

Sensorimotor mechanisms selective to numerosity: evidence from individual differences

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Giovanni Anobile , Irene Petrizzo, Daisy Paiardini, David C. Burr, Guido Marco Cicchini

Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy • School of Psychology, University of Sydney, Camperdown NSW, Australia • Institute of Neuroscience, CNR, via Moruzzi, 1, 56124, Pisa, Italy

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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 sensori-motor number channels responsible for translating symbolic numbers into action sequences.

eLife assessment

This potentially **important** paper addresses the question of how numerical information is represented in the human brain. Experimental findings are interpreted as providing evidence for a sensorimotor mechanism that involves channels, each tuned to a particular numerical range. While this is an interesting application of methodologies used to identify the presence of channels, the evidence supporting the claim that these have a sensorimotor basis is **incomplete**.

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 et 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.

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** [↗](#) & **1I** [↗](#).

Methods

Participants

An a priori power analysis for a correlation test (r) with a medium effect size of $r^2 = 0.5$, and $\alpha = 0.05$ (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 tapings 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.

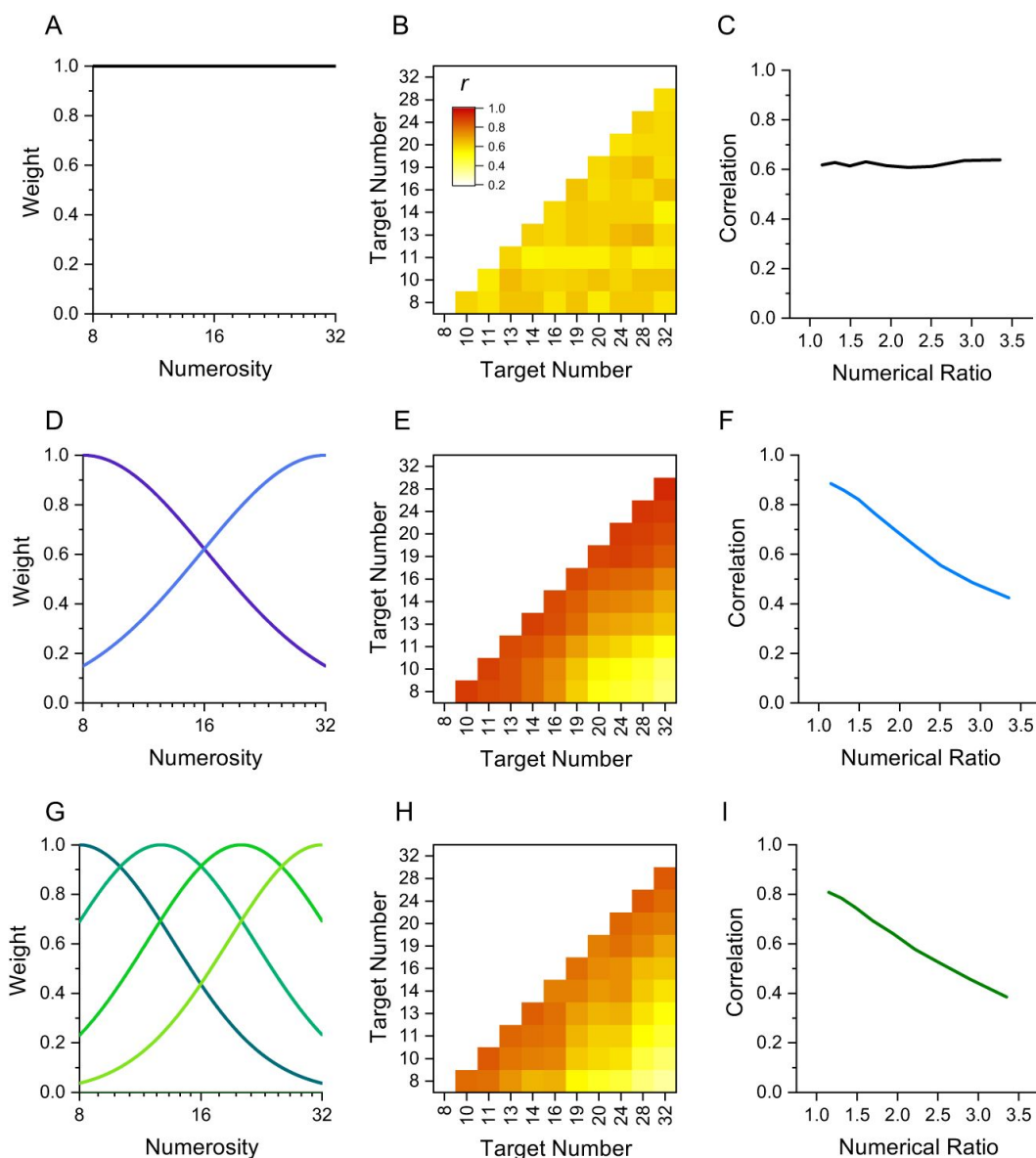


Figure 1.

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.

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 through 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.

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 (a standard index of normalized precision).

Correlation matrices and numerical distance

As a third step we computed Weber fraction correlation matrices. We first measured the precision in translating digit numbers into action sequences, for different target numbers (8, 10, 11, 13, 14, 16, 19, 21, 24, 28, 32), for all N participants. For each target number, and independently for each participant, we calculated the normalized reproduction precision (Weber Fraction). The dataset comprised a matrix where each column represents a participant, each row a target number, and each cell the corresponding Weber Fraction. This dataset was then analysed with a pairwise correlation, across participants. For example, the WFs provided by the N participants when tested at the target number “8” were correlated with those obtained with the target number 10, 11, 13, 32. If channels exist, the correlation between “8 and 10” (low numerical distance) should be higher compared to that between “8 with 32” (higher numerical distance). We therefore analysed 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

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

Table 1.

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

as the base ten logarithm ratio between itself and the remaining target numbers. The correlation coefficients 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

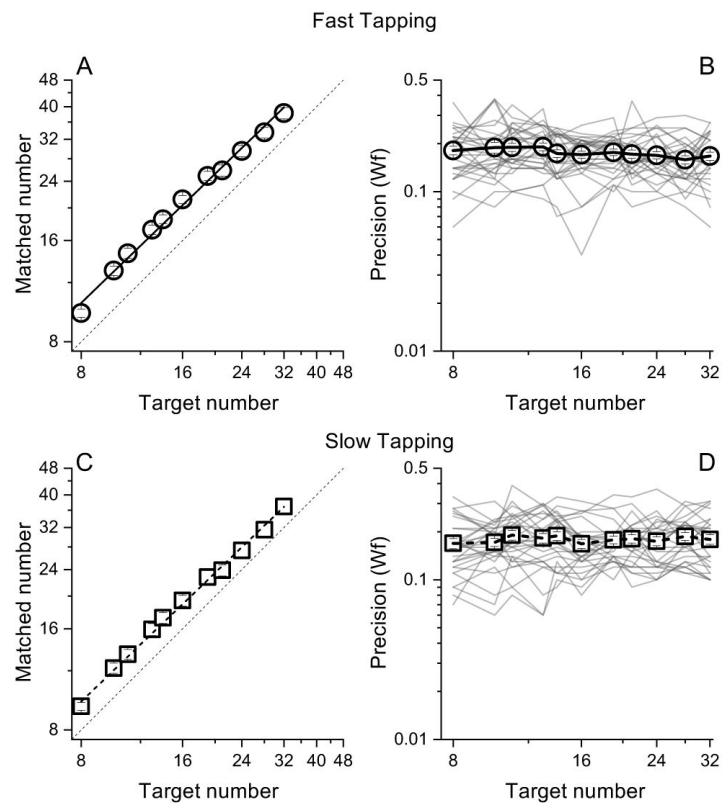


Figure 2.

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

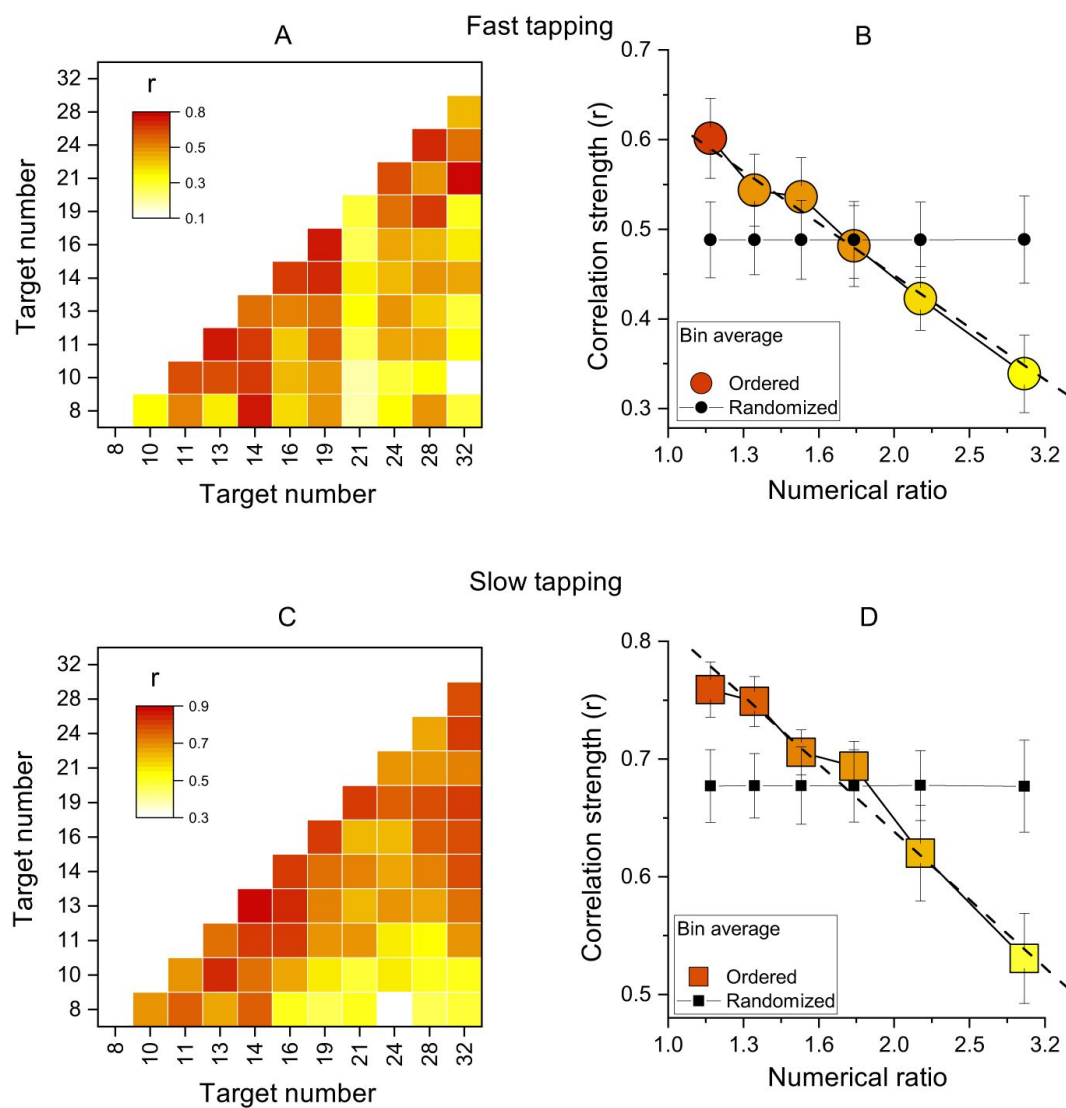


Figure 3.

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 black 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 ± 1 s.e.m. C & D. Like A & B, for the slow-tapping condition.

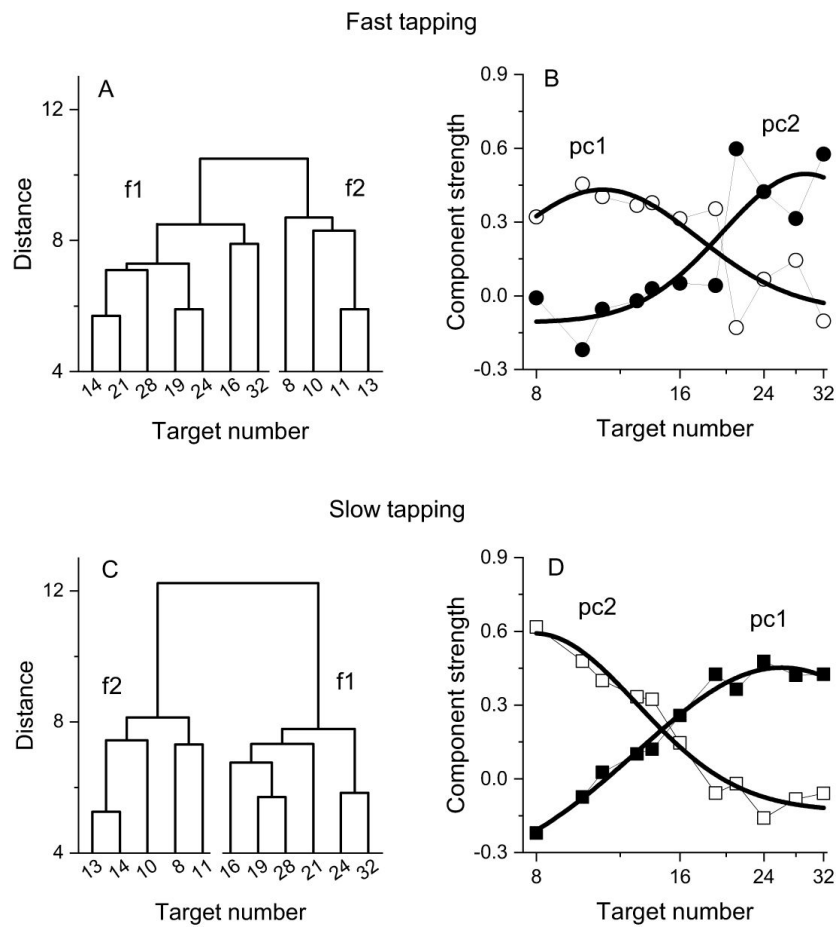


Figure 4.

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.

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** & **C**). **Figure 2B** & **D** 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.

We then computed the correlations of Wfs across participants, for all target values (see methods for details). **Figures 3A** & **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 3B & **D** show average correlation coefficients, 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 3B** & **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 black filled symbols in **Figure 3B** & **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.

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 peaked at higher target numbers (N 26) and the second component at lower numbers (N 8).

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 subsample 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 ($F(1, 80) = 19.97$, $p = 0.002$).

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). As the focus of the current study was on the individual differences in the number-to-action transformation process, we used digits as sensory stimuli. Digits encoding, at least with educated adults, is noiseless, eliminating this source of variability but leaving that associated with the sensorimotor transformation process.

Importantly, by looking at the covariance structure of the motor reproduction precision index (Weber fraction) across participants, we found evidence for sensorimotor channels tuned to number. Precision for reproducing numerically similar targets was positively correlated ($r \sim 0.8$) but for larger numerical distances, correlations decreased ($r \sim 0.1$), suggesting the action of sensorimotor 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 and higher numbers. Finally, Principal Component Analyses on Weber fractions confirmed this and went to describe two bell-shaped components, one peaking at relatively low numbers (~ 10) and the second at higher numbers (~ 27).

The covariance technique used here has been widely employed to reveal visual channels in several basic perceptual dimensions such as colour, motion, contrast and spatial frequency (Morrone et al., 1999; Peterzell et al., 1995, 2000; Peterzell & Kennedy, 2016; Peterzell & Teller, 1996, 2000; Rammsayer & Troche, 2014). The technique is based on the idea that interindividual variability conveys information that can reveal common sensory processes (Peterzell & Kennedy, 2016), as illustrated in **Figure 1**. In practice, this approach requires multiple and densely sampled measurements of different stimuli intensity, in the same sample. Regions of high intercorrelation between neighbouring stimuli intensity can be interpreted to imply that sets of stimuli are processed by the same (shared) underlying channel. This channel, while responding relatively more to its preferred stimulus, will also be activated by neighbouring stimuli that although slightly different from the preferred intensity, are nevertheless included in the same response distribution. Following this rationale, relatively lower correlations among more

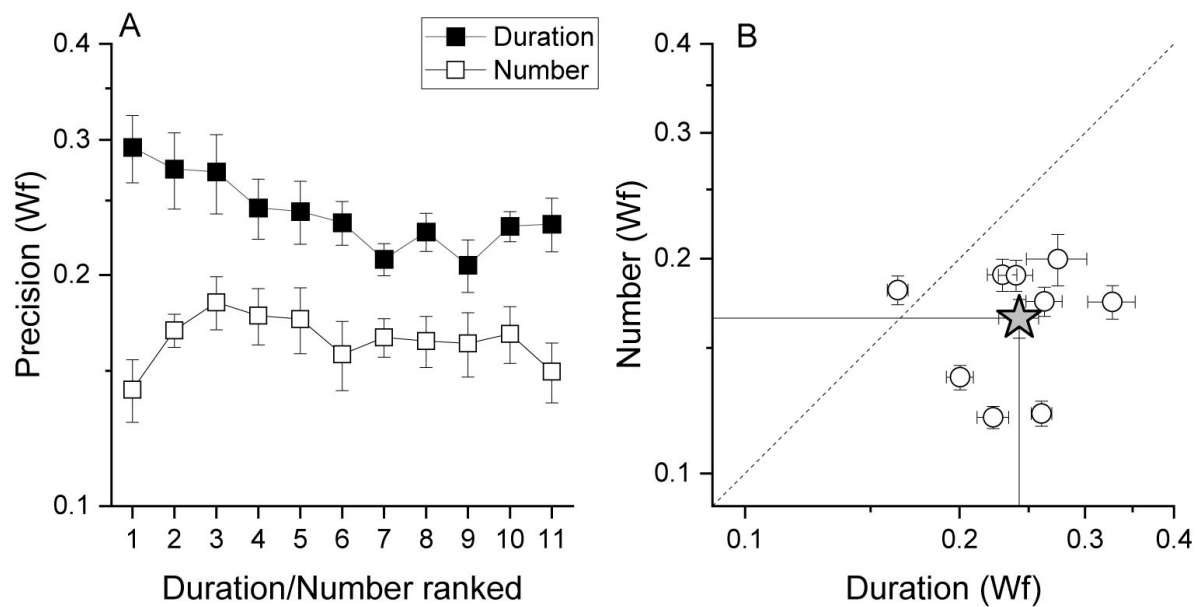


Figure 5.

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.

distant stimuli would indicate that these are processed by different, or at least partially independent, channels (Peterzell & Teller, 1996 [↗](#)). The results obtained in this study are in line with those predicted by this technique, implying the existence of sensorimotor channels tuned to different numerical targets, with a rather wide response distribution. These channels probably reflect the activity of noisy neurons responsible for translating sensory information into the corresponding numerical motor output, such as those observed in crows (Kirschhock & Nieder, 2022 [↗](#)).

The results reinforce adaptation studies showing number-selective adaptation between actions and perceived numerosity (Anobile et al., 2016 [↗](#); Maldonado Moscoso et al., 2020 [↗](#)). Those studies provided strong evidence for the existence of at least two (but possibly more) sensorimotor mechanisms, tuned to high and low numbers. The results are also broadly in line with recent evidence from animal physiology showing number selective sensorimotor neurons in the crow brain, translating visual inputs (digits and dot arrays) into number of pecks (Kirschhock & Nieder, 2022 [↗](#)). While the crow study found as many channels as the number tested (N1–5), we found evidence for only two channels (clusters and factors) over the range of 8–32. However, it is important to note that PCA aims to summarize the dataset with the minimal number of components (channels). We can therefore not exclude the possible existence of more than two (perhaps not fully independent) channels. The results should be not interpreted as evidence for only two sensorimotor channels, but rather as 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. In other words, the channels described here likely represent a coarse summary representation of several (probably sharper) underlying channels.

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. Duration could conceivably be useful proxy for numerosity, but only if the thresholds for duration were lower than those for numerosity: but the results show they are in fact higher. 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 chunks 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 [↗](#)). This is the first study showing sensorimotor channels for the transformation of numbers into action sequences in humans, and many questions remain open. Among these: is the channel preference (the peak) fixed on the absolute numerical value, or does actively recalibrate according to the numerical context (range)? Do these channels also integrate non-symbolic numerical information such as the numerosity of sets of elements and/or sequences of visual/acoustic events? Are these channels active during motor programming, or do they require action execution? Do these channels integrate non-numerical motor parameters, such as the associated effort? Are these channels motor effector-specific? These (and probably other) questions are waiting to be explored using this technique, which has the advantage of being sufficiently generalisable to be expanded to investigate most stimulus features.

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Article and author information

Giovanni Anobile

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

For correspondence: giovanni.anobile@unifi.it

ORCID iD: [0000-0003-2796-0661](https://orcid.org/0000-0003-2796-0661)

Irene Petrizzo

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

Daisy Paiardini

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

David C. Burr

Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy, School of Psychology, University of Sydney, Camperdown NSW, Australia

Guido Marco Cicchini

Institute of Neuroscience, CNR, via Moruzzi, 1, 56124, Pisa, Italy

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Reviewer #1 (Public Review):

Anobile and colleagues present a manuscript detailing an account of numerosity processing with an appeal to a two-channel model. Specifically, the authors propose that the perception of numerosity relies on (at least) two distinct channels for small and large numerosities, which should be evident in subject reports of perceived numerosity. To do this, the authors had subjects reproduce visual dot arrays of numerosities ranging from 8 to 32 dots, by having subjects repetitively press a response key at a pre-instructed rate (fast or slow) until the number of presses equaled the number of perceived dots. The subjects performed the task remarkably well, yet with a general bias to overestimate the number of presented dots. Further, no difference was observed in the precision of responses across numerosities, providing evidence for a scalar system. No differences between fast and slow tapping were observed. For behavioral analysis, the authors examined correlations between the Weber fractions for all presented numerosities. Here, it was found that the precision at each numerosity was similar to that at neighboring numerosities, but less similar to more distant ones. The authors then went on to conduct PCA and clustering analyses on the weber fractions, finding that the first two components exhibited an interaction with the presented numerosity, such that each were dominant at distinct lower and upper ranges and further well-fit by a log-Gaussian model consistent with the channel explanation proposed at the beginning.

Overall, the authors provide compelling evidence for a two-channel system supporting numerosity processing that is instantiated in sensorimotor processes. A strength of the presented work is the principled approach the authors took to identify mechanisms, as well as the controls put in place to ensure adequate data for analysis.

One remaining question regards the secondary timing task that was used as a control. There may be interesting findings here to pursue, and so I encourage the authors or other researchers to examine those findings and explore further studies there as well.

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Reviewer #2 (Public Review):

Summary:

The authors wish to apply established psychophysical methods to the study of numbers. Specifically, they wish to test the hypothesis - supported by their previous work - that human sensorimotor processes are tuned to specific number ranges. In a novel set of tasks, they ask participants to tap a button N times (either fast or slow), where N varies between 8 and 32 across trials. As I understood it, they then computed the Weber fraction (WF) for each participant for each number and correlated those values across participants and numbers. They find stronger correlations for nearby numbers than for distant numbers and interpret this as evidence of sensorimotor tuning functions. Two other analyses - cluster analyses and principal component analyses (PCA) - suggest that participants' performance relied on at least

2 mechanisms, one for encoding low numbers of taps (around 10) and another encoding larger numbers (around 27).

Strengths:

Individual differences can be a rich source of scientific insight and I applaud the authors for taking them seriously.

Weaknesses:

Implications of intercorrelation. The experiment "is based on the idea that interindividual variability conveys information that can reveal common sensory processes (Peterzell & Kennedy, 2016)" but I struggle to understand the logic of this technique. The authors explain it most clearly when they write "Regions of high intercorrelation between neighbouring stimuli intensity can be interpreted to imply that sets of stimuli are processed by the same (shared) underlying channel. This channel, while responding relatively more to its preferred stimulus, will also be activated by neighbouring stimuli that although slightly different from the preferred intensity, are nevertheless included in the same response distribution." Why does high intercorrelation imply a shared channel and why should it be calculated across participants? Shouldn't performance on any set of tasks (that vary in difficulty) correlate across participants? Why in principle should people have distinct channels for processing similar stimuli and how could such a system improve (rather than impede) discrimination abilities? What pattern of intercorrelation would disconfirm the existence of tuning mechanisms? And perhaps most fundamentally: What is a channel and why do they matter?

Different channels? I had trouble understanding much of the analyses, and this may account for at least some of my confusion. That said, as I understand it, the results are meant to provide "evidence that tuned mechanisms exist in the human brain, with at least two different tunings" because of the results of the clustering analysis and PCA. But as the authors acknowledge, "PCA aims to summarize the dataset with the minimal number of components (channels). We can therefore not exclude the possible existence of more than two (perhaps not fully independent) channels." I would go a step further and say this technique does not provide more evidence for the existence of 2 channels as for the existence of 4, 8 or 24 channels, the upper bound for a task testing 24 different numbers. If we can conclude that people may have one channel per number, what does "channel" mean?

Several other questions arise when thinking through this technique, which left me skeptical of its utility. If people did have two channels (at least in this range), why would they be so broad? Why would they be centered so near the ends of the tested range? Can such effects be explained by binning on the part of the participants, who might have categorized each number (knowingly or not) as either "small" or "large"? Or by the kind of data-binning or distributions (i.e. Gaussian) used in the analyses? Or by the physical limits and affordances of the effector participants used (i.e. their finger)? Moreover, if people had sensorimotor channels tuned to different numbers, wouldn't this cause discontinuities in their own WF? Why look at correlations across individuals rather than correlations or discontinuities within individuals? Whereas the experiment tested numbers 8-32, numbers are infinite - How could a small number of channels cover an infinite set? Or even the set 8-10,000? What would the existence of multiple such channels mean for our understanding of numerical cognition? There may be good answers to these questions, but they are not clear to this reader.

Theories of numerical cognition. An expansive literature on numerical cognition suggests that many animals, human children, and adults across cultures have two systems for representing numerosity without counting - one that can represent the exact cardinality of sets smaller than about 4 and another that represents the approximate number of larger sets. Recent accounts suggest that what appears to be two systems can be explained by a single system of numerical approximation with limited information capacity (see Cheyette &

Piantadosi, 2020). The current paper would benefit from better relating its findings to this long lineage of theories and findings in numerical approximation across cultures, ages, and species.

Specific to numbers? The authors argue that their effects are "number selective" but they do not provide compelling evidence for this selectivity. In principle, their main findings could be explained by the duration of tapping rather than the number of taps. They argue this is unlikely for two reasons. The first reason is that the overall pattern of results was unchanged across the fast and slow tapping conditions, but differences in duration were confounded with numerosity in both conditions, so the comparison is uninformative. The second reason is that temporal reproduction was less precise in their control condition than numerical reproduction, but this logic is unclear: Participants could still use duration (or some combination of speed and duration) as a helpful cue to numerosity, even if their duration reproductions were imperfect.

If the authors wish to test the role of duration, they might consider applying the same analytical techniques they use for number to their duration data. Perhaps participants show similar evidence for duration-selective channels, in the absence of number, as they do for other non-numerical domains (like spatial frequency).

<https://doi.org/10.7554/eLife.92169.2.sa1>

Reviewer #3 (Public Review):

Reviewing Editor's Summary:

The revised manuscript has clarified concerns raised by the reviewers concerning the analysis method in constructing the correlation matrix. These key results are now readily comprehensible. They have also added a final section to the Discussion, sketching some important questions for future research (e.g., number/resolution of channels and extension of the logic used here to look at number channels in other tasks).

Reviewer 1 was satisfied with these changes and has updated their review. Reviewer 2 did not think the revision tackled the theoretical issues raised in their initial review; as such, this reviewer has opted to leave their initial public review unchanged.

I also believe that the revision does not adequately address a major theoretical issue, namely whether the current data provide evidence of sensorimotor number channels, the central claim of the paper. The authors argue that since perception is noise free (stimuli were given symbolically), then the task variance comes from processes associated with sensorimotor transformation. Let's consider the task: A number is presented, the participant then attempts to produce that number of taps. To preclude counting, they are required to say the syllable "ba" as fast as possible while tapping. The sensorimotor channel idea would suppose that the symbolic stimulus activates a set of channels, each of which specifies the number of taps that should be produced. For example, a "6" channel likes to produce 6 outputs (with variability), a "10" channel 10 outputs (with variability), etc., with the actual production of the (weighted) integration of these outputs.

An alternative is that, since explicit counting is prevented by the secondary task, the participant makes an internal estimation of the number of produced taps. These judgments could be based on the output of amodal number channels. For example, the same process would be at play if the task were changed such that the participants watched a dot flash and had to estimate the number of flashes (while concurrently saying "ba"). The authors indicate in their response letter that they are conducting experiments along these lines and that the results are similar. They suggest that this provides support for the existence of both sensory

and sensorimotor number channels. Extending this, if the experiment were tones instead of flashes, the argument would be that there are auditory, visual, and sensorimotor number channels. It seems more parsimonious to interpret such a pattern as reflective of amodal number channels.

I recognize there are other intriguing reasons to think there may be intimate links between our sense of number and movement, but I remain unconvinced that the current results provide evidence for sensorimotor number channels.

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Author Response

The following is the authors' response to the original reviews.

eLife assessment

The paper addresses the important question of how numerical information is represented in the human brain. Experimental findings are interpreted as providing evidence for a sensorimotor mechanism that involves channels, each tuned to a particular numerical range. However, the logic of the channel concept as employed here, as well as the claims regarding a sensorimotor basis for these channels, is incomplete and thus requires clarification and/or modification.

Reviewer #1 Public Review

Anobile and colleagues present a manuscript detailing an account of numerosity processing with an appeal to a two-channel model. Specifically, the authors propose that the perception of numerosity relies on (at least) two distinct channels for small and large numerosities, which should be evident in subject reports of perceived numerosity. To do this, the authors had subjects reproduce visual dot arrays of numerosities ranging from 8 to 32 dots, by having subjects repetitively press a response key at a pre-instructed rate (fast or slow) until the number of presses equaled the number of perceived dots. The subjects performed the task remarkably well, yet with a general bias to overestimate the number of presented dots. Further, no difference was observed in the precision of responses across numerosities, providing evidence for a scalar system. No differences between fast and slow tapping were observed. For behavioral analysis, the authors examined correlations between the Weber fractions for all presented numerosities. Here, it was found that the precision at each numerosity was similar to that at neighboring numerosities, but less similar to more distant ones. The authors then went on to conduct PCA and clustering analyses on the weber fractions, finding that the first two components exhibited an interaction with the presented numerosity, such that each was dominant at distinct lower and upper ranges and further well-fit by a log-Gaussian model consistent with the channel explanation proposed at the beginning.

Overall, the authors provide compelling evidence for a two-channel system supporting numerosity processing that is instantiated in sensorimotor processes. A strength of the presented work is the principled approach the authors took to identify mechanisms, as well as the controls put in place to ensure adequate data for analysis. Some questions do remain in the data, and there are aspects of the presentation that could be adjusted.

- The use of a binary colormap for the correlation matrix seems unnecessary. Binary colormaps between two opposing colors (with white in the middle) are best for results spanning positive and negative values (say, correlation values between -1 and +1), but the correlations here are all positive, so a uniform*

colormap should be applied. I can appreciate that the authors were trying to emphasize that a 2+ channel system would lead to lower correlations at larger ratios, but that's emphasized better in the numerical ratio line plots.

We agree and now changed the colour maps accordingly (Fig 1 and 3, p. 4 and 11). Thank you.

- In Figure 1, the correlation matrices in Figure 1 appear blurred out. I am not sure if this was intentional but suspect it was not, and so they should appear like those presented in Figure 3.*

Sorry about that, it was a rendering problem. Now fixed.

- It's notable that the authors also collected data on a timing task to rule out a duration-based strategy in the numerosity task. If possible, it would be great to have the author also conduct the rest of the analyses on the duration task as well; that is, to look at WF correlation matrices/ratios as well as PCA. There is evidence that duration processing is also distinctly sensorimotor, and may also rely on similar channels. Evidence either for or against this would likely be of great interest.*

We agree that investigating the existence of temporal channels would be of great interest, but it goes beyond the scope of the current study. Out of curiosity, however, we analysed the duration data. Interestingly, signatures of sensorimotor channels (correlation gradient as a function on duration distance) emerge. Interestingly, this does not hold when correlating number against duration data. These results (if confirmed) would indicate the existence of independent mechanisms for the time and numerosity perception. Our research agenda is now proceeding in this direction.

- For the duration task, there was no fast-tapping condition. Why not? Was this to keep the overall task length short?*

Yes, this was the main reason.

- The number of subjects/trials seems a bit odd. Why did some subjects perform both and not others? The targets say they were presented "between 25 and 30 times", but why was this variable at all?*

The two experimental conditions were demanding, lasting around 2 hours each. Some participants, unfortunately, were available for just one slot. To make the two conditions similarly powered, we added some extra non-shared participants. Trials were divided into blocks of 55 trials (5 repetitions for each target). Most of the participants performed 6 blocks in both conditions, few of them (again for availability limits) performed 5 blocks.

- For the PCA analysis, my read of the methods and results is that this was done on all the data, across subjects. If the data were run on individual subjects and the resulting PCA components averaged, would the same results be found?*

We thank the reviewer for giving us the opportunity to clarify the technique.

In brief: we measured precision (Weber Fraction) in translating digits (target numbers) into corresponding action sequences. This creates a m by n matrix, each column (n) representing a participant, each row (m) a target number. This matrix was then submitted to PCA. The analyses provided two components. Each target number was assigned with two loading

scores: one representing the loading on the 1st and one on the 2nd component. These loadings were then displayed as a function of targets, to describe the tunings. This analysis, by its nature, is across-participants and cannot be performed on individual data.

- *For the data presented in Figure 2, it would be helpful to also see individual subject data underlaid on the plots to get a sense of individual differences. For the reproduced number, these will likely be clustered together given how small the error bars are, but for the WF data it may show how consistently "flat" the data are. Indeed, in other magnitude reproduction tasks, it is not uncommon to see the WF decrease as a function of target magnitude (or even increase). It may be possible that the reason for the observed findings is that some subjects get more variable (higher WFs) with larger target numbers and others get less variable (lower WFs).*

We agree and now added individual data, confirming flat WF distributions (Fig 2 B&D).

- *Regarding the two-channel model, I wonder how much the results would translate to different ranges of numerosities? For example, are the two channels supported here specific to these ranges of low and high numbers, or would there be a re-mapping to a higher range (say, 32 to 64 dots) or to a narrower range (say 16 to 32 dots). It would be helpful to know if there is any evidence for this kind of remapping.*

This is the first study measuring sensorimotor channels for the transformation of numbers into action sequences. Whether these channels are modulated by the numerical context is an interesting open question that we are exploring through specific experimental conditions (now discussed at p. 17, lines 451-460).

Reviewer #2 Public Review

The authors wish to apply established psychophysical methods to the study of number. Specifically, they wish to test the hypothesis - supported by their previous work - that human sensorimotor processes are tuned to specific number ranges. In a novel set of tasks, they ask participants to tap a button N times (either fast or slow), where N varies between 8 and 32 across trials. As I understood it, they then computed the Weber fraction (WF) for each participant for each number and correlated those values across participants and numbers. They find stronger correlations for nearby numbers than for distant numbers and interpret this as evidence of sensorimotor tuning functions. Two other analyses - cluster analyses and principal component analyses (PCA) - suggest that participants' performance relied on at least 2 mechanisms, one for encoding low numbers of taps (around 10) and another for encoding larger numbers (around 27).

Strengths

Individual differences can be a rich source of scientific insight and I applaud the authors for taking them seriously, and for exploring new avenues in the study of numerical cognition.

Weaknesses

Inter-subject-correlation

The experiment "is based on the idea that interindividual variability conveys information that can reveal common sensory processes (Peterzell & Kennedy, 2016)" but I struggled to understand the logic of this technique. The authors explain it most clearly when they

write "Regions of high intercorrelation between neighbouring stimuli intensity can be interpreted to imply that sets of stimuli are processed by the same (shared) underlying channel. This channel, while responding relatively more to its preferred stimulus, will also be activated by neighbouring stimuli that although slightly different from the preferred intensity, are nevertheless included in the same response distribution." As I understood it, the correlations are performed "between participants, for all targets values" - meaning that they are measuring the extent to which different participants' WFs vary together. But why is this a good measure of channels? This analysis seems to assume that if people have channels for numerical estimation, they will have the same channels, tuned to the same numerical ranges. But this is an empirical question - individual participants could have wildly different channels, and perhaps different numbers of channels (even in the tested range). If they do, then this between-subject analysis would mask these individual differences (despite the subtitle).

Yes, the technique assumes that different individuals have similar channels, and the results confirm this. If everyone had different channels, or different numbers of channels, we would not have found this pattern of results: an ordered scaling of correlations as a function of numerical distance. As specified in the ms, however, this technique (at least as we used it) is not sensitive enough to identify the exact number of channels, so it may have smoothed the results, 'masking' the existence of more than two channels. To avoid possible confounds related to accuracy (reproduction biases), we used Weber Fraction, a standard index of normalized sensory precision (p. 7, lines 182-183).

Different channels

I had trouble understanding much of the analyses, and this may account for at least some of my confusion. That said, as I understand it, the results are meant to provide "evidence that tuned mechanisms exist in the human brain, with at least two different tunings" because of the results of the clustering analysis and PCA. However, as the authors acknowledge, "PCA aims to summarize the dataset with the minimal number of components (channels). We can therefore not exclude the possible existence of more than two (perhaps not fully independent) channels." So I believe this technique does not provide more evidence for the existence of 2 channels as for the existence of 4 or 8 or 11 channels, the upper bound for a task testing 11 different numbers. If we can conclude that people may have one channel per number, what does "channel" mean?

We recognise that the technique is not particularly intuitive, and we apologize for the lack of clarity.

To clarify: we measured the precision in translating digit numbers into action sequences. This was done for different target numbers (8, 10, 11, 13, 14, 16, 19, 21, 24, 28, 32) and with N participants. For each target number, and independently for each participant, we calculated the reproduction precision (Weber Fraction). The dataset comprised a matrix where each column represents a participant, and each row a target number. Each cell contains the corresponding Weber Fraction value. This dataset was then analysed with a simple correlation, across participants. For example, the WFs provided by the N participants when tested at the target number "8" were correlated with those obtained with the target number 10, 11, 13...32. The results show that the correlation between "8 and 10" (low numerical distance) was higher compared to that obtained correlating "8 with 32" (higher numerical distance). This pattern implies that the shared variance, between numbers, scales with numerical distance, across participants: implying the existence of channels aggregating similar numbers (i.e. tuning selectivity). On the same dataset we then ran a PCA. This analysis provides two main components. Within each component, each target number is assigned with a loading score: one for the 1st and one for the 2nd component. These loadings were plotted as a function of targets, to describe the tunings shape (i.e. channels).

As stated above, we cannot really say exactly how many channels exist. These results should be interpreted as evidence for the existence of at least two channels for the transformation of numerical symbols into action sequences. This is not an obvious result at-all. There is no evidence in the literature for the existence of such mechanism in humans. In the animal (crow), there were found as many channels as the numbers tested. This does not contrast with our 2-channel results, but (very likely) arises from the different resolution of the techniques. Single cell recording has surely higher resolution compared to our interindividual covariance approach. In short, we believe that the channels revealed here are likely a coarse summary representation of several underlying channels.

We now tried to make these points clearer (p. 7 lines 186-196; p. 15 lines 382-384; p. 16 lines 401-402):

Several other questions arose for me when thinking through this technique. If people did have two channels (at least in this range), why would they be so broad? Why would they be centered so near the ends of the tested range? Can such effects be explained by binning on the part of the participants, who might have categorized each number (knowingly or not) as either "small" or "large"? Whereas the experiment tested numbers 8-32, numbers are infinite - How could a small number of channels cover an infinite set? Or even the set 8-10,000? More broadly, I was unsure what advantages channels would have - that is - how in principle would having distinct channels for processing similar stimuli improve (rather than impede) discrimination abilities?

This field of study is completely new, with many questions still open, including whether these channels are modulated by the numerical context such as the tested range and their extremes. The channels appear broad because, as stated above, they likely represent a coarse summary representation of several (probably sharper) underlying channels. We are now exploring the effect of numerical range and trying to modulate the tuning widths through ad-hoc experimental conditions. (p. 16 lines 401-402; p. 17 lines 450-459)

No number perception

I was uncertain about the analogy to studies of other continuous dimensions like spatial frequency, motion, and color. In those studies, participants view images with different spatial frequency, motion, or color - the analogy would be to see dot arrays containing different numbers of dots. Instead, here participants read written numerals (like "19"), symbols which themselves do not have any numerical properties to perceive. How does that difference change the interpretation of the effects? One disadvantage of using numerals is that they introduce a clear discontinuity: Our base-10 numerical system artificially chunks integers into decades, potentially causing category-boundary effects in people's reproductions.

We used these sensory analogies to provide a flavour of the technique. The focus of the current study was on the individual differences in the numbers-to-actions transformation process. To this aim we decided to reduce the noise associated with the encoding of the sensory stimulus di per se. Digits encoding, at least with educated adults, is indeed noiseless, eliminating this source of variability. However, we agree that looking at non-symbolic formats would be interesting. We are now collecting data with dots and flash estimations. The results (so far) are largely in line with those found here, ensuring no chunking strategies, and confirming previous literature showing sensory numerosity selective channels in humans and animals. (p. 14 lines 351-355)

Sensorimotor

The authors wished to test for "sensorimotor mechanisms selective to numerosity" but it's not clear what makes their effects sensorimotor (or selective to numerosity, see below). It's true they found effects using a tapping task (which like all behaviour is sensorimotor), but it's not clear that this effect is specific to sensorimotor number reproduction. They might find similar effects for numerical comparison or estimation tasks. Such findings would suggest the effect may be a general feature of numerical cognition across modalities.

Related to the above comment, the task here was to transform noiseless symbols (digits) into (noisy) numerical action sequences. Given that the source of variability is thus mainly driven by the sensory-to-action process, we believe that the task can be safely assumed to be considered sensorimotor in nature. (p. 14 lines 351-355)

Yes, the same pattern of results might be found for numerical comparison or estimation tasks, but using non-symbolic formats (dots/ashes). Educated adults make no errors in naming or comparing such simple digits, making this covariance analysis impossible to be performed with digit verbal estimation or comparison tasks. However, to anticipate our future results, we have preliminary data for dots and flashes verbal estimation tasks ("how many?"). The data are suggesting similar results, consolidating the technique, and confirming the large literature showing sensory channels for purely visual numerosity. (p. 17 lines 453-455)

Specific to numbers

The authors argue that their effects are "number selective" but they do not provide compelling evidence for this selectivity. In principle, their main findings could be explained by the duration of tapping rather than the number of taps. They argue this is unlikely for two reasons. The first reason is that the overall pattern of results was unchanged across the fast and slow tapping conditions, but differences in duration were confounded with numerosity in both conditions, so the comparison is uninformative. (Given this, I am not sure what we stand to learn by comparing the two tapping speeds.) The second reason is that temporal reproduction was less precise in their control condition than numerical reproduction, but this logic is unclear: Participants could still use duration (or some combination of speed and duration) as a helpful cue to numerosity, even if their duration reproductions were imperfect. If the authors wish to test the role of duration, they might consider applying the same analytical techniques they use for numbers to their duration data. Perhaps participants show similar evidence for duration-selective channels, in the absence of number, as they do for other non-numerical domains (like spatial frequency).

The fast and slow conditions were not meant to control for duration strategies but to test for the generalizability of the results over different tapping temporal dynamics (temporal frequency in this case). The results confirmed this.

The control for duration strategies is the comparison between precision in reproducing durations or numbers. In the number-to-action task, participants were free to use any cues, including response duration. However, it is safe to assume that the performance is dominated by the most precise feature, number in this case. In other words, in the number task if participants were reproducing the time required to give a certain number of presses, then in the timing task, where they are explicitly reproducing the same durations, they should show no lower precision. The results are opposite to that prediction. (p. 16 lines 418-420)

Theories of numerical cognition.

An expansive literature on numerical cognition suggests that many animals, human children, and adults across cultures have two systems for representing numerosity

without counting - one that can represent the exact cardinality of sets smaller than about 4 and another that represents the approximate number of larger sets (but see Cheyette & Piantadosi, 2020). The current paper would benefit from better relating its findings to this long lineage of theories and findings in numerical approximation across cultures, ages, and species.

The numbers used in this work were well above the subitizing limit ($>N7$). Indeed, the WFs found showed no signs of subitizing discontinuities. We believe that discussing the literature on subitizing here is too far from the scope of the current work.

Additional public comments from the Reviewing Editor:

(1) What, in the present work, makes the case that the operative mechanism is sensorimotor? The authors frame the discussion around a sensorimotor number system but the evidence here could be seen as using a sensorimotor task as one way to get at an amodal number channel. For example, the authors could do the same experiment but have people watch a circle that flashes on and off for n times, with participants reporting the number of flashes (or shown a number and asked to say more or less). They could then apply the same analyses as used here. If they got the same results, it would seem that this would be an argument against the channels being sensorimotor. I suppose if they did NOT get results in the perceptual task, then they would have (much) stronger evidence that the channels are somehow sensorimotor in nature. Either way, an experiment along these lines would be essential for addressing the nature of the channels (tied to sensorimotor or not).

We chose to use this task because the perception of simple digits (like those used here), at least in educated adults, is noiseless. This ensures that the inter-individual variability remaining on the table is that related to the motor transformation process. For this reason, we believe that the task can be safely considered sensorimotor (see also Kirschhock & Nieder, Number selective sensorimotor neurons in the crow translate perceived numerosity into number of actions, *Nature comm*, 2022). (p. 14 lines 351-355)

This is not true for verbal numerosity estimation of non-symbolic stimuli (such as dots and/or series of events). It is well known that the estimation of the latter stimuli is noisy, and there would be no sensorimotor transformation processing in the task. The inter-individual variability in estimation precision and thus the measurable channels would then reflect sensory numerosity tunings. These have been revealed with various techniques in both humans and animals. However, we are now following this idea and we have preliminary data showing that sensory channels are also detectable by the technique used in the current study. This is not in contrast with the sensorimotor nature of the channels found here, but instead indicating the existence of both sensory and sensorimotor number channels.

The authors may argue that results from other studies such as the 2016 target article make the case about a sensorimotor basis of these channels. While I don't have a great grasp of this literature, my take on the 2016 target article is that the point was not about sensorimotor channels but about interactions between action and vision. This seems more in line with the idea of amodal number channels and indeed, they speak about a "generalized number sense" in that paper.

The 2016 paper showed that a short period of hand tapping (adaptation) can distort visual numerosity perception. The results implied the existence of sensorimotor number channels, integrating non-symbolic numerosity (dots/flashes) and actions. The current study goes beyond this, describing (for the first time) sensorimotor channels transforming symbolic numbers into action sequences. Whether these channels are also in charge to encode non-symbolic numerosity is an interesting open question that we are currently investigating with

cross-tasks analyses. If the same channels are in charge to respond to non-symbolic numerosity (across space and time: dots and sequences of visual/auditory events) as well as to translate digits into actions, we could then speak about a generalized sensorimotor number sense. At present, this remains a possibility, to be tested. (p. 17 lines 450-459)

(2) There is a need for clarification on the method for creating the correlation matrices. The authors write that they look at correlations between Weber fractions between participants. By "between" do they mean "across"? That is, they calculate the Weber fraction for each individual for each cell. Then for a given cell, you correlate its Weber fraction with every other cell, using the pairs for each individual. I would call this "across" not "between." Is this just a semantic thing or have I misunderstood the process?

To make this concrete, consider the correlation for cell 10/11. I assume it is something like

Subj1 .25 .31

Subj2 .13 .09

Subj3 .22 .16

Etc

And correlation across participants will be the data point for the 10/11 cell in the matrix.

It is a semantic error; this is exactly what we did: across participants.

To clarify better: we measured the precision in transforming numbers into sequences of actions. This was done for different target numbers (8, 10, 11, 13, 14, 16, 19, 21, 24, 28, 32) and with N participants. For each target number, and independently for each participant, we then calculated the reproduction precision (Weber Fraction). The dataset then consists of a matrix where each column represents a participant, and each row a target number. Each cell contains the corresponding Weber Fraction. This dataset was then analysed with a simple correlation, across participants. For example, the WFs of the N participants obtained when testing the target number "8" were correlated with those obtained with the target numbers "10, 11, 13...32". The results show that the correlation between "8 and 10" (low numerical distance) was higher compared to that obtained correlating "8 with 32" (higher numerical distance). This pattern implies that the shared variance, between numbers (across participants) scales with numerical distance, in line with the existence of channels that aggregate similar numbers (tunings).

(p. 7 lines 186-196)

(3) The duration data should be analysed. While n is small, can't the authors correlate WFs across tasks? Suppose a similar pattern is observed, suggestive of >1 channel in this between-task correlation.

One of the strengths of this technique is that it is very general, it can be applied to virtually every stimulus feature. We are currently collecting data to test the existence of generalised sensorimotor channels for continuous magnitudes: space, time, and numerosity. The logic is exactly as suggested. These correlational analyses however require (relatively) large samples and ad-hoc experimental conditions. We do not feel confident in providing messages on this with 9 participants. Out of curiosity, however, we analysed the data as requested and the results are interesting: signatures of sensorimotor channels emerge in both the number and duration tasks but NOT when analysed in conjunction (cross-task). If these results will be confirmed, would indicate the existence of separate mechanisms for the encoding of time and numerosity (and perhaps also space?).

(4) The finding of similar results for fast and slow is quite interesting. And provides good motivation to do the duration control experiment. But two issues related to the control experiment:

(4a) Why not look at the correlation matrix for the duration task? Was this not done because there were only 9 participants? If so, why the small n here?

Yes, that is the reason. The aim of this work is not to investigate the existence of duration channels. This experimental condition was designed as a control for the use of non-numerical strategies in the number task. It worked well. The results were already obvious with 9 individuals (confirming Kirschhock & Nieder, Nature comm, 2022); we then did not consider necessary to continue in this direction. However, related to the previous point, we run a preliminary analysis on this small data set and (as mentioned above) signatures of sensorimotor channels (correlation gradients) emerge in both number and duration tasks but NOT when analysed in conjunction (cross-task), indicating different mechanism. We are now pursuing this issue using different number and duration tasks.

(4b) I don't follow why greater precision on the tapping task compared to the duration task makes a strong case against the duration hypothesis. Is the argument that, if based on duration, there should be greater precision on the duration task since the tapping task would exhibit the variability from duration PLUS added noise from tapping? If this is the argument, this should be spelled out.

Yes. The more precise feature dominates behaviour. In other words, in the number task if participants were reproducing the time required to give a certain number of presses, then in the timing task, where they are explicitly reproducing the same durations, they should show no lower precision. The results are opposite to that prediction. (p. 18 lines 418-420)

(4c) Related to point 3 above, one would expect based on things like Rammsayer's study that duration judgments would also engage channels. Is the idea that these are different channels in the tapping task? There seems a good case to have participants do both tapping and duration tasks and then do the correlation matrices, comparing within and between tasks.

Please see response to 3 and 4a.

Recommendations for the authors:

(1) On the logic of the channel concept as applied in the current context:

While the authors present the numerical channel idea by analogy to how this concept is used for other features such as spatial frequency or orientation, there is no input to activate the channels-just a written numeral. The channel concept would mean that to respond to say, "16", you get output from multiple channels, with each weighted by its "tuning" to 16 such that the aggregate results in approximately 16 taps. This seems a bit odd: it would be like saying to draw, I use the output from my spatial frequency channels to create an image with a particular power spectrum. The logic of the channel concept in the current experimental context needs to be reviewed and clarified.

The channel here reflects (probably) the activity of noisy neurons in charge to translate sensory information into a numerical motor output, such as those shown by Kirschhock & Nieder (Nature comm, 2022) in the crows. We used digits because their encoding (at least for such simple digits and educated adults) has no associated noise. The interindividual

variability left, and analysed, is thus mainly associated with the motor transformation process, revealing sensorimotor channels.

(2) A more thorough analysis of the duration task would strengthen the paper. The n is small for this interesting control condition and the analyses presented in the current version of the paper are limited. It is recommended to make this a fully powered test with complete analyses. Consider making this a new experiment in which participants do both the tapping and duration tasks to allow cross-modal analyses.

We run some exploratory analyses on this, described in comments 3 and 4a. We prefer to leave this issue to dedicated future experiments (which are just started).

(3) Expanded discussion of the limitations of the current study. The authors are clear that the methods don't provide a strong test of whether there are two or more than two channels. It would be useful to also comment on whether the estimated locations of the peaks are robust or if there is some sort of statistical bias for them to be at more extreme values. More generally, use the comments on the reviews to elaborate on various issues related to the channel concept.

We addressed these issues in the ms (p. 17 lines 450-459).

(4) Clarify the methods used to calculate the correlation matrix (see reviews).

We now specified better the correlation analyses (p. 7 lines 186-196).

(5) What is the basis for arguing that the mechanism under consideration is a "sensorimotor number system?" The data in this paper do not appear to provide evidence that the effects are linked to sensorimotor processes rather than reflect an amodal number system that is being accessed in their task through the motor system. At a minimum, present arguments for what motivates/justifies the sensorimotor claim or modify the paper to be neutral on this point.

We now specified better the sensorimotor nature of the task used here (p. 14 lines 351-355; see also comment 1).