Sensorimotor mechanisms selective to numerosity: evidence from individual differences

Giovanni Anobile[1*], Irene Petrizzo[1], Daisy Paiardini[1], David C. Burr[1,3] & Guido Marco Cicchini[2]

[1]Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy

[2]Institute of Neuroscience, CNR, via Moruzzi, 1, 56124, Pisa, Italy

[3]School of Psychology, University of Sydney, Camperdown NSW, Australia

*** Correspondence:**

Giovanni Anobile; giovanni.anobile@unifi.it

Keywords: Visuomotor numerosity, Numerosity perception, Motor system, Approximate number system

Abstract

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

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

Introduction

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

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

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

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

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

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

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

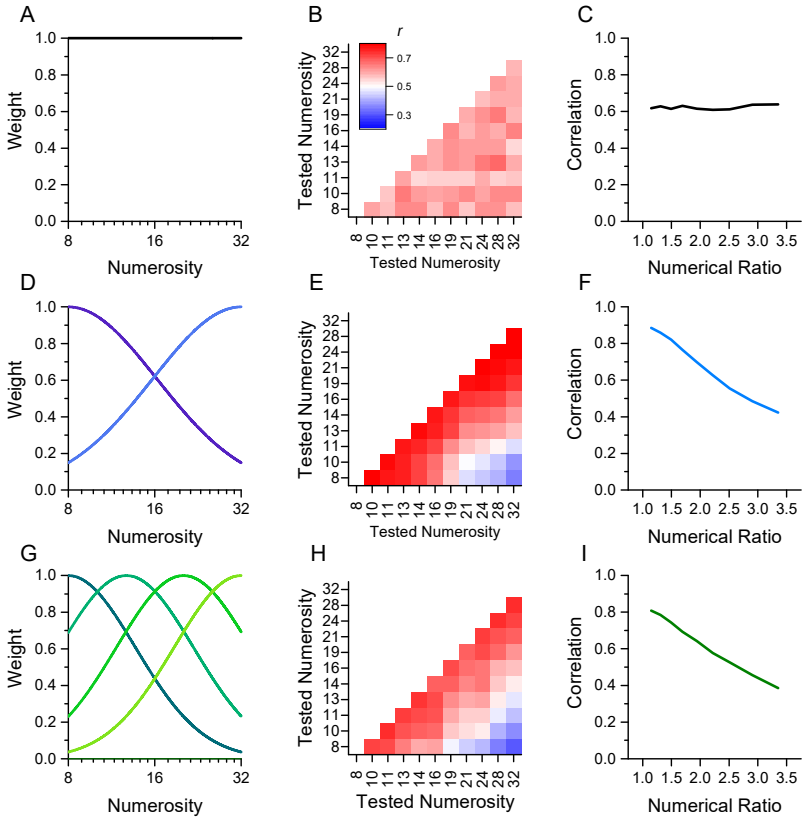

Figure 1. Simulation of behaviour with 1, 2 or 4 channels mediating numerosity judgments. A: 1-channel model shown as a flat tuning function. (B) Predicted correlation matrix between all pairs of numerosities. There is no systematic variability, only random variations induced by the noise. (C) Average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

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

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

Methods

Participants

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

Stimuli and procedures

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

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

Control duration task

A randomly selected sub-sample of 9 participants from the slow tapping condition was engaged in a duration control task. On each trial, a tone (500 Hz, ramped on and off with 20 ms raised-cosine ramps) was played though headphones, and participants asked to reproduce its duration by repeatedly tapping on a key while pronouncing the syllable 'ba' as fast as possible (to suppress counting). The between average tapping frequency rate in the number 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). Target durations were customised for each participant to perfectly match those previously produced in the number task: for each target number tested in the number matching task, we extracted the average response duration (across trials) and these eleven durations were re-presented as duration targets (Table 1). Before the experiment, participants were familiarized with the task by performing one single block of trials with feedback (2 numbers, one displaying the target duration and the second displaying the reproduced duration, in seconds). In this phase 11 trials were presented, one for each tested duration (randomly selected trial by trial). No feedbacks were provided during the rest of the experiment. As for the number task, for each participant, each duration was presented from 25 to 30 times (for a total of 2455 trials), in separate blocks.

Table 1. Responses duration (in seconds) tested in in the control duration task for each one of the nine participants (S1-S9)

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

Data analyses

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

Data processing

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

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

Correlation matrices and numerical distance

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

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

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

Hierarchical clustering and Principal component analysis

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

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

Modelling

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

Results

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

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

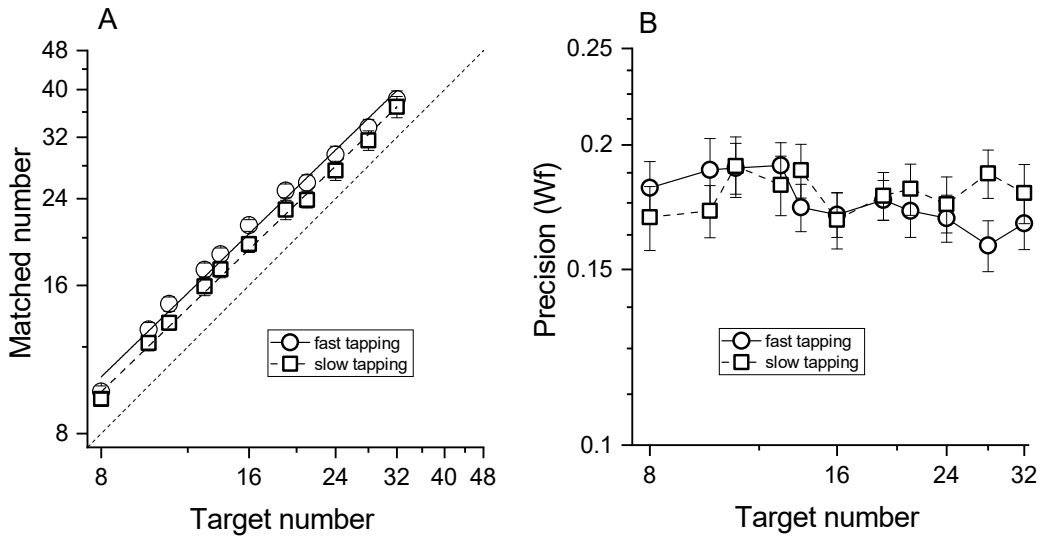

Figure 2. Matched number (A) and Weber Fractions (B) as a function of target number, separated for the fast (circles) and slow (squares) tapping conditions. Lines through the data in panel A show best linear fits. Error bars are ±1 s.e.m., across participants.

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

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

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

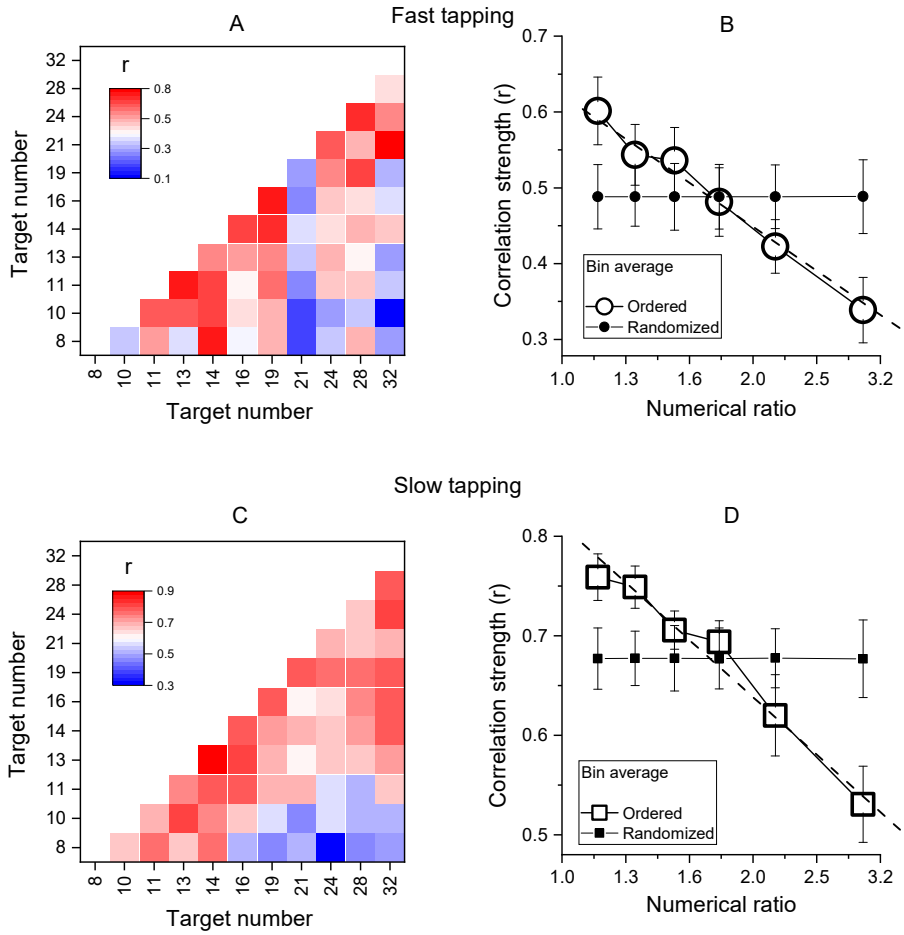

Figure 3. Inter-participant correlations. A. Correlation matrices of Wfs for all pairs of target numbers for the slow-tapping condition. B. Correlation strength as a function of numerical ratio, for the slow-tapping condition. Small, filled symbols show bootstrapped average correlation strengths of randomized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

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

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

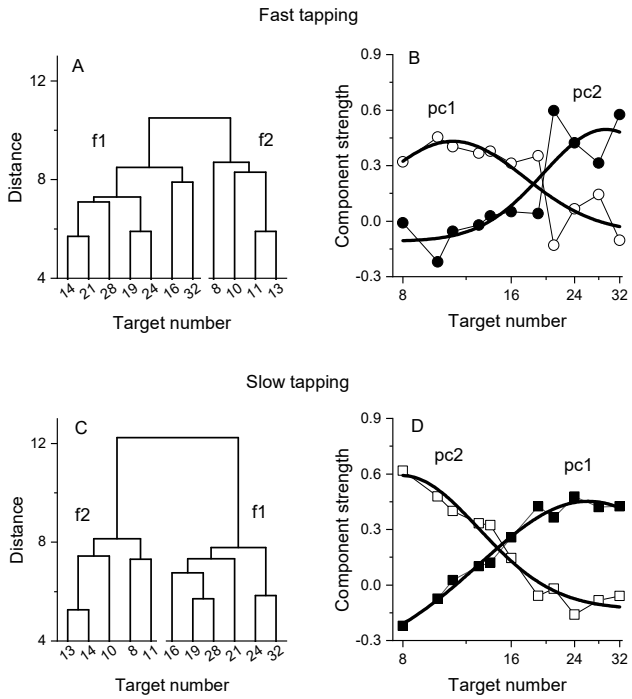

Figure 4. Dendrograms from hierarchical clustering on Wfs in the fast (A) and slow (C) tapping conditions. Panels B and D show the strength of the first two principal components from a PCA on the Wfs measured in the fast (B) and slow (D) tapping conditions. The strength of these components is shown as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

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

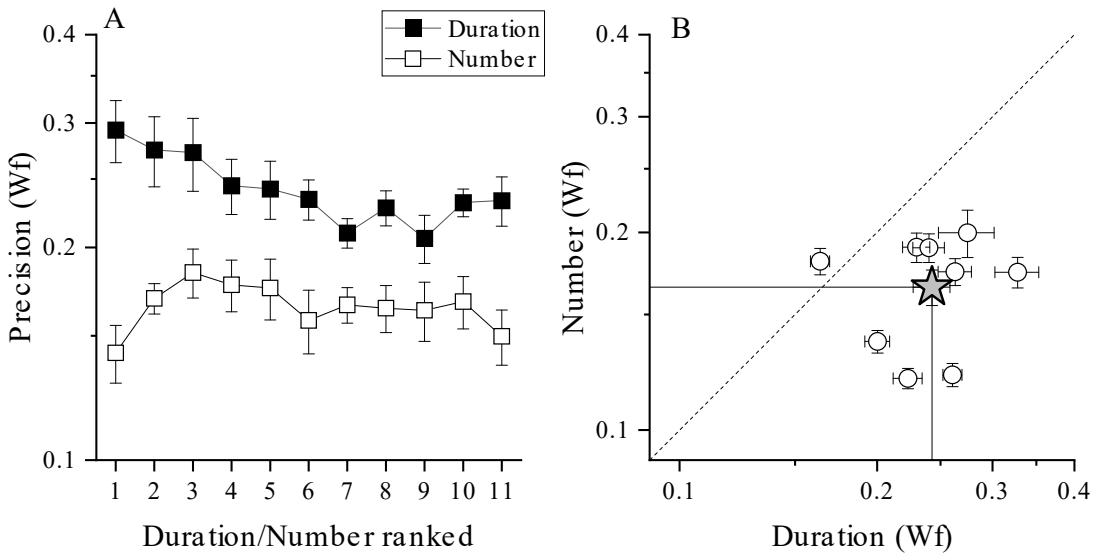

Figure 5. A) Average (across participant) Weber fraction for the number (filled squares) and duration (empty squares) matching tasks, as a function of ranked target stimulus (visual digits for the number task, and the corresponding auditory tones durations for the duration task, see methods for details).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

Discussion

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

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

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

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

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

predators (Suzuki, 2016; Templeton et al., 2005). In all cases, the use of number-related motor strategies by animals has a clear ecological value for survival and species preservation.

This system may have been preserved in humans and repurposed for our species-specific needs. Some hints come from the literature on the role of visual numerosity perception (dot arrays). Although most animal species are capable of some form of numerosity estimation (Butterworth, 2022), it appears that in humans numerosity estimation may act as a non-symbolic precursor for the development of symbolic mathematical skills (Chen & Li, 2014; Decarli et al., 2023; Halberda et al., 2008; Mazzocco et al., 2011; Piazza, 2010; Piazza et al., 2010; Schneider et al., 2017). The sensorimotor system could act as an early tool to constantly update and calibrate motor and sensory systems for the encoding and active manipulation of quantities and objects, with a potential impact on the quality of formal mathematical skills in later development. In line with this idea, there are reports of a possible co-occurrence of motor impairments in children with mathematical learning disorders such as dyscalculia (Westendorp et al., 2011), and children with developmental coordination disorders (which impair gross and fine motor function) perform poorly on math and numerosity tasks (Gomez et al., 2015, 2017). This is in line with the suggestive idea proposed by Walsh (2003) of a sensory magnitude system, encoding abstract quantities such as space, time and number, to guide planning and execution of actions. It is also in line with more recent proposal suggesting that the acquisition of number meaning is deeply grounded in sensorimotor experiences (Ranzini et al., 2022; Sixtus et al., 2023).

Funding

This research was funded by the European Union (EU) and Horizon 2020—Grant Agreement no. 832813—ERC Advanced "Spatio-temporal mechanisms of generative perception — GenPercept"; and from the Italian Ministry of Education, University, and Research under the PRIN2017 program (Grant no. 2017XBJN4F— "EnvironMag").

References

Anobile, G., Arrighi, R., Castaldi, E., & Burr, D. C. (2021). A Sensorimotor Numerosity System. *Trends in Cognitive Sciences*, *25*(1), 24–36. https://doi.org/10.1016/j.tics.2020.10.009

Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *ELife*, *5*, e16161. https://doi.org/10.7554/eLife.16161

Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate mechanisms for perception of numerosity and density. *Psychological Science*, *25*(1), 265–270. https://doi.org/10.1177/0956797613501520

Anobile, G., Domenici, N., Togoli, I., Burr, D., & Arrighi, R. (2020). Distortions of visual time induced by motor adaptation. *Journal of Experimental Psychology. General*, *149*(7), 1333–1343. https://doi.org/10.1037/xge0000709

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141791. https://doi.org/10.1098/rspb.2014.1791

Burr, D. C., Anobile, G., & Arrighi, R. (2018). Psychophysical evidence for the number sense. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20170045. https://doi.org/10.1098/rstb.2017.0045

Burr, D. C., Anobile, G., Castaldi, E., & Arrighi, R. (2021). Numbers in action. *The Behavioral and Brain Sciences*, *44*, e185. https://doi.org/10.1017/S0140525X21000996

Burr, D. C., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, *18*(6), 425–428. https://doi.org/10.1016/j.cub.2008.02.052

Butterworth, B. (2022). *Can Fish Count?: What Animals Reveal About Our Uniquely Mathematical Minds* (New edition). Basic Books.

Chen, Q., & Li, J. (2014). Association between individual differences in non-symbolic number acuity and math performance: A meta-analysis. *Acta Psychologica*, *148*, 163–172. https://doi.org/10.1016/j.actpsy.2014.01.016

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review*, *8*(4), 698–707. https://doi.org/10.3758/bf03196206

Decarli, G., Sella, F., Lanfranchi, S., Gerotto, G., Gerola, S., Cossu, G., & Zorzi, M. (2023). Severe Developmental Dyscalculia Is Characterized by Core Deficits in Both Symbolic and Nonsymbolic Number Sense. *Psychological Science*, *34*(1), 8–21. https://doi.org/10.1177/09567976221097947

Dehaene, S. (2011). *The Number Sense: How the Mind Creates Mathematics, Revised and Updated Edition* (Updated edizione). Oxford University Press, USA.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–314. https://doi.org/10.1016/j.tics.2004.05.002

Gomez, A., Piazza, M., Jobert, A., Dehaene-Lambertz, G., Dehaene, S., & Huron, C. (2015). Mathematical difficulties in developmental coordination disorder: Symbolic and nonsymbolic number processing. *Research in Developmental Disabilities*, *43–44*, 167–178. https://doi.org/10.1016/j.ridd.2015.06.011

Gomez, A., Piazza, M., Jobert, A., Dehaene-Lambertz, G., & Huron, C. (2017). Numerical abilities of school-age children with Developmental Coordination Disorder (DCD): A behavioral and eye-tracking study. *Human Movement Science*, *55*, 315–326. https://doi.org/10.1016/j.humov.2016.08.008

Halberda, J., Mazzocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665–668. https://doi.org/10.1038/nature07246

Kirschhock, M. E., & Nieder, A. (2022). Number selective sensorimotor neurons in the crow translate perceived numerosity into number of actions. *Nature Communications*, *13*(1), 6913. https://doi.org/10.1038/s41467-022-34457-5

Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R., & Burr, D. C. (2020). Adaptation to hand-tapping affects sensory processing of numerosity directly: Evidence from reaction times and confidence. *Proceedings. Biological Sciences*, *287*(1927), 20200801. https://doi.org/10.1098/rspb.2020.0801

Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011). Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). *Child Development*, *82*(4), 1224–1237. https://doi.org/10.1111/j.1467-8624.2011.01608.x

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology: CB*, *9*(14), 763–766. https://doi.org/10.1016/s0960-9822(99)80338-8

Peterzell, D. H., Chang, S. K., & Teller, D. Y. (2000). Spatial frequency tuned covariance channels for red-green and luminance-modulated gratings: Psychophysical data from human infants. *Vision Research*, *40*(4), 431–444. https://doi.org/10.1016/s0042-6989(99)00188-1

Peterzell, D. H., & Kennedy, J. F. (2016). Discovering Sensory Processes Using Individual Differences: A Review and Factor Analytic Manifesto. *Electronic Imaging*, *28*(16), 1–11. https://doi.org/10.2352/ISSN.2470-1173.2016.16.HVEI-112

Peterzell, D. H., & Teller, D. Y. (1996). Individual differences in contrast sensitivity functions: The lowest spatial frequency channels. *Vision Research*, *36*(19), 3077–3085. https://doi.org/10.1016/0042-6989(96)00061-2

Peterzell, D. H., & Teller, D. Y. (2000). Spatial frequency tuned covariance channels for red-green and luminance-modulated gratings: Psychophysical data from human adults. *Vision Research*, *40*(4), 417–430. https://doi.org/10.1016/s0042-6989(99)00187-x

Peterzell, D. H., Werner, J. S., & Kaplan, P. S. (1995). Individual differences in contrast sensitivity functions: Longitudinal study of 4-, 6- and 8-month-old human infants. *Vision Research*, *35*(7), 961–979. https://doi.org/10.1016/0042-6989(94)00117-5

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences*, *14*(12), 542–551. https://doi.org/10.1016/j.tics.2010.09.008

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S., & Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, *116*(1), 33–41. https://doi.org/10.1016/j.cognition.2010.03.012

Rammsayer, T. H., & Troche, S. J. (2014). In search of the internal structure of the processes underlying interval timing in the sub-second and the second range: A confirmatory factor analysis approach. *Acta Psychologica*, *147*, 68–74. https://doi.org/10.1016/j.actpsy.2013.05.004

Ranzini, M., Semenza, S., Zorzi, M., & Cutini, S. (2022). Influences of hand action on the processing of symbolic numbers: A special role of pointing? *PloS One*, *17*(6). https://doi.org/10.1371/journal.pone.0269557

Reynaud, A., & Hess, R. F. (2017). Characterization of Spatial Frequency Channels Underlying Disparity Sensitivity by Factor Analysis of Population Data. *Frontiers in Computational Neuroscience*, *11*. https://www.frontiersin.org/articles/10.3389/fncom.2017.00063

Rose, G. J. (2017). The numerical abilities of anurans and their neural correlates: Insights from neuroethological studies of acoustic communication. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1740), 20160512. https://doi.org/10.1098/rstb.2016.0512

Ross, J. (2003). Visual discrimination of number without counting. *Perception*, *32*(7), 867–870. https://doi.org/10.1068/p5029

Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature*, *415*(6874), Article 6874. https://doi.org/10.1038/415918a

Schneider, M., Beeres, K., Coban, L., Merz, S., Susan Schmidt, S., Stricker, J., & De Smedt, B. (2017). Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: A meta-analysis. *Developmental Science*, *20*(3). https://doi.org/10.1111/desc.12372

Simpson, W. A., & McFadden, S. M. (2005). Spatial frequency channels derived from individual differences. *Vision Research*, *45*(21), 2723–2727. https://doi.org/10.1016/j.visres.2005.01.015

Sixtus, E., Krause, F., Lindemann, O., & Fischer, M. H. (2023). A sensorimotor perspective on numerical cognition. *Trends in Cognitive Sciences*, *27*(4), 367–378. https://doi.org/10.1016/j.tics.2023.01.002

Suzuki, T. N. (2016). Semantic communication in birds: Evidence from field research over the past two decades. *Ecological Research*, *31*(3), 307–319. https://doi.org/10.1007/s11284-016-1339-x

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science (New York, N.Y.)*, *308*(5730), 1934–1937. https://doi.org/10.1126/science.1108841

Togoli, I., Crollen, V., Arrighi, R., & Collignon, O. (2020). The shared numerical representation for action and perception develops independently from vision. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *129*, 436–445. https://doi.org/10.1016/j.cortex.2020.05.004

Togoli, I., Marlair, C., Collignon, O., Arrighi, R., & Crollen, V. (2021). Tactile numerosity is coded in external space. *Cortex*, *134*, 43–51. https://doi.org/10.1016/j.cortex.2020.10.008

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488. https://doi.org/10.1016/j.tics.2003.09.002

Westendorp, M., Hartman, E., Houwen, S., Smith, J., & Visscher, C. (2011). The relationship between gross motor skills and academic achievement in children with learning disabilities. *Research in Developmental Disabilities*, *32*(6), 2773–2779. https://doi.org/10.1016/j.ridd.2011.05.032

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137. https://doi.org/10.1111/1467-9280.00120

Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: Stepping on stilts and stumps. *Science (New York, N.Y.)*, *312*(5782), 1965–1967. https://doi.org/10.1126/science.1126912