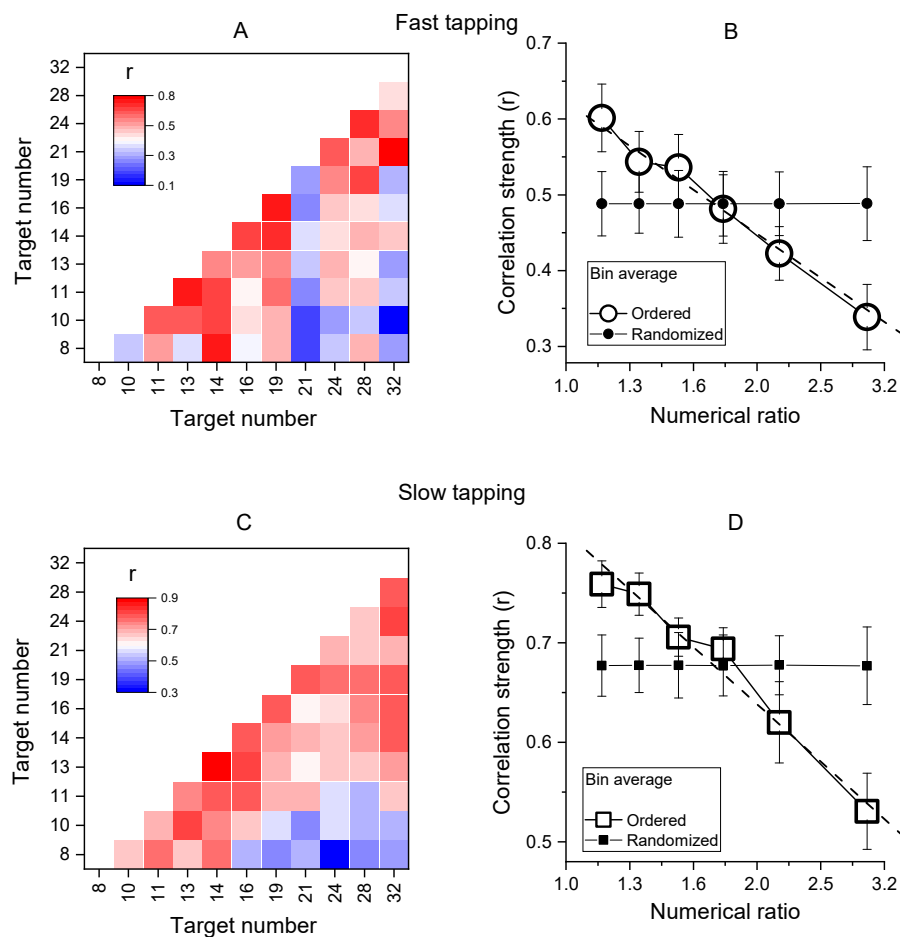
260 **Figure 2.** Matched number (A) and Weber Fractions (B) as a function of target number,
261 separated for the fast (circles) and slow (squares) tapping conditions. Lines through the data
262 in panel A show best linear fits. Error bars are ± 1 s.e.m., across participants.

263

264 We then computed the correlations between Wfs between participants, for all targets values.
265 Figures 3 A&C show correlation matrices across all participants (like the simulations of
266 Figure 1), with each cell representing the Pearson correlation coefficient between the two
267 target numbers. The correlations were all positive, ranging from 0.1 to 0.75 in the fast
268 condition and 0.3 to 0.88 in the slow condition. Importantly, the correlations were clearly not
269 randomly distributed, but most of the higher correlations (reddish) lie near the diagonal,
270 indicating that the motor matching performance was more similar for neighbouring numbers,
271 compared to higher numerical distance.

272 Figure 3 B&D show average correlation coefficients between participants, averaged into six
273 bins as a function of numerical distance. There is a systematic decreasing trend in both fast
274 and slow tapping conditions (linear fit on unbinned data shown by dashed lines in Figure 3
275 B&D: slopes= -0.58 ± 0.11 , -0.57 ± 0.07 for fast and slow respectively, both $p < 0.001$),
276 clearly different to that predicted by a random pattern of matching precision levels (curves
277 with filled symbols in Figure 3 B&D, see methods). Overall, these analyses confirm that the
278 degree of performance similarity was systematically modulated by the numerical difference
279 between targets, in line with the existence of underlying tuning functions.

280 As a preliminary analysis we modelled the data with simulations like that of Figure 1,
281 assuming one, two or four numerosity-selective channels. The average WFs for the
282 participants was taken from the data, and channel width, variability, and measurement noise
283 free parameters. The fits with a single channel were very poor, with $R^2 = 0.003$ and 0.002
284 (essentially no better than the mean) for the fast and slow tapping respectively. However, the
285 two-channel model gave much better fits, with $R^2 = 0.54$ and 0.29 . The four-channel model
286 had similarly good fits, with $R^2 = 0.52$ and 0.28 . The parameters to yield best fits seemed
287 reasonable, with channel width of 1.2 and 1.8 octaves, and channel variability between 0.051
288 and 0.106.



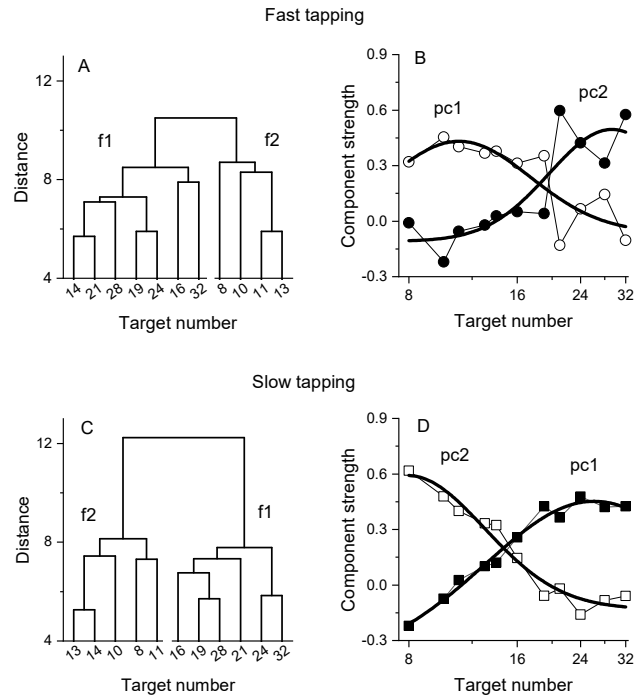
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290 **Figure 3.** Inter-participant correlations. A. Correlation matrices of Wfs for all pairs of target
291 numbers for the slow-tapping condition. B. Correlation strength as a function of numerical
292 ratio, for the slow-tapping condition. Small, filled symbols show bootstrapped average
293 correlation strengths of randomized Wfs matrices. Dashed lines are the best linear fit on
294 unbinned data and error bars are ± 1 s.e.m. C & D. Like A & B, for the fast-tapping condition.

295

296 We then investigated the structure underlying the number sensorimotor translation system
297 with a hierarchical clustering analysis (see methods for details). Figure 4 (A&C) shows the
298 resulting dendrograms. In both the fast and slow tapping conditions, the analyses returned a
299 two-cluster solution with one cluster aggregating low numbers (N8-13 and N8-14 in the fast
300 and slow conditions) and the other aggregating high numbers (N>13 and N>14 respectively).
301 This analysis corroborates the results obtained from the correlation analysis and add on this
302 suggests the existence (at least) of two channels dealing with relatively different numerical
303 targets. A control analysis on randomised data (see methods) yielded clusters containing
304 contiguous numbers only in 0.005% of cases (for both the fast and slow tapping conditions),
305 suggesting that the results with the original dataset likely represent a structure genuinely
306 organised as a function of the highest similarity between neighbouring numbers.

307 To study the tuning of these two hypothetical channels, we then performed a factor analysis
308 on Wfs. In both fast and slow tapping conditions, two factors emerged (see methods),
309 explaining a total of 68% and 81% of the total variance (for the fast and slow tapping
310 conditions respectively). Figure 4 shows the rotated component strength as a function of
311 target number. The results revealed two bell-shaped tuning functions for both fast (panel B)
312 and slow (panel D) tapping conditions, with factor strength distributions reasonably described
313 by logGaussian functions (fast tapping: $R^2 = 0.6$ and $R^2 = 0.65$; slow tapping: $R^2 = 0.97$, $R^2 =$
314 0.94 for 1st and 2nd components). In the fast-tapping condition, the first component peaked at
315 lower target numbers (N 11) and the second component at higher numbers (N 29). In the slow
316 motor condition, the first component peaked at higher target numbers (N 26) and the second
317 component at lower numbers (N 8).

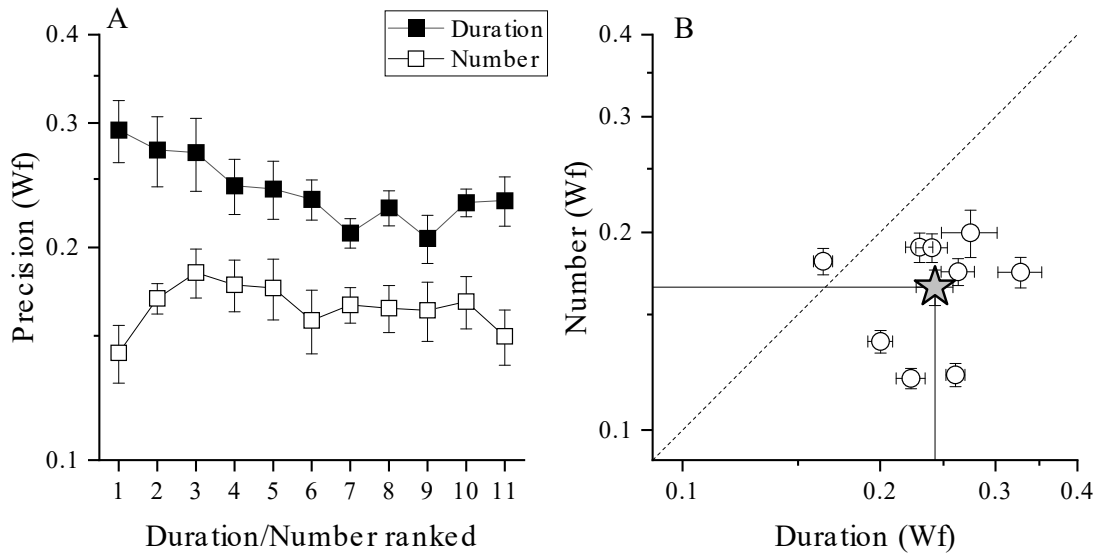


318

319 **Figure 4.** Dendrograms from hierarchical clustering on Wfs in the fast (A) and slow (C)
320 tapping conditions. Panels B and D show the strength of the first two principal components
321 from a PCA on the Wfs measured in the fast (B) and slow (D) tapping conditions. The
322 strength of these components is shown as a function of the different numerical target levels.
323 The smooth curves are logGaussian fits to the component strengths.

324

325 That fast and slow tapping conditions provided similar results despite the very different
326 tapping rates suggests that temporal frequency of the tapping did not play a major role.
327 However, as total response duration was positively correlated with target numbers ($r = 0.95$,
328 $r = 0.36$, for fast and slow tapping, both $p < 0.001$), participants might have used response
329 duration instead of number of taps as a stop criterion. To test this possibility, a sub-sample of
330 9 participants were given a control task to match the duration of a tone (see methods). If the
331 number task was performed through duration, this latter must have an equal or lower
332 precision level compared to that measured in the number task. Figure 5 A&B shows that this
333 was not the case with the precision level (Wfs) in the number task being clearly lower (higher
334 precision) than the duration task, making the use of duration strategies during the number
335 task unlikely (number: average=0.16, SD= 0.03; duration: average= 0.24, SD= 0.04). A RM
336 ANOVA with task (duration, number) and stimuli intensity (11 levels) confirmed the
337 difference ($F(1, 80) = 19.97$, $p = 0.002$).



338

339 **Figure 5.** A) Average (across participant) Weber fraction for the number (filled squares) and
340 duration (empty squares) matching tasks, as a function of ranked target stimulus (visual digits
341 for the number task, and the corresponding auditory tones durations for the duration task, see
342 methods for details). B) Individual Weber fractions for the number task plotted against those
343 for the duration task, averaged across stimulus intensity. The star symbol reports average
344 across participants. Error bars are ± 1 s.e.m.

345

346

347

348 Discussion

349 Using a motor reproduction task, we measured the precision with which number digits were
350 translated into sequences of actions. Replicating previous evidence from both human and
351 animal studies (Cordes et al., 2001; Kirschhock & Nieder, 2022; Whalen et al., 1999),
352 precision followed Weber's law, a well-established signature of the Approximate Number
353 System (Anobile et al., 2014; Dehaene, 2011; Feigenson et al., 2004; Ross, 2003). More
354 importantly, by looking at the covariance structure of the precision index (Weber fraction)
355 between participants, we found evidence for sensorimotor channels tuned to number.
356 Precision for reproducing numerically similar targets was positively correlated ($r \sim 0.8$) but for
357 larger numerical distances, correlations decreased ($r \sim 0.1$), suggesting the action of sensori-
358 motor channels sharing the encoding of neighbouring numbers. In line with this, cluster
359 analyses identified two main clusters, one aggregating low numbers (from 8 to ~ 13) and the
360 other higher numbers (from ~ 13 to 32), pointing to (at least) two mechanisms encoding low

361 and higher numbers. Finally, Principal Component Analyses on Weber fractions confirmed
362 this and went to describe two bell-shaped components, one peaking at relatively low numbers
363 (~10) and the second at higher numbers (~27).

364 The covariance technique used here has been widely employed to reveal visual channels in
365 several basic perceptual dimensions such as colour, motion, contrast and spatial frequency
366 (Morrone et al., 1999; Peterzell et al., 1995, 2000; Peterzell & Kennedy, 2016; Peterzell &
367 Teller, 1996, 2000; Rammsayer & Troche, 2014). The technique is based on the idea that
368 interindividual variability conveys information that can reveal common sensory processes
369 (Peterzell & Kennedy, 2016), as illustrated in Figure 0. In practice, this approach requires
370 multiple and densely sampled measurements of different stimuli intensity, in the same
371 sample. Regions of high intercorrelation between neighbouring stimuli intensity can be
372 interpreted to imply that sets of stimuli are processed by the same (shared) underlying
373 channel. This channel, while responding relatively more to its preferred stimulus, will also be
374 activated by neighbouring stimuli that although slightly different from the preferred intensity,
375 are nevertheless included in the same response distribution. Following this rationale,
376 relatively lower correlations among more distant stimuli would indicate that these are
377 processed by different, or at least partially independent, channels (Peterzell & Teller, 1996).
378 The results obtained in this study are in line with those predicted by this technique, implying
379 the existence of sensorimotor channels tuned to different numerical targets, with a rather
380 wide response distribution.

381 The results reinforce adaptation studies showing number-selective adaptation between actions
382 and perceived numerosity (Anobile et al., 2016; Maldonado Moscoso et al., 2020). Those
383 studies provided strong evidence for the existence of at least two (but possibly more)
384 sensorimotor mechanisms, tuned to high and low numbers. The results are also broadly in
385 line with recent evidence from animal physiology showing number selective sensorimotor
386 neurons in the crow brain, translating visual inputs (digits and dot arrays) into number of
387 pecks (Kirschhock & Nieder, 2022). While the crow study found as many channels as the
388 number tested (N1–5), we found evidence for only two channels (clusters and factors) over
389 the range of 8–32. However, it is important to note that PCA aims to summarize the dataset
390 with the minimal number of components (channels). We can therefore not exclude the
391 possible existence of more than two (perhaps not fully independent) channels. The results
392 should be not interpreted as evidence for only two sensorimotor channels, but rather as
393 evidence that tuned mechanisms exist in the human brain, with at least two different tunings.

394 This is also apparent from the simulations of Figure 1, showing that the predictions of two or
395 multiple channels are very similar, difficult to distinguish with the current technique. Indeed,
396 the fits to the data using two or four channels were very similar, but both almost infinitely
397 better than the one-channel fit.

398 The results reported here are unlikely to be contaminated by strategies capitalizing on
399 duration of motor responses and/or temporal frequency. Despite the very different tapping
400 rates in the slow (~3 Hz) and fast motor conditions (~7 Hz), the overall pattern of results
401 remained almost unchanged. The only difference was an inversion of the order of the
402 principal components and factors, with the first component peaking at lower numbers for the
403 fast-tapping condition and higher numbers for the slow tapping condition (and vice versa for
404 the second component). This result suggests that for fast actions lower number targets show
405 more variance than higher numbers, and vice versa for slower actions. Although we have no
406 definitive explanation for this pattern of results, it could arise from different effects of the
407 matching motor noise associated with different tapping rates across the number ranges. In
408 any event, the results showed two covariance channels for both conditions, similarly
409 distributed along the numerical targets, supporting the existence of at least two mechanisms,
410 one tuned to the lower numbers and one to the higher (at least within this numerical range).

411 Even if total duration of responses were positively correlated with target number, and
412 although participants were free to use duration as a viable stopping criterion, the exploitation
413 of this non-numerical strategy seems unlikely. In the control task, where participants
414 reproduced duration rather than number, clearly showed lower precision levels, making it
415 unlikely to account for the precision measured on motor numerosity reproduction. Once
416 again, these results are in line with previous studies showing lower sensitivities for motor
417 matching duration tasks compared with motor number matching tasks. The
418 electrophysiological study on crows also found similar neural response curves across very
419 different motor response timing conditions (Kirschhock & Nieder, 2022). In summary, the
420 results seem to suggest that the channels found here, like those in crows, reflect a genuine
421 number selective sensorimotor transformation processes.

422 What may be the adaptive value of this mechanism? The spontaneous use of the number of
423 actions in the animal kingdom is now well-established. For example, desert ants rely on the
424 number of steps to return to the nest (Wittlinger et al., 2006), some species of male frogs
425 match or exceed the chunks of competitors to attract female partner (Rose, 2017), and some
426 songbirds modulate the numbers of syllables in their calls to signal dangerousness of

427 predators (Suzuki, 2016; Templeton et al., 2005). In all cases, the use of number-related
428 motor strategies by animals has a clear ecological value for survival and species preservation.
429 This system may have been preserved in humans and repurposed for our species-specific
430 needs. Some hints come from the literature on the role of visual numerosity perception (dot
431 arrays). Although most animal species are capable of some form of numerosity estimation
432 (Butterworth, 2022), it appears that in humans numerosity estimation may act as a non-
433 symbolic precursor for the development of symbolic mathematical skills (Chen & Li, 2014;
434 Decarli et al., 2023; Halberda et al., 2008; Mazocco et al., 2011; Piazza, 2010; Piazza et al.,
435 2010; Schneider et al., 2017). The sensorimotor system could act as an early tool to
436 constantly update and calibrate motor and sensory systems for the encoding and active
437 manipulation of quantities and objects, with a potential impact on the quality of formal
438 mathematical skills in later development. In line with this idea, there are reports of a possible
439 co-occurrence of motor impairments in children with mathematical learning disorders such as
440 dyscalculia (Westendorp et al., 2011), and children with developmental coordination
441 disorders (which impair gross and fine motor function) perform poorly on math and
442 numerosity tasks (Gomez et al., 2015, 2017). This is in line with the suggestive idea proposed
443 by Walsh (2003) of a sensory magnitude system, encoding abstract quantities such as space,
444 time and number, to guide planning and execution of actions. It is also in line with more
445 recent proposal suggesting that the acquisition of number meaning is deeply grounded in
446 sensorimotor experiences (Ranzini et al., 2022; Sixtus et al., 2023).

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456 **References**

- 457 Anobile, G., Arrighi, R., Castaldi, E., & Burr, D. C. (2021). A Sensorimotor Numerosity
458 System. *Trends in Cognitive Sciences*, 25(1), 24–36.
459 <https://doi.org/10.1016/j.tics.2020.10.009>
- 460 Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation
461 for action and perception. *ELife*, 5, e16161. <https://doi.org/10.7554/eLife.16161>
- 462 Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate mechanisms for perception of
463 numerosity and density. *Psychological Science*, 25(1), 265–270.
464 <https://doi.org/10.1177/0956797613501520>
- 465 Anobile, G., Domenici, N., Togoli, I., Burr, D., & Arrighi, R. (2020). Distortions of visual
466 time induced by motor adaptation. *Journal of Experimental Psychology. General*,
467 149(7), 1333–1343. <https://doi.org/10.1037/xge0000709>
- 468 Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of*
469 *the Royal Society B: Biological Sciences*, 281(1797), 20141791.
470 <https://doi.org/10.1098/rspb.2014.1791>
- 471 Burr, D. C., Anobile, G., & Arrighi, R. (2018). Psychophysical evidence for the number
472 sense. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
473 373(1740), 20170045. <https://doi.org/10.1098/rstb.2017.0045>
- 474 Burr, D. C., Anobile, G., Castaldi, E., & Arrighi, R. (2021). Numbers in action. *The*
475 *Behavioral and Brain Sciences*, 44, e185.
476 <https://doi.org/10.1017/S0140525X21000996>
- 477 Burr, D. C., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, 18(6), 425–428.
478 <https://doi.org/10.1016/j.cub.2008.02.052>
- 479 Butterworth, B. (2022). *Can Fish Count?: What Animals Reveal About Our Uniquely*
480 *Mathematical Minds* (New edition). Basic Books.

- 481 Chen, Q., & Li, J. (2014). Association between individual differences in non-symbolic
482 number acuity and math performance: A meta-analysis. *Acta Psychologica, 148*, 163–
483 172. <https://doi.org/10.1016/j.actpsy.2014.01.016>
- 484 Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures
485 distinguish verbal from nonverbal counting for both large and small numbers.
486 *Psychonomic Bulletin & Review, 8*(4), 698–707. <https://doi.org/10.3758/bf03196206>
- 487 Decarli, G., Sella, F., Lanfranchi, S., Gerotto, G., Gerola, S., Cossu, G., & Zorzi, M. (2023).
488 Severe Developmental Dyscalculia Is Characterized by Core Deficits in Both
489 Symbolic and Nonsymbolic Number Sense. *Psychological Science, 34*(1), 8–21.
490 <https://doi.org/10.1177/09567976221097947>
- 491 Dehaene, S. (2011). *The Number Sense: How the Mind Creates Mathematics, Revised and*
492 *Updated Edition* (Updated edizione). Oxford University Press, USA.
- 493 Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in*
494 *Cognitive Sciences, 8*(7), 307–314. <https://doi.org/10.1016/j.tics.2004.05.002>
- 495 Gomez, A., Piazza, M., Jobert, A., Dehaene-Lambertz, G., Dehaene, S., & Huron, C. (2015).
496 Mathematical difficulties in developmental coordination disorder: Symbolic and
497 nonsymbolic number processing. *Research in Developmental Disabilities, 43–44*,
498 167–178. <https://doi.org/10.1016/j.ridd.2015.06.011>
- 499 Gomez, A., Piazza, M., Jobert, A., Dehaene-Lambertz, G., & Huron, C. (2017). Numerical
500 abilities of school-age children with Developmental Coordination Disorder (DCD): A
501 behavioral and eye-tracking study. *Human Movement Science, 55*, 315–326.
502 <https://doi.org/10.1016/j.humov.2016.08.008>
- 503 Halberda, J., Mazocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-
504 verbal number acuity correlate with maths achievement. *Nature, 455*(7213), 665–668.
505 <https://doi.org/10.1038/nature07246>

- 506 Kirschhock, M. E., & Nieder, A. (2022). Number selective sensorimotor neurons in the crow
507 translate perceived numerosity into number of actions. *Nature Communications*,
508 *13*(1), 6913. <https://doi.org/10.1038/s41467-022-34457-5>
- 509 Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R., & Burr, D. C. (2020). Adaptation to
510 hand-tapping affects sensory processing of numerosity directly: Evidence from
511 reaction times and confidence. *Proceedings. Biological Sciences*, *287*(1927),
512 20200801. <https://doi.org/10.1098/rspb.2020.0801>
- 513 Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011). Impaired acuity of the
514 approximate number system underlies mathematical learning disability (dyscalculia).
515 *Child Development*, *82*(4), 1224–1237. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-8624.2011.01608.x)
516 [8624.2011.01608.x](https://doi.org/10.1111/j.1467-8624.2011.01608.x)
- 517 Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for
518 visual optic flow. *Current Biology: CB*, *9*(14), 763–766.
519 [https://doi.org/10.1016/s0960-9822\(99\)80338-8](https://doi.org/10.1016/s0960-9822(99)80338-8)
- 520 Peterzell, D. H., Chang, S. K., & Teller, D. Y. (2000). Spatial frequency tuned covariance
521 channels for red-green and luminance-modulated gratings: Psychophysical data from
522 human infants. *Vision Research*, *40*(4), 431–444. [https://doi.org/10.1016/s0042-](https://doi.org/10.1016/s0042-6989(99)00188-1)
523 [6989\(99\)00188-1](https://doi.org/10.1016/s0042-6989(99)00188-1)
- 524 Peterzell, D. H., & Kennedy, J. F. (2016). Discovering Sensory Processes Using Individual
525 Differences: A Review and Factor Analytic Manifesto. *Electronic Imaging*, *28*(16),
526 1–11. <https://doi.org/10.2352/ISSN.2470-1173.2016.16.HVEI-112>
- 527 Peterzell, D. H., & Teller, D. Y. (1996). Individual differences in contrast sensitivity
528 functions: The lowest spatial frequency channels. *Vision Research*, *36*(19), 3077–
529 3085. [https://doi.org/10.1016/0042-6989\(96\)00061-2](https://doi.org/10.1016/0042-6989(96)00061-2)

- 530 Peterzell, D. H., & Teller, D. Y. (2000). Spatial frequency tuned covariance channels for red-
531 green and luminance-modulated gratings: Psychophysical data from human adults.
532 *Vision Research*, 40(4), 417–430. [https://doi.org/10.1016/s0042-6989\(99\)00187-x](https://doi.org/10.1016/s0042-6989(99)00187-x)
- 533 Peterzell, D. H., Werner, J. S., & Kaplan, P. S. (1995). Individual differences in contrast
534 sensitivity functions: Longitudinal study of 4-, 6- and 8-month-old human infants.
535 *Vision Research*, 35(7), 961–979. [https://doi.org/10.1016/0042-6989\(94\)00117-5](https://doi.org/10.1016/0042-6989(94)00117-5)
- 536 Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations.
537 *Trends in Cognitive Sciences*, 14(12), 542–551.
538 <https://doi.org/10.1016/j.tics.2010.09.008>
- 539 Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S.,
540 & Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe
541 impairment in developmental dyscalculia. *Cognition*, 116(1), 33–41.
542 <https://doi.org/10.1016/j.cognition.2010.03.012>
- 543 Rammsayer, T. H., & Troche, S. J. (2014). In search of the internal structure of the processes
544 underlying interval timing in the sub-second and the second range: A confirmatory
545 factor analysis approach. *Acta Psychologica*, 147, 68–74.
546 <https://doi.org/10.1016/j.actpsy.2013.05.004>
- 547 Ranzini, M., Semenza, S., Zorzi, M., & Cutini, S. (2022). Influences of hand action on the
548 processing of symbolic numbers: A special role of pointing? *PloS One*, 17(6).
549 <https://doi.org/10.1371/journal.pone.0269557>
- 550 Reynaud, A., & Hess, R. F. (2017). Characterization of Spatial Frequency Channels
551 Underlying Disparity Sensitivity by Factor Analysis of Population Data. *Frontiers in*
552 *Computational Neuroscience*, 11.
553 <https://www.frontiersin.org/articles/10.3389/fncom.2017.00063>

- 554 Rose, G. J. (2017). The numerical abilities of anurans and their neural correlates: Insights
555 from neuroethological studies of acoustic communication. *Philosophical Transactions*
556 *of the Royal Society of London. Series B, Biological Sciences*, 373(1740), 20160512.
557 <https://doi.org/10.1098/rstb.2016.0512>
- 558 Ross, J. (2003). Visual discrimination of number without counting. *Perception*, 32(7), 867–
559 870. <https://doi.org/10.1068/p5029>
- 560 Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the
561 parietal cortex of the monkey. *Nature*, 415(6874), Article 6874.
562 <https://doi.org/10.1038/415918a>
- 563 Schneider, M., Beeres, K., Coban, L., Merz, S., Susan Schmidt, S., Stricker, J., & De Smedt,
564 B. (2017). Associations of non-symbolic and symbolic numerical magnitude
565 processing with mathematical competence: A meta-analysis. *Developmental Science*,
566 20(3). <https://doi.org/10.1111/desc.12372>
- 567 Simpson, W. A., & McFadden, S. M. (2005). Spatial frequency channels derived from
568 individual differences. *Vision Research*, 45(21), 2723–2727.
569 <https://doi.org/10.1016/j.visres.2005.01.015>
- 570 Sixtus, E., Krause, F., Lindemann, O., & Fischer, M. H. (2023). A sensorimotor perspective
571 on numerical cognition. *Trends in Cognitive Sciences*, 27(4), 367–378.
572 <https://doi.org/10.1016/j.tics.2023.01.002>
- 573 Suzuki, T. N. (2016). Semantic communication in birds: Evidence from field research over
574 the past two decades. *Ecological Research*, 31(3), 307–319.
575 <https://doi.org/10.1007/s11284-016-1339-x>
- 576 Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped
577 chickadees encode information about predator size. *Science (New York, N.Y.)*,
578 308(5730), 1934–1937. <https://doi.org/10.1126/science.1108841>

- 579 Togoli, I., Crollen, V., Arrighi, R., & Collignon, O. (2020). The shared numerical
580 representation for action and perception develops independently from vision. *Cortex;*
581 *a Journal Devoted to the Study of the Nervous System and Behavior*, *129*, 436–445.
582 <https://doi.org/10.1016/j.cortex.2020.05.004>
- 583 Togoli, I., Marlair, C., Collignon, O., Arrighi, R., & Crollen, V. (2021). Tactile numerosity is
584 coded in external space. *Cortex*, *134*, 43–51.
585 <https://doi.org/10.1016/j.cortex.2020.10.008>
- 586 Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and
587 quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488.
588 <https://doi.org/10.1016/j.tics.2003.09.002>
- 589 Westendorp, M., Hartman, E., Houwen, S., Smith, J., & Visscher, C. (2011). The relationship
590 between gross motor skills and academic achievement in children with learning
591 disabilities. *Research in Developmental Disabilities*, *32*(6), 2773–2779.
592 <https://doi.org/10.1016/j.ridd.2011.05.032>
- 593 Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The
594 Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137.
595 <https://doi.org/10.1111/1467-9280.00120>
- 596 Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: Stepping on stilts and
597 stumps. *Science (New York, N.Y.)*, *312*(5782), 1965–1967.
598 <https://doi.org/10.1126/science.1126912>
- 599
600
601
602