BRILL

Multisensory Research 38 (2025) 383–402

MULTISENSORY RESEARCH

brill.com/msr

Multisensory Number Channels Derived from Individual Differences

Irene Petrizzo [1,*], **Guido Marco Cicchini** [2], **David Charles Burr** [3,4] **and Giovanni Anobile** [3]

[1] Center for Mind/Brain Sciences, University of Trento, Trento, Italy
[2] Institute of Neuroscience, CNR, *via* Moruzzi, 1, 56124, Pisa, Italy
[3] Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy
[4] School of Psychology, University of Sydney, Camperdown, NSW 2050, Australia
[*]Corresponding author; e-mail: irene.petrizzo@unitn.it
ORCID iDs: Petrizzo: 0000-0001-8736-8278; Cicchini: 0000-0002-3303-0420; Burr: 0000-0003-1541-8832; Anobile: 0000-0003-2796-0661

Received 9 September 2024; accepted 26 June 2025; published online 15 July 2025; published in print 15 December 2025

Abstract

Recently, analysis of differences in individual performance has provided evidence to support the existence of sensorimotor number mechanisms. The individual difference technique assumes that performance for stimuli processed by the same mechanism should be more correlated between individuals than are stimuli processed by different mechanisms. Here we replicated this finding and generalized the results to other sensory modalities. We measured performance for the same participants on three different numerical tasks: a sensorimotor task (series of actions), a temporal numerosity task (series of flashes) and a spatial numerosity task (array of dots). We then searched for tuning selectivity within each task and between task pairs by analysing patterns of correlation between tested numerosities. Correlation within each task showed tuning selectivity in all the three cases, with high positive correlations for nearby target numbers that decreased with numerical distance, providing psychophysical and physiological evidence for the existence of multisensory numerosity channels. Cross-task correlations also suggested a shared tuning between the sensorimotor and temporal visual numerosity, which points to channels responsible for performance in both visual and motor temporal number tasks. However, no shared tuning emerged between spatial visual numerosity and the other two tasks, suggesting partially different patterns of encoding for temporal and spatial numerosity. Taken together our results provide evidence for a similar functional architecture for the three tasks tested here, but also imply that there is no full overlap of shared resources between numerosity domains, suggesting at least partially separated mechanisms of encoding.

Published with license by Koninklijke Brill BV | DOI: 10.1163/22134808-bja10154
 | ISSN: 2213-4794 (print) 2213-4808 (online)

Keywords
Multisensory numerosity, individual differences, Weber fraction, numerosity tunings

1. Introduction

Humans and many other animals can roughly estimate the numerosity of objects and events in the external environment: an approximate number system (Dehaene, 2011; Feigenson *et al*., 2004). This system has been predominantly investigated from a purely sensory perspective, leading to a consensus for the existence of visual and auditory number selective neurons (Castelli *et al*., 2006; Nieder, 2012, 2016; Piazza *et al*., 2004), mainly located in the parietal and prefrontal cortex (Castaldi *et al*., 2019; Harvey *et al*., 2013; Piazza *et al*., 2006) but also in the human medial temporal lobe (Kutter *et al*., 2018).

1.1. Motor and Sensorimotor Number Mechanisms

Recently, the investigation of numerosity has been extended to motor and sensorimotor systems. In a seminal paper, Sawamura *et al*. (2002) discovered motor cells in the monkey parietal cortex selectively tuned to the number of self-produced arm actions. Some years later Kirschhock and Nieder (2022) described sensorimotor cells in the crow brain translating visual numbers (dot arrays and digits) into the corresponding number of actions (pecks). Unlike the cells showed by Sawamura *et al*. (2002), these neurons were active when animals were programming the actions, between the disappearance of the sensory instruction (visual digits and dot arrays) and the start of the motor routine (the series of pecks). The same research group (Kirschhock and Nieder, 2023) went on to show that number production in the crow obeys Weber Law (variability scales linearly with stimuli intensity), a behavioral hallmark of the number sense, previously found for the judgement of sensory numerosity in animals and humans (Anobile *et al*., 2014; Feigenson *et al*., 2004; Ross, 2003).

Human psychophysics has also provided strong evidence for the existence of sensorimotor number mechanisms, with adaptation and individual differences studies. Adaptation is a well-established tool to identify brain mechanisms involved in a task: post-adaptation perceptual distortion implies the existence of neurons tuned to that (adapted) feature (Clifford and Rhodes, 2005; Thompson and Burr, 2009). Burr and Ross (2008) showed that after a sustained presentation of a set of dots with high numerosity, the subsequent array was underestimated (and overestimated after adaptation to a few dots). Arrighi *et al*. (2014) extended this phenomenon to cross-modal and cross-format conditions. Adapting to streams of flashes affected the perceived numerosity of series of flashes (same modality and format) but also of series of tones (different modality, same format) as well as spatial visual arrays of

dots (different modality and format), suggesting a generalised (spatiotemporal) sensory number system.

Numerosity adaptation was then extended to the motor domain. Anobile *et al*. (2016) showed that after a few seconds of fast up-down hand tapping (motor adaptation) the numerosity of arrays of dots and sequences of flashes presented near the adapted region was underestimated (while overestimated after slow tapping). This evidence has been recently replicated (Yang *et al*., 2024), expanded to auditory stimuli (Togoli *et al*., 2020), and demonstrated to reflect a genuine sensory phenomenon (Maldonado Moscoso *et al*., 2020a). Overall these results all point to the existence of a sensorimotor number system (Anobile *et al*., 2021).

1.2. Sensorimotor Number Channels Revealed by Individual Differences

Sensorimotor number mechanisms have also been recently revealed by an individual differences approach. This technique is based on the assumption that performance (usually precision) for stimuli processed by the same mechanism should be more correlated between individuals than those stimulating different mechanisms (Peterzell and Kennedy, 2016): higher correlations between intensity of neighbouring stimuli imply that the sets of stimuli are processed by a shared channel. Channels will respond maximally to their preferred stimuli but will also be activated by neighbouring (slightly similar) stimuli that are included within the response distribution. Conversely, relatively lower correlations between more distant stimuli would indicate that these are processed by separate channels (Peterzell and Teller, 1996). Thus it is possible to infer and describe brain mechanisms by looking at the covariance structure of performance between individuals (Peterzell and Kennedy, 2016). This method has been successfully exploited in the past, to reveal covariance channels tuned to basic visual features such as motion (Morrone *et al*., 1999), spatial frequency (Reynaud and Hess, 2017; Simpson and McFadden, 2005), contrast sensitivity (Peterzell and Teller, 1996; Peterzell *et al*., 1995) colour (Peterzell and Teller, 2000; Peterzell *et al*., 2000), and more recently to compare mechanisms for colour and visual motion (Emery *et al*., 2023).

Following this rationale, Anobile and colleagues (2024) measured participants' precision (Weber fractions) in converting visual digits into the corresponding number of keypresses (without counting). As predicted by the existence of sensorimotor number channels, precision for similar numbers (e.g. 10 *vs* 12, low numerical distance) were more correlated than that for more different numbers (e.g. 10 *vs* 32, high numerical distance), implying tuning selectivity for the translation of digit numbers into action sequences (similar to Kirschhock and Nieder, 2022).

1.3. The Current Study

Whether the numerical sensorimotor channels described above are specific for the number-to-action transformation or also activated by the encoding of purely sensory numerical stimuli (in space and time) is currently unknown. In other words, is the mechanism involved in translating the digit '12' into twelve actions also activated when passively visually inspecting 12 dots and/or 12 flashes? Here we addressed this question with the individual difference approach, described above. We measured the precision in converting digits to actions, as well as precision in estimating dots arrays (visual spatial numerosity) and flash sequences (visual temporal numerosity). Following the individual differences technique, we then calculated the covariance structure emerging within each task and between tasks. In both cases the existence of tuning selectivity predicts relatively higher correlations for similar numbers (low numerical distance), decreasing as numerical distance increases (e.g. the performance for the target number pairs 10–12 should be more correlated than those for the pair 10–32). Given the available physiological and behavioural evidence showing visual (dots and flashes) and visual-to-action mechanisms (described above), we hypothesized the emergence of tuning selectivity within each of the three tasks, considered separately. Regarding the cross-task analyses, two different scenarios are equally possible. If shared mechanisms exist, the prediction is that the correlations obtained by similar numbers – but measured in different tasks – should be higher than those obtained for numbers that are numerically more distant. A lack of this correlation gradient would instead indicate the activation of (at least partially) separate mechanisms.

2. Materials and Methods

2.1. Participants

A total of 48 young people participated in this study (mean age = 24.2 ± 6.3, min = 19, max = 51, 45 right-handed, three left-handed, 34 females). All participants had normal, or corrected-to-normal, vision. 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 was obtained from all participants prior to the experiment.

2.2. Stimuli and General Procedures

Stimuli were generated and presented with PsychToolbox (Brainard, 1997; Kleiner *et al*., 2007; Pelli, 1997) routines for Matlab (ver. R2020b). Participants were tested in a dimly lit, quiet room on three numerical tasks (described below). Participants observed a screen (iMac Retina display 27–inch) placed

frontally approx. 60 cm from the eyes and target numbers were: 8, 10, 11, 13, 14, 16, 19, 21, 24, 28, 32. Each target was presented (in random order) 30 times (90 across the three tasks) divided into 6 separate blocks of 55 trials (for a total of 990 trials across the three tasks). The three numerical tasks (Digit-to-Action, Digit-to-Visual-Sequence, Visual-Dots-Estimation) were administered in separate conditions. Overall, the experiment required approx. 3 h of testing for each participant. To minimise fatigue, participants were tested in two separate days (approx. 1.5 h of testing each day). The order of conditions was counter-balanced across participants. Before the testing, participants were familiarized with the tasks performing one block of trials presenting each target once (in random order), with feedback (a digit displaying: the number of tapping's performed, or the number of flashes presented or the number of dots in the array, see below for details). These data were not analysed, and no feedback was provided during the rest of the experiment.

2.2.1. Digit to Action Task

This task follows that previously published by Anobile and colleagues (2024) and was designed to index the ability to translate digits into numerical action sequences (Fig. 1A). On each trial a digit (5° of visual angle) was presented in the centre of the screen for 1 s. As soon as the digit disappeared participants started to tap (up-down) as fast as possible with the dominant hand,

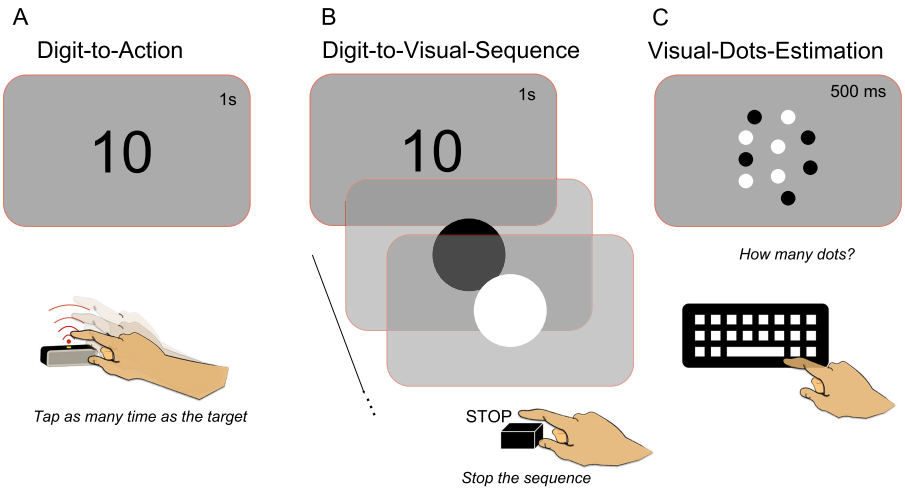

Figure 1. Schematic representation of the three tasks. (A) Digit-to-action: on each trial participants were asked to tap mid-air as many times as a target digit. (B) Digit-to-visual-sequence: on each trial participants were first presented with a visual target digit and soon after with a series of visual flashes. The task was to stop the sequence (by key press) when the number of flashes matched the target number. (C) Visual-dots-estimation: on each trial participants were presented with a dot array and asked to estimate the number of dots. In tasks A and B serial counting was prevented by subvocal suppression.

until they felt that the number of actions matched the target. To minimize sensory feedback, participants tapped mid-air with the hand positioned behind a vertical black panel positioned to the right (or left) to the monitor so that the moving hand and arm were hidden from view. Hand movements were monitored by an infrared motion sensor device (Leap motion controller https://www.leapmotion.com/) running at 60 Hz. Serial counting was prevented by vocal suppression, repeating aloud the syllable 'ba' (for a similar procedure see: Anobile *et al*., 2024; Cordes *et al*., 2001; Whalen *et al*., 1999).

Digit to Visual Sequence Task. This task was designed to mimic the Digit-to-Action task, but without the motor production component (Fig. 1B). On each trial a target digit was presented in the centre of the screen (same as above), then replaced with a series of flashes (50 ms black or white circles, subtending 5° of visual angle). Participants were asked to interrupt (by keypress) the visual sequence when they felt that the number of flashes matched the target. The temporal frequency of the flashes was 7.5 Hz, and to avoid regular patterns, each flash was slightly jittered in time (max 50 ms). As before, counting was prevented by vocal suppression.

2.2.1.1. Visual Dots Estimation Task. This task was designed to measure visual numerosity perception in the spatial domain (Fig. 1C). On each trial, a circular (5° radius) array of white and black (50%, to balance luminance) dots (0.25° diameter) was briefly (500 ms) presented in the centre of the screen and participants were asked to estimate their numerosity and to enter the response *via* keypress. In this case, given the brief presentation time, no vocal suppression was needed.

2.2.2. Data Analyses

2.2.2.1. Pre-processing. In the Visual Dots Estimation task, the first tested numerosity (N8) might have triggered groupitizing strategies (Maldonado Moscoso *et al*., 2020b) resulting in a much higher performance, compared with the other target numerosities. For this reason, to avoid spurious results, we removed N8 from further analyses (as a precaution, we also analysed the data including this target number and the results remained unchanged). We then detected and eliminated outlier responses separately for each participant and for each target number (responses falling beyond 1.5 interquartile, approx. 3% of trials for each task).

After this step, we indexed performance as accuracy and precision separately for the three task, target number and participant. Accuracy was indexed as the mean reproduction or response (depending on the task) across trials and precision as Weber fraction, computed as responses standard deviation divided by the average reproduction/response. All the analyses were performed with Matlab software (ver. R2020b) and JASP software (version 0.19).

2.2.3. Correlation Matrices and Correlation Gradient: Within-Task Analysis
In the next step we computed WF correlation matrices separately for each of the three tasks. The dataset comprised a matrix where each column represents a participant, each row a target number, and each cell the corresponding WF. This dataset was analysed with a pairwise correlation (Pearson). For example, the WFs provided by the participants when tested with the target number '10' were correlated with those obtained with the target numbers 11, 13, 14, …, 32. According to the technique rationale, if channels exist, the correlation between '10 and 11′ (low numerical distance) should be higher than that between '10 and 32′ (higher numerical distance). To better visualize the results, we then analysed the correlation strength obtained with the described procedure as a function of numerical distance. This analysis was performed on binned data. Bins were created to have an approximately equal number of observations for each bin (6, 6, 7, 7, 6, 6, 6). For each target, the numerical distance was expressed as the base ten logarithm ratio between itself and the remaining target numbers (e.g. 6 and 60 would be one log-unit away). The correlation coefficients were then averaged in the following bins (log10 ratios): <0.06, 0.06–0.11, 0.11–0.16, 0.16–0.22, 0.22–0.28, 0.28–0.35, >0.35. To test whether the correlation coefficients decreased as a function of numerical distance (as predicted), we fitted the unbinned correlation coefficients with a linear fit.

We checked significance with a bootstrap procedure, performing the same analysis on randomized correlation matrices. On each of 10,000 iterations, separately for each participant, the WFs were assigned at random to the target numbers and a new correlation matrix computed. Then (as before) the correlation coefficients were averaged within the reported bins (for visualization) and fitted with best linear fit, yielding a null-hypothesis distribution.

Following previous studies using similar covariance techniques (Emery *et al*., 2023; Morrone *et al*., 1999; Peterzell and Teller, 2000; Peterzell *et al*., 2000; Reynaud and Hess, 2017; Simpson and McFadden, 2005), we also ran Principal Component Analysis (PCA) on WFs. This analysis provides an efficient data visualization of the tuning structure. The principal component analysis was performed on normalized WFs and factors rotated with the non-orthogonal promax method. We selected the number of components explaining at least 70% of the variance (see Anobile *et al*., 2024 for a similar procedure).

2.2.4. Correlation Matrices and Correlation Gradient: Between-Task Analysis
Before looking at the correlation strength as a function of numerical distance, we first run a more classic correlation analysis between tasks. This analysis was performed on between-participants average WFs, across numerical targets (raw WFs). Shared resources between tasks predict positive correlations.

Calculating correlations across tasks as function of numerical distance presents a specific challenge. Correlation between raw values of WFs in two tasks reflects both the correlation of the underlying perceptual systems (which we seek) and the correlation between tasks (which we do not want to measure in this analysis). The presence of correlation between tasks is a strong nuisance factor and can have positive as well as negative effects on the ability to detect the genuine correlation specific to the numerosity. For instance, pairs of numerosities and tasks which impinge on the same mechanism may not turn out fully correlated if the two tasks are not perfectly correlated. Likewise, pairs of numerosities and tasks which do not share the neural substrate may still yield a positive correlation if the two tasks are correlated. For this reason, to isolate the genuine component that is specific to the numerosities we standardized participant performance across each task. This was done calculating Z scores. So, for each participant we first considered individual WFs at all numerosities for a given task and then removed the mean and divided by the standard deviation of the set. As before we then analysed the correlation strength between each pair of numerosity across tasks as a function of numerical distance with bins created to have an approximately equal number of observations (10, 12, 12, 14, 14, 12, 12, 12). The correlation coefficients were averaged within the following numerical distance bins (absolute value of log10 ratios): <0.01, 0.01–0.06, 0.06–0.11, 0.11–0.16, 0.16–0.22, 0.22–0.28, 0.28–0.35, >0.35. As before, to test whether the correlation coefficients decreased as a function of numerical distance, we fitted the unbinned correlation coefficients with linear fit, and as the same analysis was also performed on values obtained from randomized correlation matrices to obtain the null-hypothesis distribution.

3. Results

3.1. Within-Modality Covariance Channels

In three separate tasks, we asked participants to perform a specific number of mid-air hand taps to match a visual target number (Digit-to-Action), or to stop a sequence of visual flashes when their number reached a target (Digit-to-Visual-Sequence), or to estimate the numerosity of dot arrays (Visual-Dots-Estimation). Performance was indexed by average responses/reproduction and precision (variability of response, given by Weber fraction, WF). Figure 2A shows between-participants responses/reproduction as a function of target numbers. For all tasks the average response was near veridical, close to the diagonal (Fig. 2A). Figure 2B shows precision (WF). Precision was higher (lower WFs) in the Visual-Dots-Estimation task (0.16 ± 0.004 standard error of the mean [SEM]), compared with the other two tasks (0.21 ± 0.009 SEM

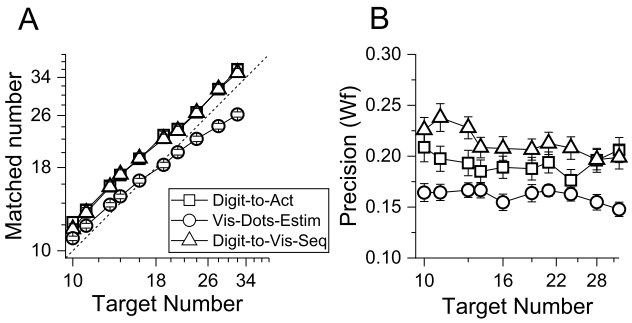

Figure 2. Numerical accuracy and precision. (A) Average estimated/reproduced numerosity as a function of target numbers divided by tasks (squares: digit-to-actions, circles: dots estimation, triangles: digit-to-visual sequences). (B) Average Weber fractions (WFs) as a function of target numbers for the three tasks (same conventions as in A). Error bars are ±1 SEM.

and 0.19 ± 0.01 SEM for Digit-to-Visual-Sequences and Digit-to-Action tasks respectively, t-test $p < 0.003$ for both).

Following the individual difference approach (Peterzell and Kennedy, 2016), we then analysed the data of each of the three tasks separately, to extract sensorimotor and visual covariance tuning channels. Figure 3A,C,E shows WF's correlation matrices (from top to bottom: Digit-to-Action, Digit-to-Visual-Sequences, Visual-Dots-Estimation). The colour of each cell indicates the correlation strength (red high) obtained for a specific numerical comparison. All correlations were positive, ranging from 0.1 to 0.9. Importantly, the correlation values were not uniformly distributed within the matrices, but there were higher correlations around the diagonal (low numerical distance), as predicted by tuning selectivity. To better visualize and quantify this trend, Fig. 3 (panels B, D and F, same task order) shows average binned correlations as a function of numerical distance (see Section 2. Materials and Methods). For all the three tasks there was a descending trend as numerical distance increases, indicating that participant performance correlated more for neighbouring numbers. Linear fits of (unbinned) data confirmed the negative slopes (Digit-to-Action: $b = -0.32$, Digit-to-Visual-Sequence: $b = -0.31$, Visual-Dots-Estimation: $b = -0.64$) all different from zero ($p < 0.012$ for all the tasks). Importantly, the negative trend does not emerge when the matrices were randomized (black symbols, see Section 2), confirming that the negative trend found with original data was genuinely driven by the numerical distance structure and not by a statistical artefact. Each randomized distribution was linearly fit, and the distribution of the slopes confirmed to be statistically different from the slope obtained with the real data ($p < 0.02$ in all cases). These results suggest the existence of tuning selectivity for each of the three tasks.

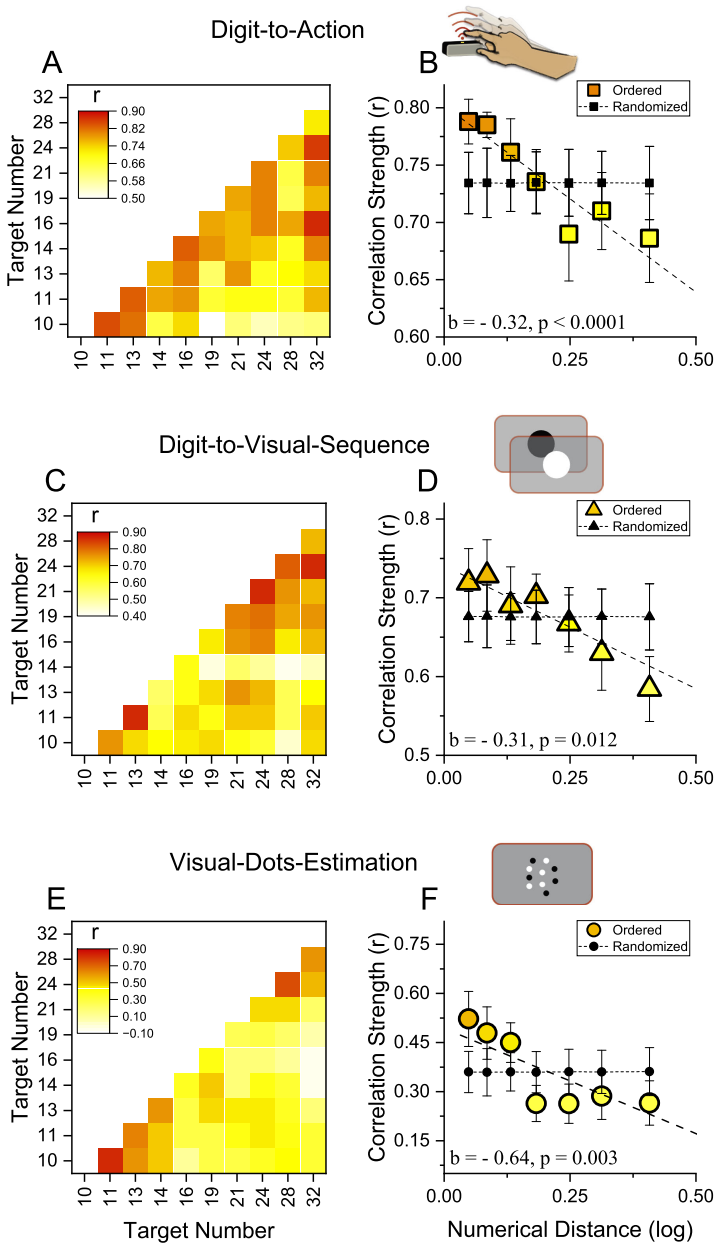

Figure 3. Sensorimotor and visual covariance numerosity channels. (A,C,E) Correlation matrices of Weber fractions for all pairs of target numbers. (B,D,F) Correlation strength as a function of numerical ratio. Coloured symbols show binned data obtained from the analyses of original ordered data. Small, black symbols show bootstrapped average correlation strengths of randomized Weber fraction (WF) matrices. Dashed lines are the best linear fit on unbinned data and error bars are ±1 SEM.

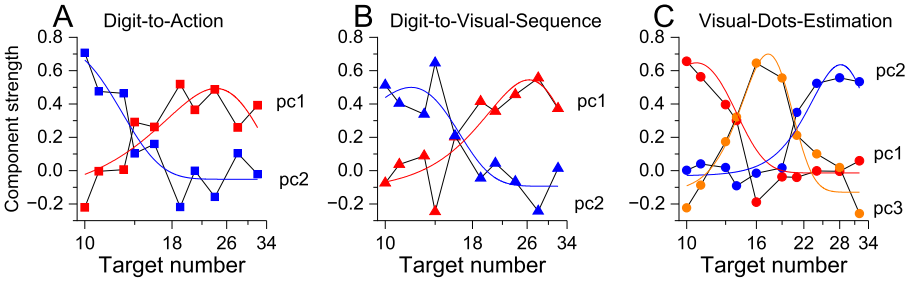

Figure 4. Principal components factor loadings as a function of target numbers. The strength of the extracted principal components from principal components analysis (PCA) on the Weber fractions measured in the digit-to-action (A), the digit-to-visual-sequence (B) and the visual-dots-estimation tasks. The strength of the components is shown as a function of the different numerical target levels. The smooth curves are logGaussian fits to the component strengths.

To further characterize the structure of the number channels we applied PCA) on WFs, separately for each task. Figure 4 shows the (rotated) component strength as a function of target numbers. The results revealed two bell-shaped tuning functions for the Digit-to-Action and the Digit-to-Visual-Sequence tasks (Fig. 4A,B) and three components in the Visual-Dots-Estimation task (Fig.4C, the values of the third component were multiplied by -1 to ease interpretation). For all the tasks, the factor strength distributions were reasonably well described by Gaussian functions (all $R^2 > 0.70$) peaking at different target numbers (Digit-to-Action: N8 and N24; Digit-to-Visual Sequence: N10 and N28; Visual-Dots-Estimation: N10, N17 and N28).

3.2. Between-Modality Covariance Channels

So far, the results have replicated previous evidence for sensorimotor mechanisms tuned to the number of actions triggered by sensory inputs (Anobile *et al.*, 2024) and extended the results to visual numerosity perception in temporal and spatial domains.

We then asked whether these three numerical tasks share common or separate mechanisms. Before looking at the cross-task covariance structure as a function of numerical distance, we ran a more typical correlation analysis between tasks. Figure 5 shows WFs averaged across numerical targets. Overall, the analysis shows positive trends between task performance, indicating that participants doing better (higher precision) on a specific numerical task also perform generally better in the others ($r = 0.40$, $p = 0.004$; $r = 0.35$, $p = 0.013$ and $r = 0.28$, $p = 0.05$ for panels A, B and C, respectively).

The positive correlations between tasks suggest shared resources. However, this analysis is too coarse to describe common channels. We then ran the same covariance analyses used before on individual tasks, between tasks. The rationale is the same: if the different tasks tap shared numerical channels,

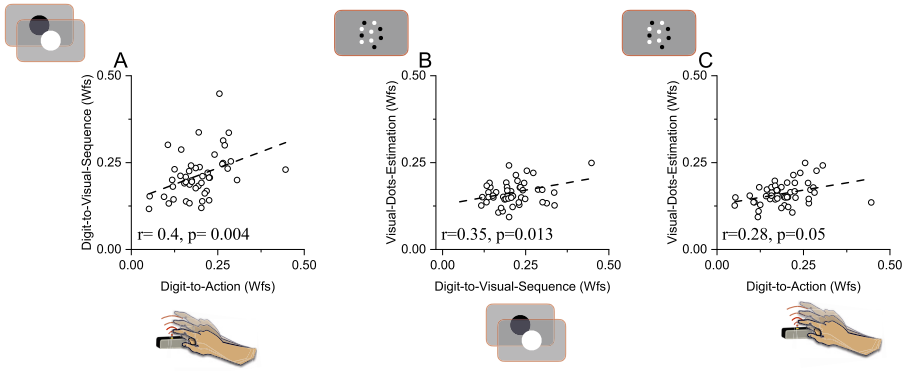

Figure 5. Correlation between tasks. Scatter plots between Weber fractions (WFs; averaged across numerical targets) obtained in the three numerical tasks. Dashed lines are the best linear fit.

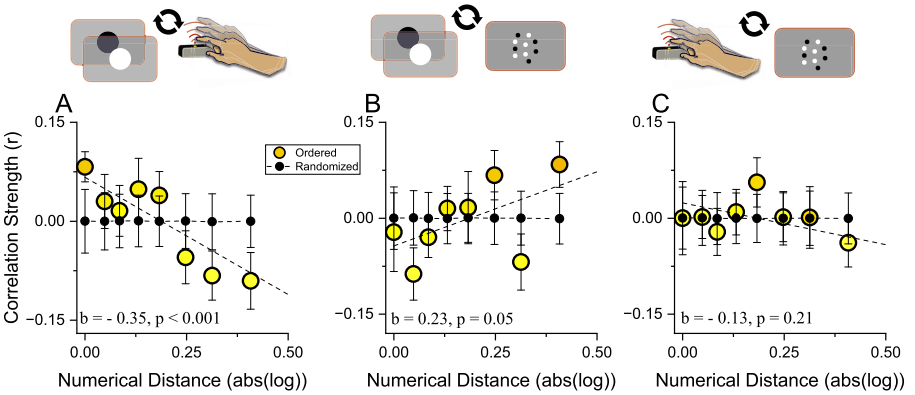

Figure 6. Between-tasks covariance channels. Correlation strength as a function of numerical ratio. Empty symbols report bin average correlation coefficients calculated from the original, ordered data. Black symbols show the results as bootstrapped average correlation strengths obtained by the same analyses but performed on randomized Weber fraction matrices. Dashed lines are the best linear fit on unbinned data and error bars are ±1 SEM.

the performance (WFs) for similar numbers (low numerical distance) should be more correlated than that obtained for different numbers (high numerical distance). Figure 6A–C shows the results for the three tasks pairs. Correlation values in this analysis are lower than those obtained before for within-task analysis (e.g. Fig. 3). However, it is worth mentioning that the correlations presented here originate from standardized values from which the common correlation across numerosities has been removed, so are necessarily smaller. In any event, the expected pattern of the results is the same as before: if similar

numerosities shared perceptual systems, similar numerosities should display the highest correlations.

This prediction held true when comparing the performance of the Digit-to-Action task with that of the Digit-to-Visual-Sequence task (Fig. 6A), with the results showing a clear descending trend of correlations strength as a function of numerical distance ($b = -0.35$, $p < 0.0001$, clearly different from that obtained by randomized data depicted in Figure 6A as filled symbols, with a sign-test yielding $p = 0.002$). The results for the other two task comparisons showed no reliable descending pattern, with results similar to the control randomized data (Digit-to-Visual-Sequence *vs* Visual-Dots-Estimation task $b = 0.23$, $p = 0.05$, sign-test with random distribution $p = 0.03$; Digit-to-Action *versus* Visual-Dots-Estimation $b = -0.13$, $p = 0.21$, bootstrap sign-test $p = 0.15$; Fig, 6B, C respectively).

4. Discussion

This study had two main aims. The first was to generalize the covariance technique previously used to reveal sensorimotor number channels to purely visual numerical stimuli in space (dots) and time (series of flashes). The second was to test for shared tuning selectivity between these three numerosity formats. To this aim we measured the same participants on three different numerical tasks and then, with a well-established covariance technique based on individual differences (Peterzell and Kennedy, 2016), searched for tuning selectivity within each task and between task pairs.

The tasks measured numerosity perception and reproduction in the visual and sensorimotor domains across space and time. In the temporal sensorimotor task participants had to transform symbolic numbers (visual digits) into the corresponding number of hand actions (up-down tapping). In two visual tasks they had to stop a sequence of visual flashes when reaching a previously presented target digit (temporal) or to verbally estimate the perceived number of dots simultaneously presented as briefly spatial arrays (spatial). To measure an intuitive sense of numerical quantities (Anobile *et al*., 2014), all the tasks were performed without the possibility to serially count the events/objects and performance was indexed by estimation/reproduction precision (Weber fraction).

The results within each task show tuning selectivity in all the three cases, confirming psychophysical and physiological evidence for the existence of tuning selectivity for visual (Burr *et al*., 2018; Ditz and Nieder, 2015, 2020; Piazza *et al*., 2004) and sensorimotor (Anobile *et al*., 2016a, 2024; Kirschhock and Nieder, 2022, 2023; Sawamura *et al*., 2002) numerosity. In line with the rationale of this technique, in all cases, the performance for similar numbers correlated more than that from different numbers and Principal Component

Analyses revealed partially overlapping bell-shaped tuning channels, peaking at different target numbers. Moreover, the performance obtained in the three separate tasks follows Weber Law (precision scales linearly with stimulus intensity, consistent with the activation of the Approximate Number System) and average performance (averaged Weber fraction across numerical targets) correlated positively between tasks, suggesting that the three tasks used shared resources or at least similar mechanisms. Overall, the results performed within each task highlight the usefulness of this technique to characterize the structure of the non-symbolic number system, regardless of the numerical format of the stimuli and the task being used.

However, clear patterns also emerged between tasks. Performance in the spatial numerosity task (Visual-Dots-Estimation) was much higher than both visual and sensorimotor temporal tasks, and while the two temporal tasks revealed two qualitatively similar tuning channels, three channels emerged from the spatial numerosity task, suggesting different organizational principles. In line with this, the between-task covariance analysis contrasting the performance in the spatial (Visual-Dots-Estimation) and temporal (Digit-to-Visual-Sequence) visual numerosity tasks revealed no shared tuning with correlations even showing a weak but positive trend (probably indicating differences in the way numbers are represented across different formats).

These results suggest a different functional architecture for temporal and spatial numerosity in the visual domain, with a finer grain representation of spatial numerosity (three channels and lower WF). That visual and spatial numerosity might rely on (at least) partially different mechanisms fits well with a previous imaging investigation showing the activation of different brain areas (Cavdaroglu and Knops, 2019), and with a developmental study showing that visual spatial but not temporal numerosity sensitivity (Weber fraction) correlates with math scores in children (Anobile *et al*., 2018).

Other evidence for partially separated systems for these two numerical formats comes from a psychophysical adaptation study. Arrighi *et al*. (2014) demonstrated that adapting to a series of flashes distorted the subsequent estimation of numerosity of sets of spatial items (dots), suggesting shared mechanisms. However, this cross-format adaptation effect was much attenuated for the opposite condition in which the authors adapted to a set of elements and tested with a series of flashes. While the reasons behind the asymmetry in the adaptation effect are unknown, it suggests that the encoding of these two numerical formats might not share completely overlapping mechanisms. This is in line with an animal study from Nieder and colleagues (Ditz and Nieder, 2020). The authors recorded neuronal activity in the crow's brain while performing visual numerosity tasks (delayed match-to-sample task) with spatial (dots) and temporal (series of flashes) numerical formats. During the

sensory representation stage (when inspecting the stimuli), temporal and spatial numerosity were extracted by different populations of neurons. However, after this encoding phase, while animals kept numbers into working memory to solve the task, another neural population represented numerosity in both formats.

Overall, these results suggest that visual numerosity perception of spatial ensembles and temporal sequences share resources during their processing hierarchy, but also have different basic encoding properties and different functional architectures. Previous studies have suggested that various numerosity tasks share common resources. This was predicted because of task correlations, behavioural similarities (e.g. both follows Weber Law) and cross adaptation (Anobile *et al*., 2016a, b, 2018; Arrighi *et al*., 2014; Dehaene, 2003). The technique presented here, however, represents a step forward as it addresses the mechanism for processing individual numerosities. Our research has revealed that there is very little correlation specific to similar numerosities. While this interpretation seems to us plausible, and fits with the observation in crows, we cannot completely discard the possibility that the lack of shared covariance channels was due to the difference between the tasks. Subsequent studies are needed to re-examine this issue using more similar tasks designed to equate possible sources of noise.

Going beyond visual numerosity, the results obtained by the sensorimotor number task (Digit-to-Action) fully replicated a recent work (Anobile *et al*., 2024) showing a clear descending pattern of correlations as a function of numerical distance and two bell-shaped tuning channels (at least in this numerical range). Interestingly, the overall precision (across numerical targets) in this task was (positively) correlated with that in both temporal (Digit-to-Visual-Sequence) and spatial (Visual-Dots-Estimation) visual tasks, again suggesting similar mechanisms. Importantly, the results of the between-task covariance analyses revealed clear evidence for shared tuning channels between the visual and visuomotor temporal number tasks. The correlational analyses as a function of numerical distance demonstrated a strong descending pattern, meaning that similar numbers tested by these two different tasks correlated more than different numbers. These results are in line with a study showing that a period of hand tapping (motor adaptation) distorted the numerosity estimation of subsequently presented flash sequences (Anobile *et al*., 2016a), indicating the existence of a sensorimotor number system (Anobile *et al*., 2021). Similar results have been then obtained with temporal auditory stimuli (series of tones), suggesting that the system might be generalized across visual and auditory numerical formats (Togoli *et al*., 2020), an issue worth investigating with the covariance technique in the future.

Some might argue that the emergence of this shared tuning could reflect the temporal rather than numerical features of the stimuli/responses. With the

current data we cannot definitely discard this possibility. However, the literature indicates that the Digit-to-Action task is based on the number of discrete actions, rather than the overall response duration. Indeed, a previous study using the same task (Anobile *et al*., 2024) showed that if instead of asking individuals to translate a digit number into a series of actions, they are asked to reproduce (again by tapping) the duration of a sound, the precision in the latter task was significantly lower compared to the numerical task, suggesting that no temporal strategies were used during the numerical task. Similar results come also from animal physiology (Kirschhock and Nieder, 2022), showing that the visual-number-to-action neuronal tunings in crows were independent from the temporal structure of the motor response phase (series of pecks in that case). Overall, the results are in line with the existence of tuned channels in the human brain dealing with both visual and motor temporal number tasks.

At odds with this, the results contrasting the sensorimotor performance with the spatial visual task (Visual-Dots-Estimation) did not reveal robust evidence for shared tuning. While the correlation strengths show a qualitatively negative trend as a function of numerical distance (Fig. 6C), the trend was quantitatively weak (slope −0.13). This result is somehow different from that previously obtained with motor adaptation, as a series of hand tappings was found to also reliably distort spatial numerosity estimation (Anobile *et al*., 2016a; Maldonado Moscoso *et al*., 2020a; Yang *et al*., 2024), suggesting that the two techniques (covariance channels and adaptation) might capture different aspects of cross-modal numerical processing. However, as mentioned before, also in this case we cannot rule out the possibility that post-perceptual noise sources might have mitigated the current results.

The investigation of the mechanisms underlying numerosity perception has attracted increasing attention in the scientific community, generating results from many different disciplines. However, most of these studies have focused on purely sensory mechanisms (visual and acoustic predominantly), leaving out the motor and sensorimotor systems. Only recently the link between action and numerosity perception is gaining attention (Anobile *et al*., 2016a, 2021, 2024; Kirschhock and Nieder, 2023; Ranzini *et al*., 2022). The current study shows, with a relatively fast and non-invasive behavioural technique, that there exist brain mechanisms that integrate the number of visual events in the external environment with that internally self-generated by actions. While the investigation of this multisensory numerical mechanism has just started, and many questions are still open, the current study reinforces the idea that it exists and proposes the covariance technique as a useful tool to investigate its nature.

Besides the specific number-related results of the current study, some more general implications can be drawn. While the covariance technique used here has been extensively applied to reveal channels for visual features (Emery *et*

al., 2023; Morrone *et al*., 1999; Peterzell and Kennedy, 2016; Peterzell and Teller, 2000; Peterzell *et al*., 1995; Reynaud and Hess, 2017; Simpson and McFadden, 2005), to the best of our knowledge, this is the first time it has been applied in a multisensory perspective, to reveal channels shared between different stimuli and tasks. The results indicate that this technique is general and robust enough to be applied to multisensory research, paving the way for other investigations. Taken together, it would be interesting to fully understand what this technique can bring compared with other techniques more typically used to reveal cross-modal mechanisms, such as cross-modal adaptation.

Since the use of individual differences to reveal number channels is a rather novel design, this study has limitations. The observed descending pattern of correlations as a function of numerical distance, although possibly caused by tuning selectivity, could also emerge for other reasons. If participants all obeyed to a sort of 'imperfect Weber's Law', with each observer starting from a specific baseline and then evolving an idiosyncratic manner, there would be higher correlations for similar numerosities, as those highlighted in Figure 3. It is worth noting however, that the reverse is also true. A pool of observers with two channels which cross-faded into each other as function of numerosity would exhibit a pattern of Weber fractions akin to that of an idiosyncratic violation of Weber's law. The two scenarios are thus intertwined and hard to be teased apart without specific ad hoc experiments.

Acknowledgement

The first two authors should be considered shared first authors. 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 by the European Union Next Generation EU–PRIN 2022 (DD 104, 02/02/22)–PNRR–M4–C2–INV1.1–PRIN – Project title: 'Sense of number *vs* sense of quantity: Modeling, neuroimaging, behavior' (ID: 2022EBC78W – CUP E53D23008820006). Data for the main findings of this study are available at: 10.5281/zenodo.13711231.

References

Anobile, G., Cicchini, G. M. and Burr, D. C. (2014). Separate mechanisms for perception of numerosity and density, *Psychol. Sci.* **25**, 265–270. DOI:10.1177/0956797613501520.

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

Anobile, G., Cicchini, G. M. and Burr, D. C. (2016b). Number as a primary perceptual attribute: a review, *Perception* **45**, 5–31. DOI:10.1177/0301006615602599.

Anobile, G., Arrighi, R., Castaldi, E., Grassi, E., Pedonese, L., Moscoso, P. A. M. and Burr, D. C. (2018). Spatial but not temporal numerosity thresholds correlate with formal math skills in children, *Dev. Psychol.* **54**, 458–473. DOI:10.1037/dev0000448.

Anobile, G., Arrighi, R., Castaldi, E. and Burr, D. C. (2021). A sensorimotor numerosity system, *Trends Cogn. Sci.* **25**, 24–36. DOI:10.1016/j.tics.2020.10.009.

Anobile, G., Petrizzo, I., Paiardini, D., Burr, D. C. and Cicchini, G. M. (2024). Sensorimotor mechanisms selective to numerosity: evidence from individual differences, *eLife* **12**, RP92169. DOI:10.7554/eLife.92169.2.

Arrighi, R., Togoli, I. and Burr, D. C. (2014). A generalized sense of number, *Proc. R. Soc. B Biol. Sci.* **281**, 20141791. DOI:10.1098/rspb.2014.1791.

Brainard, D. H. (1997). The Psychophysics Toolbox, *Spat. Vis.* **10**, 433–436.

Burr, D. and Ross, J. (2008). A visual sense of number, *Curr. Biol.* **18**, 425–428. DOI:10.1016/j.cub.2008.02.052.

Burr, D., Anobile, G. and Arrighi, R. (2018). Psychophysical evidence for the number sense, *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20170045. DOI:10.1098/rstb.2017.0045.

Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A. and Eger, E. (2019). Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream, *eLife* **8**, e45160. DOI:10.7554/eLife.45160.

Castelli, F., Glaser, D. E. and Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: a functional MRI study, *Proc. Natl Acad. Sci. U. S. A.* **103**, 4693–4698. DOI:10.1073/pnas.0600444103.

Cavdaroglu, S. and Knops, A. (2019). Evidence for a posterior parietal cortex contribution to spatial but not temporal numerosity perception, *Cereb. Cortex* **29**, 2965–2977. DOI:10.1093/cercor/bhy163.

Clifford, C. W. G. and Rhodes, G. (2005). *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. Oxford University Press, Oxford, United Kingdom. DOI:10.1093/acprof:oso/9780198529699.001.0001.

Cordes, S., Gelman, R., Gallistel, C. R. and Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers, *Psychon. Bull. Rev.* **8**, 698–707. DOI:10.3758/BF03196206.

Dehaene, S. (2003). The neural basis of the Weber–Fechner law: a logarithmic mental number line, *Trends Cogn. Sci.* **7**, 145–147. DOI:10.1016/S1364-6613(03)00055-X.

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

Ditz, H. M. and Nieder, A. (2015). Neurons selective to the number of visual items in the corvid songbird endbrain, *Proc. Natl Acad. Sci. U. S. A.* **112**, 7827–7832. DOI:10.1073/pnas.1504245112.

Ditz, H. M. and Nieder, A. (2020). Format-dependent and format-independent representation of sequential and simultaneous numerosity in the crow endbrain, *Nat. Commun.* **11**, 686. DOI:10.1038/s41467-020-14519-2.

Emery, K. J., Volbrecht, V. J., Peterzell, D. H. and Webster, M. A. (2023). Fundamentally different representations of color and motion revealed by individual differences in perceptual scaling, *Proc. Natl Acad. Sci. U. S. A.* **120**, e2202262120. DOI:10.1073/pnas.2202262120.

Feigenson, L., Dehaene, S. and Spelke, E. (2004). Core systems of number, *Trends Cogn. Sci.* **8**, 307–314. DOI:10.1016/j.tics.2004.05.002.

Harvey, B. M., Klein, B. P., Petridou, N. and Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex, *Science* **341**, 1123–1126. DOI:10.1126/science.1239052.

Kirschhock, M. E. and Nieder, A. (2022). Number selective sensorimotor neurons in the crow translate perceived numerosity into number of actions, *Nat. Commun.* **13**, 6913. DOI:10.1038/s41467-022-34457-5.

Kirschhock, M. E. and Nieder, A. (2023). Numerical representation for action in crows obeys the Weber–Fechner law, *Psychol. Sci.* **34**, 1322–1335. DOI:10.1177/09567976231201624.

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R. and Broussard, C. (2007). What's new in Psychtoolbox-3, *Perception ECVP 2007 Abstr. Suppl.* **36**, 1–16.

Kutter, E. F., Bostroem, J., Elger, C. E., Mormann, F. and Nieder, A. (2018). Single neurons in the human brain encode numbers, *Neuron* **100**, 753–761.e4. DOI:10.1016/j.neuron.2018.08.036.

Maldonado Moscoso, P. A., Castaldi, E., Burr, D. C., Arrighi, R. and Anobile, G. (2020a). Grouping strategies in number estimation extend the subitizing range, *Sci. Rep.* **10**, 14979. DOI:10.1038/s41598-020-71871-5.

Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R. and Burr, D. (2020b). Adaptation to hand-tapping affects sensory processing of numerosity directly: evidence from reaction times and confidence, *Proc. R. Soc. B Biol. Sci.* **287**, 20200801. DOI:10.1098/rspb.2020.0801.

Morrone, M. C., Burr, D. C., Di Pietro, S. and Stefanelli, M.-A. (1999). Cardinal directions for visual optic flow, *Curr. Biol.* **9**, 763–766. DOI:10.1016/S0960-9822(99)80338-8.

Nieder, A. (2012). Supramodal numerosity selectivity of neurons in primate prefrontal and posterior parietal cortices, *Proc. Natl Acad. Sci. U. S. A.* **109**, 11860–11865. DOI:10.1073/pnas.1204580109.

Nieder, A. (2016). The neuronal code for number, *Nat. Rev. Neurosci.* **17**, 366–382. DOI:10.1038/nrn.2016.40.

Pelli, D. G. (1997). The *VideoToolbox* software for visual psychophysics: transforming numbers into movies, *Spat. Vis.* **10**, 437–442. DOI:10.1163/156856897X00366.

Peterzell, D. H. and Kennedy, J. F. (2016). Discovering sensory processes using individual differences: a review and factor analytic manifesto, *Electr. Imaging* **28**, 1–11. DOI:10.2352/ISSN.2470-1173.2016.16.HVEI-112.

Peterzell, D. H. and Teller, D. Y. (1996). Individual differences in contrast sensitivity functions: the lowest spatial frequency channels, *Vision Res.* **36**, 3077–3085. DOI:10.1016/0042-6989(96)00061-2.

Peterzell, D. H. and Teller, D. Y. (2000). Spatial frequency tuned covariance channels for red–green and luminance-modulated gratings: psychophysical data from human adults, *Vision Res.* **40**, 417–430. DOI:10.1016/S0042-6989(99)00187-X.

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

Peterzell, D. H., Chang, S. K. and Teller, D. Y. (2000). Spatial frequency tuned covariance channels for red–green and luminance-modulated gratings: psychophysical data from human infants, *Vision Res.* **40**, 431–444. DOI:10.1016/S0042-6989(99)00188-1.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D. and Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus, *Neuron* **44**, 547–555. DOI:10.1016/j.neuron.2004.10.014.

Piazza, M., Mechelli, A., Price, C. J. and Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: an fMRI study, *Brain Res.* **1106**, 177–188. DOI:10.1016/j.brainres.2006.05.104.

Ranzini, M., Scarpazza, C., Radua, J., Cutini, S., Semenza, C. and Zorzi, M. (2022). A common neural substrate for number comparison, hand reaching and grasping: A SDM-PSI meta-analysis of neuroimaging studies, *Cortex* **148**, 31–67. DOI:10.1016/j.cortex.2021.12.007.

Reynaud, A. and Hess, R. F. (2017). Characterization of spatial frequency channels underlying disparity sensitivity by factor analysis of population data, *Front. Comput. Neurosci.* **11**, 63. DOI:10.3389/fncom.2017.00063.

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

Sawamura, H., Shima, K. and Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey, *Nature* **415**, 918–922. DOI:10.1038/415918a.

Simpson, W. A. and McFadden, S. M. (2005). Spatial frequency channels derived from individual differences, *Vision Res.* **45**, 2723–2727. DOI:10.1016/j.visres.2005.01.015.

Thompson, P. and Burr, D. (2009). Visual aftereffects, *Curr. Biol.* **19**, R11–R14. DOI:10.1016/j.cub.2008.10.014.

Togoli, I., Crollen, V., Arrighi, R. and Collignon, O. (2020). The shared numerical representation for action and perception develops independently from vision, *Cortex* **129**, 436–445. DOI:10.1016/j.cortex.2020.05.004.

Whalen, J., Gallistel, C. R. and Gelman, R. (1999). Nonverbal counting in humans: the psychophysics of number representation, *Psychol. Sci.* **10**, 130–137. DOI:10.1111/1467-9280.00120.

Yang, H., Jia, L., Zhu, J., Zhang, J., Li, M., Li, C. and Pan, Y. (2024). The interplay of motor adaptation and groupitizing in numerosity perception: insights from visual motion adaptation and proprioceptive motor adaptation, *PeerJ* **12**, e16887. DOI:10.7717/peerj.16887.