

## Opinion

## A Sensorimotor Numerosity System

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**Incoming sensory input provides information for the planning and execution of actions, which yield motor outcomes that are themselves sensory inputs. One dimension where action and perception strongly interact is numerosity perception. Many non-human animals can estimate approximately the number of external elements as well as their own actions, and neurons have been identified that respond to both. Recent psychophysical adaptation studies on humans also provide evidence for neural mechanisms responding to both the number of externally generated events and self-produced actions. Here we advance the idea that these strong connections may arise from dedicated sensorimotor mechanisms in the brain, part of a more generalized system interfacing action with the processing of other quantitative magnitudes such as space and time.**

**A Sensorimotor Numerosity System**

Early physiological studies suggested that the cerebral cortex is organized in many areas, each functionally specialized to analyze different features of the perceptual environment [1,2]. Recent work, however, is beginning to show very strong interactions between different perceptual features, pointing to shared associative mechanisms. Perhaps the most prominent proposal is the A Theory Of Magnitude (ATOM) model [3], positing that the human parietal cortex processes jointly quantitative information about space, time, and number to optimize action planning and execution [3,4]. This theory has spawned multiple studies investigating how the perception of space, time, and number relies on shared mechanisms, with less attention dedicated to how perceptual information combines with action programming and execution.

Here we propose that, for the perception of number, or **numerosity** (see [Glossary](#)), there exists a common neural system subserving both action and perception: a sensorimotor numerosity system, tuned to numerosity signals from both perception and action planning and execution. This proposal is supported by a range of studies suggesting that mechanisms processing the numerosity of externally generated events (regardless of sensory modality or presentation format) may also process internally generated events, such as goal-directed motor routines. We also review evidence suggesting that a sensorimotor system of this type may process quantitative information of non-numerical dimensions such as space and time.

**Numerosity Estimation**

The number of items is represented in humans by two distinct processes: a cultural and language-dependent system that encodes precisely the cardinality of elements; and a more primitive system shared with a variety of non-human species termed the approximate number system (ANS), which encodes quantity (or numerosity) in an approximate, non-symbolic manner [5,6]. Numerosity perception differs from both symbolic number representation (digits) and serial counting, in that it is rapid, parallel, and approximate. Numerosity estimation errors scale proportionally to physical numerosity, following Weber's law, at least over a limited range [7,8]. This opinion deals almost exclusively with the notion of numerosity, so the proposed functional and anatomical mechanisms may be distinct from those dedicated to processing exact quantities.

**Highlights**

Behavioral studies show that humans and other animals can estimate the numerosity of both external stimuli and self-produced actions.

Recent psychophysical studies using motor-adaptation techniques have characterized the link between action and magnitude perception, advancing the concept of a sensorimotor system encoding both external stimuli and internally generated actions.

The sensorimotor numerosity system might reside in the parietal cortex.

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Humans and animals can estimate the numerosity not only of external events, but also of self-generated actions. For example, mice learn to press a lever a defined number of times for a reward, with average responses and variability increasing proportionally to the target number of repetitions (scalar variability) [9]. Bees estimate the distance between the nest and a feeder by combining the number of visual landmarks with other cues of travelled distance, some of them likely to be related to internal variables such as estimates of energy spent or flight duration [10]. Desert ants estimate the number of steps to infer walked distance; if their legs are elongated or shortened, they over- or underestimate distance [11]. Processing of the numerosity of internally generated events plays a critical role in frog mating behavior: in some species female frogs select mates by the number of 'chuck sounds' they make, which in turn affects male responses, which must match or exceed the chucks of competitors [12].

When humans are asked to reproduce a target number with a series of fast motor repetitions (without counting), both the mean and the variability of the estimates scale linearly with target number. The pattern of results closely resembles that of a perceptual version of the task where participants verbally estimate the numerosity of impulses of rapid sequences of flashes [13].

Taken together, the studies suggest that humans and other species estimate the numerosity of self-generated actions and that the characteristics of this function closely resemble those associated with the estimation of sensory stimuli. Further evidence for interactions between action and numerosity perception comes from studies on saccadic eye movements in humans. At the time of fast saccadic eye movements, visual estimates of the numerosity of a cloud of dots become strongly compressed [14], paralleling similar effects that occur in space and time [15, 16]. Fast saccades toward the more numerous of two arrays can be executed very quickly (latencies as short as 190 ms), suggesting a link between action and numerosity systems through dedicated pre-attentive mechanisms operating on feed-forward signals [17]. Distortions also occur with manipulations of symbolic numbers, where participants underestimate the results of additions and subtractions when digits are presented at the time of saccades [18].

### Perceptual and Motor Number Neurons

The neural substrates of numerosity perception in both animals and humans is reasonably well understood. A series of seminal electrophysiological studies [19–23] has shown that single-cell activity in the prefrontal and parietal cortices of macaques is specifically tuned to the numerosities of both spatial arrays and temporal sequences (Figure 1A,B). In humans, similarly tuned responses to numerosity have been recorded from the horizontal part of the intraparietal sulcus (HIPS) with an fMRI habituation paradigm [24]. Interestingly, in monkeys, cells in parietal sensorimotor area 5 [located near the ventral intraparietal area (VIP)] respond to the number of self-generated motor actions (Figure 1C [25]). Monkeys were trained to perform an arm movement (e.g., push) five times, then to switch to another movement (e.g., turn) for another five times and then back to the initial movement. Around a third of the cells in sensorimotor area 5 were selectively tuned to a specific repetition of the motor routine, shown by the normalized activity of the number-action cells in Figure 1C. Furthermore, transient pharmacological inactivation caused numerical errors in repetition of actions (while not producing motor deficits), demonstrating a causal link between the activity of these neurons and action numerosity [26]. Given the low numerosities involved (around 5), monkeys may have engaged in counting rather than estimation, but the study nevertheless demonstrates a clear link between number and action.

There is also evidence for numerosity tuning of single-cell activity from the medial temporal lobe (MTL) of human neurosurgical patients performing calculation tasks on symbolic and non-symbolic stimuli [27]. The first operand and the subsequent delay period elicited clear responses

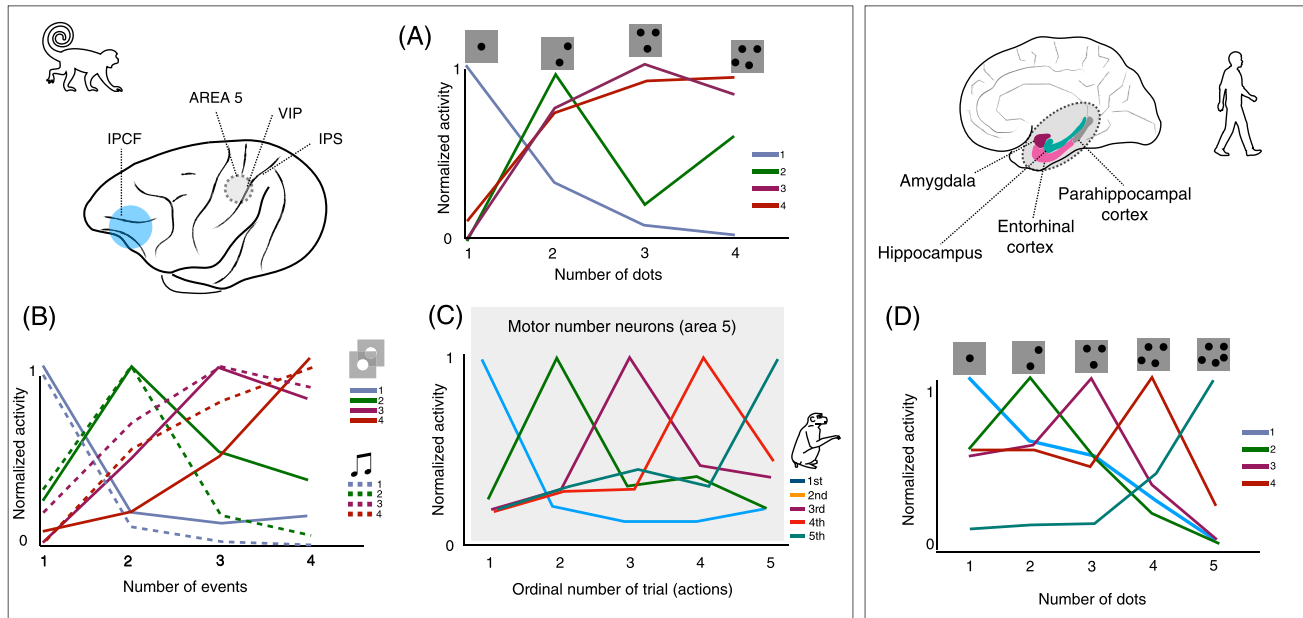
### Glossary

**Numerosity:** number is represented in humans by two distinct processes – a cultural and language-dependent system that encodes precisely the cardinality of elements and a more primitive system termed the ANS, which encodes quantity (or numerosity) in an approximate, non-symbolic manner. Numerosity perception is rapid, parallel, and approximate, and errors scale proportionally to physical numerosity following Weber's law, at least over a limited range.

**Perceptive field:** the portion of space that elicits perceptual responses. Perceptive fields can be estimated by psychophysical adaptation techniques by varying the spatial interval between the adaptor and the test. When the adaptor stimulates a portion of space outside the receptive field activated by the test stimulus, no adaptation effects are expected. Perceptive fields are often considered to be the perceptual correlate of neural perceptive fields.

**Point of subjective equality (PSE):** the point along a stimulus dimension at which a variable stimulus is judged to be equal to a standard stimulus. At that point the probability of judging the variable stimulus as larger or smaller than the other is 50%. The PSE is usually given by the median (50%) of psychometric functions describing the probability of judging the variable stimulus as larger than the other.

**Weber fraction:** the smallest variation that can be perceived, normalized by the perceived (or sometimes physical) magnitude test stimulus. In discrimination experiments it is typically derived from psychometric functions as the stimulus change needed to pass from the PSE to a certain criterion (e.g., 75% correct response), normalized by the PSE. In magnitude estimation experiments it can be measured as the ratio of the standard deviation and the perceived mean of the responses.



## Trends In Cognitive Sciences

**Figure 1. Numerosity-Tuned Neurons.** (A) Numerosity neurons recorded from monkey prefrontal cortex. Monkeys memorized the numerosity of a dot ensemble (sample), then after a delay period of 1 s indicated whether a second stimulus (match) had the same or different numerosity. The graph shows the normalized activity of neurons during sample presentation, clearly tuned to spatial numerosity (dots). (B) Neurons tuned to temporal numerosity (flashes and sounds) recorded from monkey prefrontal and parietal cortices. Monkeys memorized the numerosity of a sequence of pulses to compare with the numerosity of a dot ensemble. Tuning similar to numerosity perception of spatial ensembles emerged. (C) Action numerosity neurons recorded from monkey area 5. Monkeys performed a specific arm movement five times, then made another movement another five times, then the initial movements again. The graph shows the normalized activity of neurons during the waiting period between each movement. Several units showed preferential activation when the monkey was waiting for a given number of movement repetitions. (D) Numerosity selective neurons recorded from intracranial electrodes in human medial temporal lobe of surgical patients performing a calculation task, summing or subtracting two successive dot clouds. The figure shows the average activity of neurons recorded during the presentation of the first stimulus. As with monkeys, some neurons show stronger responses for a given, preferred numerosity. Reproduced, with permission: (A,B) [20], (C) [26], and (D) [27]. Abbreviations: IPCF, lateral prefrontal cortex; IPS, intraparietal sulcus; VIP, ventral intraparietal area.

from the hippocampus, parahippocampal cortex, entorhinal cortex, and amygdala for both non-symbolic (Figure 1D) and symbolic numbers. Most number-selective cells were found in the parahippocampal cortex, which is highly interconnected with frontal and parietal areas. It also contains cells activated by hand-grasping execution and observation [28], opening the possibility that this area could mediate the interaction between number and action.

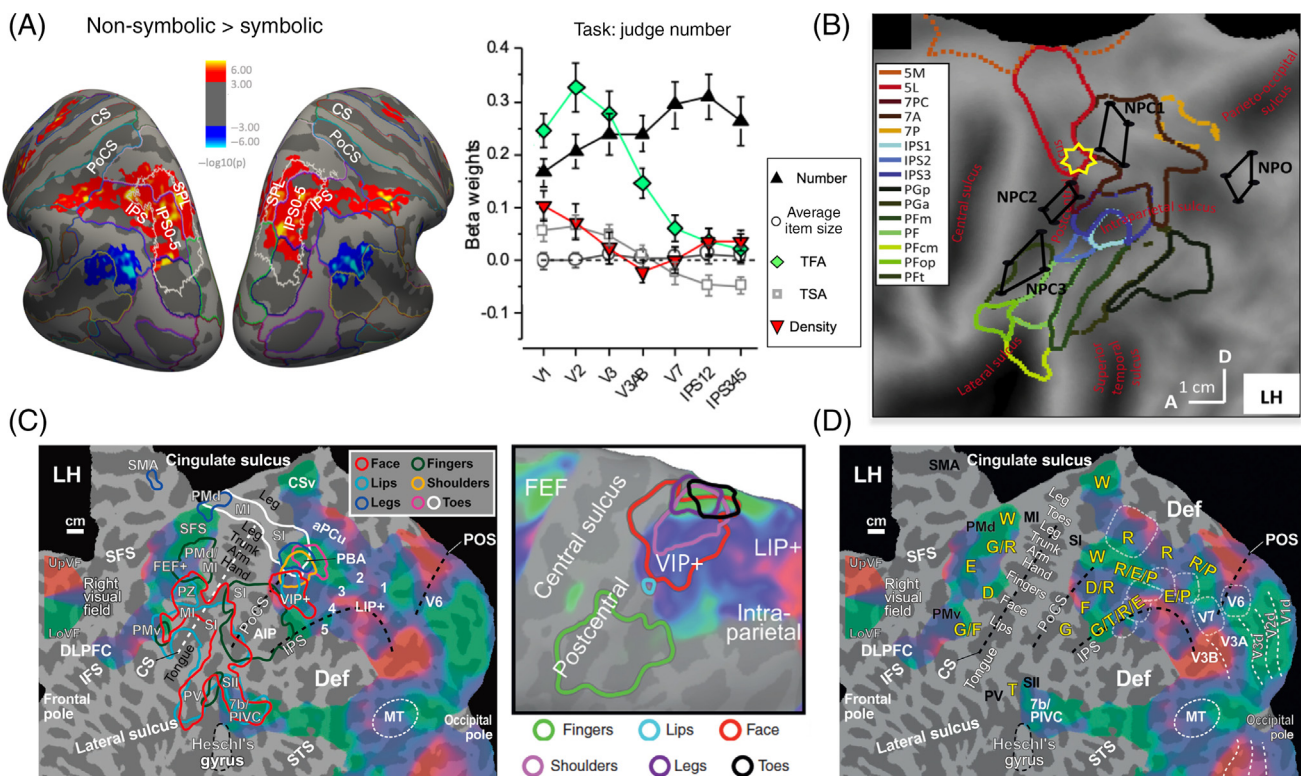
### Numerosity and Action in the Human Brain

Imaging studies in humans have shown that regions activated during numerosity perception are located nearby and in partial overlap with action areas (eye or hand movements) in the parietal cortex [29,30]. Recent studies have used functional and structural criteria to define putative human homologs of macaque areas [31–37]. For example, a decoder trained to distinguish leftward from rightward saccades in a likely homolog of area lateral intraparietal (LIP) generalized to distinguish between subtraction and addition [35], both symbolic and non-symbolic, nicely complementing the psychophysical studies showing the influence of saccades on arithmetic [18]. In addition to the LIP, another study [32] localized the human homolog of area VIP with visual motion and tactile stimulation of the face and found that both regions encode the numerosity of visual arrays in multivoxel patterns of evoked activity.

Using a phase-encoding mapping technique, six field maps have been identified along the human IPS, the most posterior (IPS1/2) a candidate homolog of the monkey LIP, and the most anterior

(IPS3/4/5) candidate homolog of the monkey VIP [38]. These regions, located in the superior/medial parts of the IPS and superior parietal gyrus, are more active when visually processing non-symbolic numerical quantities than digits [39] and selectively encode the numerosity of visual arrays in patterns of activity [31] (Figure 2A). Population receptive-field mapping techniques [34,36] have revealed topographically organized maps (NCP1–3) in partial overlap with these regions, which are selective to non-symbolic numerosities. Like the macaque VIP, area NCP1 is located posterior to a region of visual tactile convergence (Figure 2B [33]). This region may correspond to area 5 [40], which in monkeys hosts neurons involved in the sensorimotor control of limb action [41], including numerosity [25,26].

Interestingly, a recent study found that a nearby parietal area with another numerosity map (area NCP3) is recruited during numerical processing of observed actions [42]. Other studies identified a multisensory homunculus along the posterior central sulcus (PoCS), posterior to the primary somatosensory cortex and extending into the inferior PoCs and anterior intraparietal sulcus. The hand representation is ‘out of order’ and located lateral and anterior to the region VIP+ [responsive to tactile stimulation of the face (Figure 2C); for a review see [43]]. Upper and lower



**Figure 2. Multisensory and Number-Responsive Regions.** (A) Areas in the intraparietal cortex recruited for visual processing of arrays of items over Arabic numerals. Colored outlines identify the major anatomical sulci and gyri based on the Destrieux Atlas [83] on a FreeSurfer average surface; white outlines identify the field maps IPS0–5 based on visual topography [84]. Beta weights obtained from the RSA multiple regression analysis for number (black triangles), average item size (circles), total field area (TFA) (diamonds), total surface area (TSA) (squares), and density (red triangles) while participants were judging the numerosity of the arrays. (B) Flattened maps of left parietal lobe of human PALS B12 brain atlas. Black lines identify the human numerosity maps, with the yellow star approximately corresponding to a region of visuotactile integration. (C,D) A group-average map of somatotopic areas activated by passive tactile stimulation on six body parts (C) and a model of action representation (D). D, defense; E, eye movements; F, feeding; G, grasping; P, pointing; R, reaching; T, touching; W, walking. Reproduced, with permission: (A) [31,37], (B) [33], and (C) [43,85].

limbs are also represented intermingled in a more medial region in the superior parietal lobe. These areas have been implicated in the sensory and visuomotor control of actions such as reaching and grasping and defensive and feeding behaviors (Figure 2D). The proximity of areas supporting hand movements and numerosity representation may mediate the psychophysical interaction between hand tapping and numerosity, which we will discuss in some detail.

Overall, given the role in sensorimotor integration and action guidance played by these areas, it is likely that they are implicated in the behavioral interactions between numerosity and action. Together with the prefrontal cortex, implicated in the maintenance of working memory of supramodal (visual, auditory, and tactile) numerosity information [44,45], and with the mediotemporal regions containing numerosity selective neurons [27], these parietal areas may constitute the neural substrate of the proposed sensorimotor number system in humans. Although these hypotheses are largely speculative, the anatomical proximity of areas recruited for numerosity and action processing could favor their interaction, as has been proposed for numerosity and size processing [46].

### Psychophysical Evidence for a Sensorimotor Numerosity System

The animal electrophysiological and human imaging evidence for brain mechanisms dedicated to numerosity find strong support from psychophysical studies in humans leveraging the technique of adaptation (Box 1). Perceptual adaptation is one of the most simple, powerful, and robust behavioral techniques to probe sensory mechanisms: after observing a particular stimulus (adapter) for some time, subsequent stimuli are usually misperceived, showing strong negative aftereffects. Adaptation aftereffects are assumed to reflect changes in the response functions of the neurons selective to a particular feature [47–50] and hence reveal properties of the underlying perceptual mechanisms: ‘if you can adapt it, it’s there’ [51].

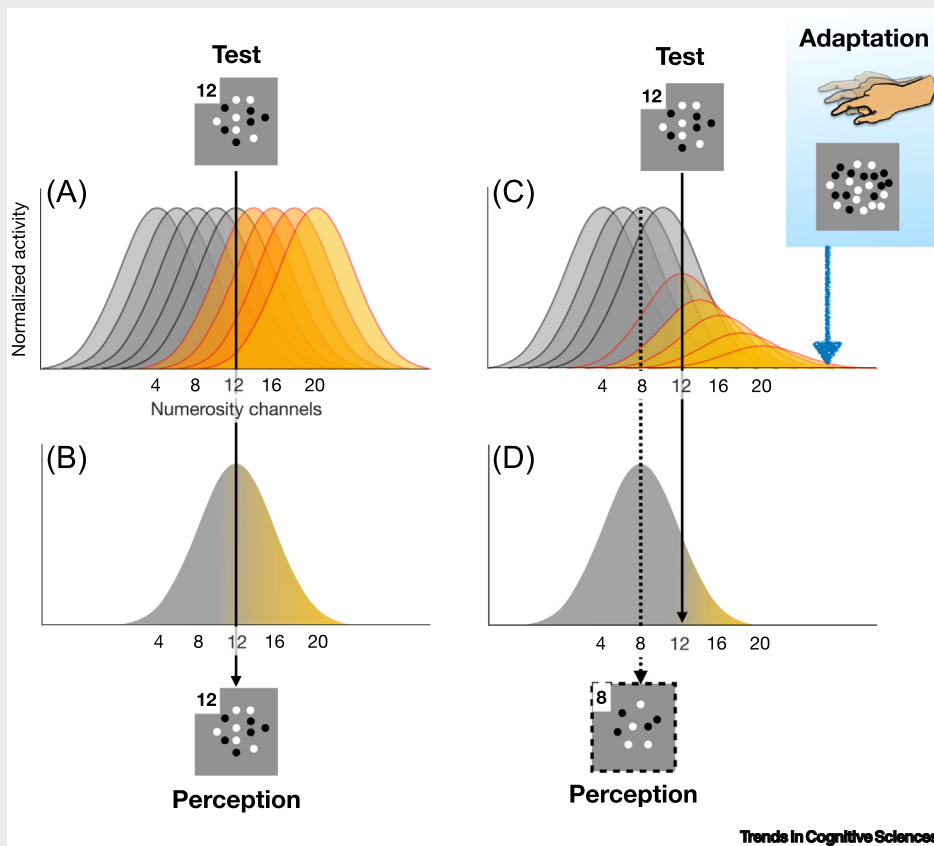
Burr and Ross [52] demonstrated that, like most perceptual attributes, visual numerosity is highly susceptible to adaptation (see also [53]). After exposure to a dense dot array for several seconds, the numerosity of a subsequent array was strongly underestimated (and vice versa for low-numerosity adapters). The period of adaptation need not be long, with strong adaptation effects after less than 1 s of exposure [54]. Numerosity adaptation changes the pattern of numerosity-evoked activity in the parietal region: classifiers trained to discriminate between numerosities before adaptation did not generalize to the same numerosity after adaptation and vice versa [55].

Adaptation is not limited to the numerosity of spatial arrays. Adapting to a series of rapid flashes causes underestimation in the apparent numerosity of subsequent sequences of flashes and vice versa [56]. The adaptation effects occur with sounds as well as flashes and also cross-modally: adapting to sound sequences distorts the numerosity of both sounds and flashes and vice versa. Most surprisingly, the effects are cross-format: adapting to sequences of flashes distorts the apparent numerosity of spatial arrays of dots. Taken together, these psychophysical results support the idea that the numerosity of stimuli is a primary perceptual attribute like color, orientation, or motion. At some stage of encoding, numerosity becomes independent of perceptual characteristics such as sensory modality or presentation format [52,56,57]. These adaptation studies, together with electrophysiological studies [20] reporting supramodal and cross-format numerosity neurons in the monkey, strongly point to a generalized number sense.

Anobile *et al.* [57] developed a psychophysical adaptation technique to further characterize sensorimotor numerosity mechanisms in humans. Participants were required to tap in mid-air for several seconds (adaptation phase) then judge the numerosity of a visual stimulus displayed

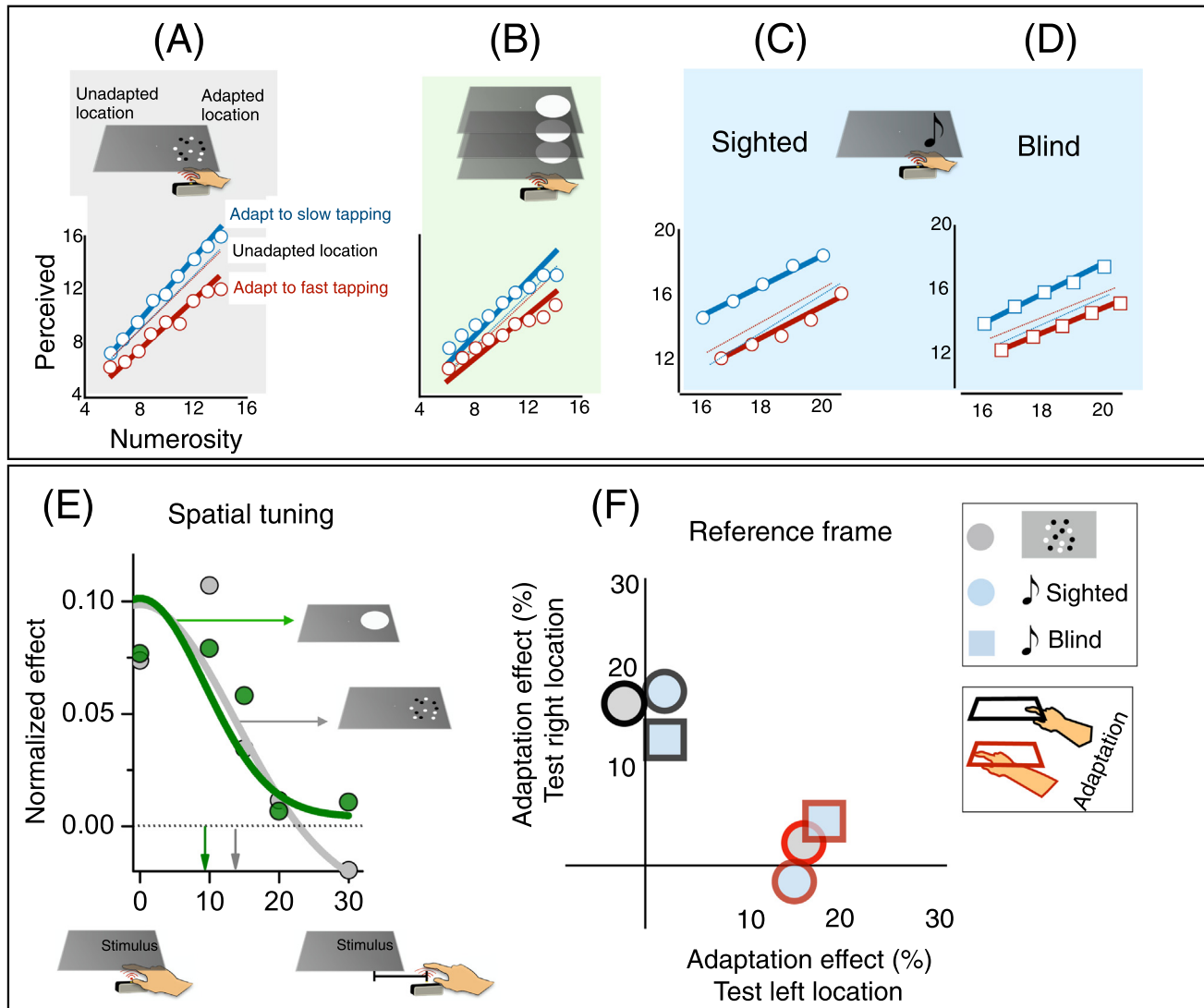
**Box 1. Perceptual Adaptation**

Perceptual adaptation is a psychophysical technique that can reveal and characterize specific sensory mechanisms. The technique typically involves an adaptation phase where the participant passively observes an adaptor stimulus for a period and is then asked to judge a test stimulus, typically by comparing it with another stimulus in an unadapted location. Adaptation usually causes misperception of specific aspects of the stimulus, such as direction of motion, which become biased in the opposite direction to the adaptor: after observing for a few seconds the downward movement of a waterfall, shifting gaze to the adjacent region will cause it to appear to move upward [78]. This phenomenon is attributed to an imbalance in the relative activities of neurons tuned to vertical motion after sustained stimulation of those tuned to downward motion. The test stimulus will then tap a system that is functionally unbalanced, producing measurable illusory perceptual aftereffects. This technique can reveal neural populations sensitive to the tested feature (e.g., numerosity) and give information on how it is functionally organized, revealing selectivity to specific stimulus features such as motion direction, orientation, size, perceptual numerosity (Figure 1), and many others [49]. Adaptation is ubiquitous throughout all sensory systems, representing a form of short-term plasticity, probably serving as a tool to calibrate perception to their environment statistics [68,69,79–81].



**Figure 1. Schematic Representation of the Adaptation Aftereffect.** (A) Activity of hypothetical numerosity channels tuned to specific numerosities (4, 8, 12, 16, and 20 in the example). Before adaptation, a test stimulus of 12 dots would cause the strongest activity in the channel tuned to 12 (B) and the perception will be veridical. (C) Repeated exposure to a highly numerous dot array (or numerous actions) would decrease the activity of the neurons encoding high numerosities, leaving relatively unchanged those encoding lower numerosities. (D) A test stimulus of 12 dots would now cause stronger activity in a channel tuned to a lower numerosity (eight in the example), shifting the perception toward lower numbers and causing the classic negative aftereffect.

near the tapping region. Motor adaptation distorted apparent numerosity in the same way as visual adaptation (Figure 3A,B [57]): after a short period of adaptation to rapid tapping, participants underestimated the number of stimuli presented near the tapping region, while adaptation to slow tapping caused overestimation. During the motor adaptation phase, participants were asked not to



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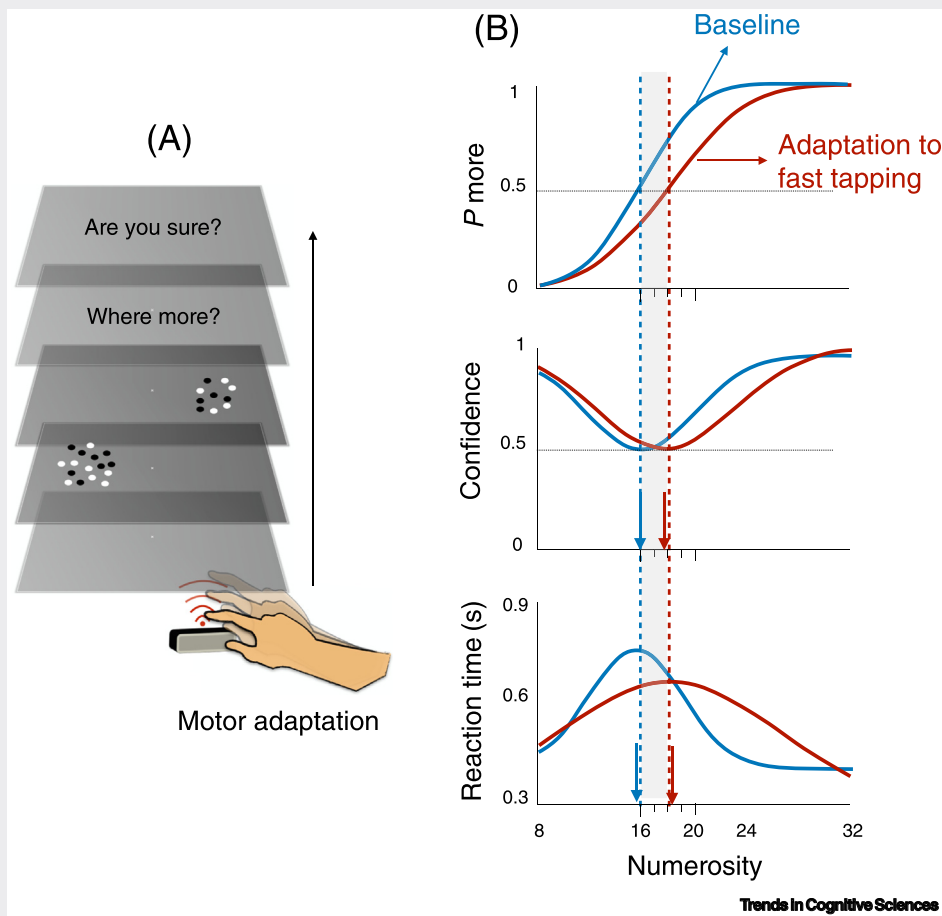
**Figure 3. Motor Adaptation Effect on Numerosity Perception.** (A–D) Participants tapped rapidly or slowly in mid-air while fixating a central point on a blank monitor (motor adaptation). After the adaptation phase (~6 s) a stimulus was briefly (~250 ms) presented around the motorically adapted region or in the opposite hemifield. After a sequence of fast tapping, the perceived numerosity of dots (A), flashes (B), and sounds (C) were all underestimated compared with slow adaptation (red compared with blue symbols). The motor adaptation effects were all spatially selective, occurring only for stimuli presented around the adapted location (unbroken lines) and not extending to stimuli presented in the opposite hemifield (broken lines). The effect on the auditory numerosity also occurred in congenitally blind adults (D). (E) The spatial selectivity of the adaptation effect was broad, occurring for all stimuli falling within a radius of ~10° (arrows) around the motorically adapted region. In this case motor adaptation was performed in separate blocks at various distances relative to the visual stimuli (flashes and dots). (F) The reference frame of the motor adaption effect on numerosity was world centered: tapping with the right hand in the right hemisphere affected stimuli presented in the right hemisphere (black), while tapping with the right hand in the left hemisphere affected stimuli presented in the left hemisphere (red). The same reference frame describes selectivity in blind adult participants (square symbols). Reproduced, with permission: (A–D) [57,66], (E) [58], and (F) [6,57,66].

count the number of actions, and given the high tapping rate in the ‘fast’ condition, it was unlikely that they did. Motor adaptation modified the perceived numerosity of both simultaneously presented dot arrays (Figure 3A) and sequentially presented streams of flashes (Figure 3B). Importantly, the adaptation effect was spatially selective, affecting only stimuli presented around the adapted region, suggesting a genuine sensory effect rather than a cognitive bias (Box 2). A

**Box 2. Motor Adaptation Directly Acts on Sensory Processing**

Much evidence for sensory–motor neural interactions comes from adaptation studies. It is therefore critical to demonstrate that this type of adaptation affects sensory processing directly rather than simply biasing decision changes. A recent study shows that motor adaptation directly affects perceptual rather than decision processes. Using a technique pioneered by Gallagher *et al.* [82], Maldonado-Moscoso *et al.* [72] measured both visual and motor adaptation of numerosity with a standard forced-choice technique and asked observers to indicate how confident they were with their decision (Figure IA), reasoning that minimum confidence should occur where the adapted test and unadapted probe appear to be most similar. If adaptation works at a perceptual level, this point of minimal confidence should occur at the PSE of the adapted psychometric functions. Figure I show that this prediction was verified. Adaptation to tapping shifted the psychometric functions (Figure IB) rightward, changing the PSE by at ~15%, and the shift was accompanied by a commensurate shift in the confidence curves, with the point of minimal confidence aligning with the PSE. Maximal reaction times (another index of certainty) also shifted to align with the PSE. This is strong evidence that the adaptation effects occur at perceptual, pre-decision stages.

In a control experiment where responses were cognitively biased with a reward technique rather than by perceptual adaptation, shifts in PSE were not accompanied by shifts in either confidence or reaction times.



**Figure I. Motor Adaptation Effects Occur at Perceptual Stages.** (A) After judging which of two arrays appeared to be more numerous (baseline, blue; adaptation to fast tapping, red), subjects reported their level of confidence of the judgment. (B) The broken lines indicate point of subjective equality (PSE) values from psychometric functions (upper panel) and arrows show the peaks of the best-fit Gaussians to the confidence or reaction time distributions. Adapted, with permission, from [72].

subsequent study [58] characterized better the spatial selectivity of motor adaptation (**perceptive field**), showing that for both simultaneous and sequential numerosity, adaptation was restricted to an area of radius 12° around the adapted region (Figure 3E).



Adaptation perceptible fields are broad, characteristic of high-level neural populations [59], suggesting that the motor activity might distort high-level sensorimotor areas. Other evidence for a relatively high level of sensory processing is the adaptation reference frame. Features encoded at a relatively high level are often organized within spatiotopic rather than retinotopic coordinates [60–63], at least when attention can be directed toward the stimulus location [64]. Interestingly, adaptation to temporal numerosity (sequences of flashes) was spatiotopic rather than retinotopic [56], demonstrated by interspersing a saccadic eye movement between the adaptation and test phases. Similarly, numerosity motor adaptation occurs in external (real world) coordinates: when the right hand tapped in the left spatial hemifield, the adaptation aftereffect was confined to the left hemifield, around the adapted region ([57]; Figure 3F). That motor adaptation occurs in real-world coordinates presumably allows interactions between vision, audition, touch, and action, all of which have different coordinate systems [65].

Motor adaptation also changes the perceived numerosity of sequences of auditory tones [66], in a similar repulsive way. Again, adaptation is spatially selective in a world-centered reference frame, as with vision. Interestingly, congenitally blind adults showed a comparably strong effect of motor adaptation of auditory numerosity ([66]; Figure 3D), and the effect remained selective in word-centered coordinates (Figure 3F). This demonstrates that early visual experience is not essential for the development of connections between numerosity and action.

All of these studies rely on the psychophysical technique of adaptation, which is thought to directly affect neural responsiveness, as illustrated schematically in Box 1. Many explanations have been advanced for adaptation, including simple neural fatigue [67], calibration and normalization [50,68], and optimization of neural function [69,70]. Whatever the mechanism driving adaptation, to serve as a tool to uncover the neural substrate of numerosity encoding it should act on sensory or perceptual processes rather than just biasing decisions. For example, Morgan [71] showed that encouraging participants to adopt a simple rule like “if unsure respond “greater than”” caused substantial shifts in psychometric functions, mimicking adaptation effects. That numerosity adaptation is spatially specific makes this explanation unlikely (as cognitive biasing should be more generalized), but the potential criticism is nevertheless relevant and important.

To address this issue, Maldonado Moscoso *et al.* [72] measured observer confidence and reaction times during motor adaptation. As may be expected, minimal confidence and maximal reaction times occurred when test and probe stimuli were most similar, at the **point of subjective equality (PSE)** of the psychometric function. Crucially, these minima and maxima shifted with adaptation, to follow the perceived rather than physical point of stimulus equality (Box 2). This shows that adaptation acts early in processing at a sensory level before confidence judgements rather than as a consequence of them.

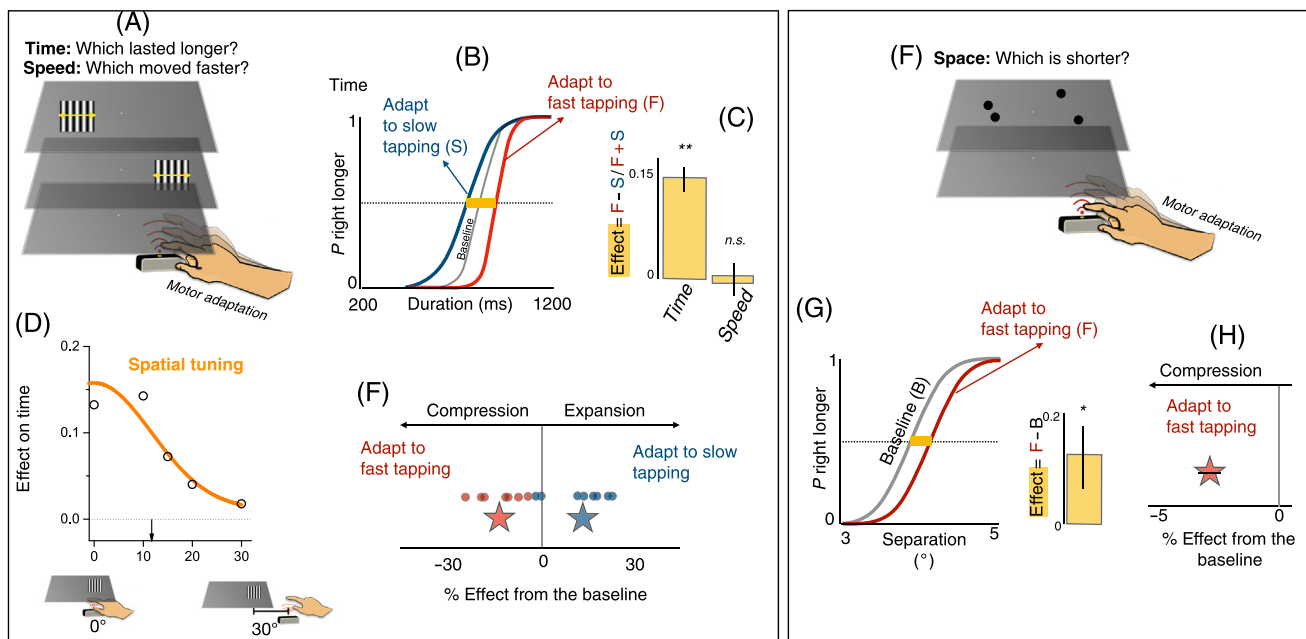
### Beyond Number: Motor Adaptation of Time and Space

The previous section presented evidence for the existence of a sensorimotor number system for perception and action, most likely residing in parietal cortex. As parietal cortex also encodes space and time [4], motor adaptation may also distort these non-numerical features. However, we would not expect motor adaptation to generalize to all perceptual features, especially those not involving magnitude coding along the lines of the ATOM model [4].

Two recent studies have directly investigated and confirmed these predictions. One measured the perceived duration of peripherally presented drifting gratings after tapping quickly or slowly for a few seconds (Figure 4A). As with numerosity, fast tapping caused a substantial underestimation of the perceived duration of the stimulus presented in the motorically adapted region, while slow tapping expanded the perceived duration ([58]; Figure 4B,E). Again, the selectivity was in real-world coordinates. The spatial region affected by motor adaptation was broad but selective, a 12° radius around the adapted region (Figure 4D). Again, the spatial selectivity points to a genuine perceptual effect rather than a generic cognitive phenomenon.

Motor adaptation also alters the perception of visual space [73], although the effects were weaker than those for time and number. Motor adaptation compressed the perceived distance between dot pairs by about 3% (Figure 4F–H).

It may seem that fast and slow tapping affects all perceptual judgements. However, this is not the case. Motion perception (the first reported visual aftereffect [47]) was not affected by motor adaptation [58]: the perceived speed of drifting gratings remained veridical after extensive periods of hand tapping (Figure 4C). This result suggests that the motor–sensory interactions are specific for representations of the magnitudes time, space, and numerosity, rather than acting on all perceptual attributes.



**Figure 4. Motor Adaptation Distorts Time and Space But Not Motion Speed Perception.** (A) Participants made a series of fast or slow mid-air tapping movements for a few seconds with the right hand in the right visual hemifield. After a pause, a drifting grating with variable duration was presented in the adapted location, followed by one of fixed duration presented in the opposite hemifield; participants judged either which lasted longer or which moved faster. (B) Data were fitted with psychometric functions to estimate the points of subjective equality (PSEs). Fast tapping caused the perceived duration to be underestimated (rightward shift of red psychometric function) compared with baseline (broken-line psychometric function) and slow tapping overestimation (blue psychometric function). (C) The shift of PSEs induced by fast and slow motor adaptation. Motor adaptation strongly affected perceived duration, but not perceived speed. (D,E) The adaptation effect on duration was spatially selective, occurring for stimuli presented within ~12° of the adapted location (black arrow; same technique as for numerosity), symmetrically expanding and compressing perceived time by about 15%. (F) Space: After the adaptation phase, subjects were presented with two simultaneous dot pairs and indicated which was shorter. (G) Data were fitted with psychometric functions to estimate the PSE. Compared with the baseline, adaptation to fast tapping causes a small rightward shift of the psychometric. (G,H) Motor adaptation on average compressed the perceived spatial separation of about 0.13°, an effect of about 3%. Reproduced, with permission: (A–E) [58] and (F–H) [73].

### Concluding Remarks and Future Directions

In recent years there has been growing scientific interest in the idea that humans and other species possess a number sense facilitating quick but rough estimates of the number of objects in space and events in time. Here we suggest that the number sense is intimately linked to action, to constitute a 'sensorimotor numerosity system' keeping track of the numerosity of internally self-produced actions as well as events in the environment. This system seems to be tightly linked with perception of space and time as well as numerosity. Considering the number sense not as a passive perceptual system but as an active system intimately connected with action opens new research horizons (see Outstanding Questions).

No electrophysiological study has to date searched for sensorimotor neurons specific for numerosity. The perceptual adaptation studies reviewed here predict their existence, providing theoretical motivation to conduct electrophysiological studies designed to reveal this type of mechanism. A similar question should be also addressed in humans, to investigate the neurofunctional links between numerosity and action processing and to delineate a possible neural hierarchical model of the sensorimotor number system, which goes beyond the simple anatomical proximity of number- and action-sensitive regions. For example, some of the stages may be affected by attentional resources or cognitive processes.

Many studies have reported positive correlations between numerosity precision (**Weber fraction**) and cognitive arithmetic skills [74], suggesting that the number sense may serve as a 'start-up tool' for mathematics acquisition [75]. Interestingly, a link between mathematics acquisition and motor skills has also been reported in children with learning disabilities, showing a correlation between motor skills and proficiency in solving mathematical problems [76]. Children with developmental coordination disorder (DCD), which impairs both gross and fine motor functions [77], perform poorly on symbolic mathematics, numerosity discrimination, and motor tasks. If numerosity precision interacts with the symbolic system supporting the development of arithmetic skills, and also with the action system, it becomes crucial to assess the importance of the motor component of numerosity mechanisms in shaping symbolic mathematical skills. Answering these open questions could provide further practical guidance for education methods, perhaps suggesting alternative strategies to teach and potentiate mathematical learning. For example, the often-used training programs that aim to boost visual numerical acuity could be supplemented by other exercises focused on enhancing sensitivity for motor numerosity.

The development of the sensorimotor system for numerosity does not require visual experience, as congenitally blind adults have adaptation similar to that of sighted adults [66]. It would be interesting to test clinical populations with congenital or acquired motor deficits to test to what extent a motor deprivation can impact the perception of numerosity and whether this in turn can have cognitive repercussions on the development of arithmetic skills.

In conclusion, parallel lines of research have shown that humans and other animals are able to estimate the numerosity of incoming stimuli as well as the numerosity of self-produced actions. Here we suggest, with ample supporting evidence, that these two tasks – numerosity for action and for perception – are mediated by a common shared mechanism. As perception and action are strongly linked in everyday life, the emergence of a sensorimotor mechanism would seem to be a parsimonious and evolutionary useful strategy.

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### Outstanding Questions

Does motor adaptation arise from imbalance in the activities of perceptual motor neurons?

Is it necessary to actually execute movements to trigger motor adaptation or is movement programming sufficient?

Is it necessary to provide semantic verbal instructions (tap fast/slow) to obtain the motor adaptation effect? Will passive adaptation (without instructions) also be effective?

Is perceptive field measurement influenced by the shift of spatial attention?

Is it necessary to attend to the motor adaptation sequence for the effects to work? Will passive adaptation be as effective as active adaptation?

Does the 'mirror neuron system' encode the number of observed actions?

External or hand coordinates? If the hand changes location after motor adaptation, would the effect remain in the external space where the adaptation occurs or it will follow the hand position?

Are motor skills causally linked to symbolic mathematics learning?

Is motor experience necessary for perceptual motor number sense?

Can adapting to visual or auditory numerosity adapt and distort motor actions?

During development, how do the sensorimotor units for numerosity become calibrated?

Might the proposed sensorimotor system for numerosity also play a key role in the acquisition of symbolic mathematical knowledge?

Do patients with congenital or acquired motor deficits show deficits in the perception of numerosity and does this have cognitive repercussions for the development of arithmetic skills?

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References

1. Zeki, S. (1993) *A Vision of the Brain*, Blackwell Scientific
2. Zeki, S.M. (1978) Functional specialisation in the visual cortex of the rhesus monkey. *Nature* 274, 423–428
3. Walsh, V. (2003) A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn. Sci.* 7, 483–488
4. Buetti, D. and Walsh, V. (2009) The parietal cortex and the representation of time, space, number and other magnitudes. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 364, 1831–1840
5. Dehaene, S. (2011) *The Number Sense: How the Mind Creates Mathematics, Revised and Updated Edition*, Oxford University Press
6. Burr, D.C. et al. (2017) Psychophysical evidence for the number sense. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 373, 20170045
7. Ross, J. (2003) Visual discrimination of number without counting. *Perception* 32, 867–870
8. Anobile, G. et al. (2014) Separate mechanisms for perception of numerosity and density. *Psychol. Sci.* 25, 265–270
9. Cavdaroglu, B. and Balci, F. (2016) Mice can count and optimize count-based decisions. *Psychon. Bull. Rev.* 23, 871–876
10. Chittka, L. and Geiger, K. (1995) Can honey-bees count landmarks. *Anim. Behav.* 49, 159–164
11. Wittlinger, M. et al. (2006) The ant odometer: stepping on stilts and stumps. *Science* 312, 1965–1967
12. Rose, G.J. (2018) The numerical abilities of anurans and their neural correlates: insights from neuroethological studies of acoustic communication. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 373, 20160512
13. Whalen, J. et al. (1999) Nonverbal counting in humans: the psychophysics of number representation. *Psychol. Sci.* 10, 130–137
14. Binda, P. et al. (2011) Underestimation of perceived number at the time of saccades. *Vis. Res.* 51, 34–42
15. Morrone, M.C. et al. (2005) Saccadic eye movements cause compression of time as well as space. *Nat. Neurosci.* 8, 950–954
16. Ross, J. et al. (1997) Compression of visual space before saccades. *Nature* 386, 598–601
17. Castaldi, E. et al. (2020) Fast saccadic eye-movements in humans suggest that numerosity perception is automatic and direct. *Proc. Biol. Sci.* 287, 20201884
18. Binda, P. et al. (2012) Saccadic compression of symbolic numerical magnitude. *PLoS One* 7, e49587
19. 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
20. Nieder, A. (2016) The neuronal code for number. *Nat. Rev. Neurosci.* 17, 366–382
21. Nieder, A. et al. (2006) Temporal and spatial enumeration processes in the primate parietal cortex. *Science* 313, 1431–1435
22. Nieder, A. et al. (2002) Representation of the quantity of visual items in the primate prefrontal cortex. *Science* 297, 1708–1711
23. Viswanathan, P. and Nieder, A. (2013) Neuronal correlates of a visual “sense of number” in primate parietal and prefrontal cortices. *Proc. Natl. Acad. Sci. U. S. A.* 110, 11187–11192
24. Piazza, M. et al. (2004) Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44, 547–555
25. Sawamura, H. et al. (2002) Numerical representation for action in the parietal cortex of the monkey. *Nature* 415, 918–922
26. Sawamura, H. et al. (2010) Deficits in action selection based on numerical information after inactivation of the posterior parietal cortex in monkeys. *J. Neurophysiol.* 104, 902–910
27. Kutter, E.F. et al. (2018) Single neurons in the human brain encode numbers. *Neuron* 100, 753–761.e4
28. Mukamel, R. et al. (2010) Single-neuron responses in humans during execution and observation of actions. *Curr. Biol.* 20, 750–756
29. Simon, O. et al. (2002) Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33, 475–487
30. Hubbard, E.M. et al. (2005) Interactions between number and space in parietal cortex. *Nat. Rev. Neurosci.* 6, 435–448
31. Castaldi, E. et al. (2019) Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. *eLife* 8, e45160
32. Eger, E. et al. (2015) Spatially invariant coding of numerical information in functionally defined subregions of human parietal cortex. *Cereb. Cortex* 25, 1319–1329
33. Harvey, B.M. et al. (2017) Comparing parietal quantity-processing mechanisms between humans and macaques. *Trends Cogn. Sci.* 21, 779–793
34. Harvey, B.M. et al. (2013) Topographic representation of numerosity in the human parietal cortex. *Science* 341, 1123–1126
35. Knops, A. et al. (2009) Recruitment of an area involved in eye movements during mental arithmetic. *Science* 324, 1583–1585
36. Harvey, B.M. and Dumoulin, S.O. (2017) A network of topographic numerosity maps in human association cortex. *Nat. Hum. Behav.* 1, 0036
37. Castaldi, E. et al. (2020) Mapping subcomponents of numerical cognition in relation to functional and anatomical landmarks of human parietal cortex. *Neuroimage* 221, 117210
38. Kastner, S. et al. (2017) A brief comparative review of primate posterior parietal cortex: a novel hypothesis on the human toolmaker. *Neuropsychologia* 105, 123–134
39. Castaldi, E. et al. (2019) Mapping numerical perception and operations in relation to functional and anatomical landmarks of human parietal cortex. *bioRxiv* Published online April 9, 2019. <https://doi.org/10.1101/602599>
40. Gentile, G. et al. (2011) Integration of visual and tactile signals from the hand in the human brain: an fMRI study. *J. Neurophysiol.* 105, 910–922
41. Gamberini, M. et al. (2020) Structural connectivity and functional properties of the macaque superior parietal lobule. *Brain Struct. Funct.* 225, 1349–1367
42. Sawamura, H. et al. (2020) A parietal region processing numerosity of observed actions: an fMRI study. *Eur. J. Neurosci.* Published online August 3, 2020. <https://doi.org/10.1111/ejn.14930>
43. Huang, R.S. and Sereno, M.I. (2018) Multisensory and sensorimotor maps. *Handb. Clin. Neuro.* 151, 141–161
44. Spitzer, B. et al. (2014) Parametric alpha- and beta-band signatures of supramodal numerosity information in human working memory. *J. Neurosci.* 34, 4293–4302
45. Uluç, I. et al. (2020) Parametric representation of tactile numerosity in working memory. *eNeuro* 7 ENEURO.0090-19.2019
46. Harvey, B.M. et al. (2015) Topographic representations of object size and relationships with numerosity reveal generalized quantity processing in human parietal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13525–13530
47. Barlow, H.B. and Hill, R.M. (1963) Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature* 200, 1345–1347
48. Clifford, C.W. et al. (2007) Visual adaptation: neural, psychological and computational aspects. *Vis. Res.* 47, 3125–3131
49. Thompson, P. and Burr, D. (2009) Visual aftereffects. *Curr. Biol.* 19, R11–R14
50. Benucci, A. et al. (2013) Adaptation maintains population homeostasis in primary visual cortex. *Nat. Neurosci.* 16, 724–729
51. Mollon, J.D. (1874) After-effects in the brain. *New Sci.* 61, 4
52. Burr, D.C. and Ross, J. (2008) A visual sense of number. *Curr. Biol.* 18, 425–428
53. Butterworth, B. (2008) Numerosity perception: how many speckles on the hen? *Curr. Biol.* 18, R388–R389

54. Aagten-Murphy, D. and Burr, D. (2016) Adaptation to numerosity requires only brief exposures, and is determined by number of events, not exposure duration. *J. Vis.* 16, 22
55. Castaldi, E. et al. (2016) Effects of adaptation on numerosity decoding in the human brain. *Neuroimage* 143, 364–377
56. Arrighi, R. et al. (2014) A generalized sense of number. *Proc. Biol. Sci.* 281, 20141791
57. Cicchini, G.M. et al. (2016) Spontaneous perception of numerosity in humans. *Nat. Commun.* 7, 12536
58. Anobile, G. et al. (2019) Distortions of visual time induced by motor adaptation. *J. Exp. Psychol. Gen.* 149, 1333–1343
59. Blatt, G.J. et al. (1990) Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. *J. Comp. Neurol.* 299, 421–445
60. Burr, D. et al. (2007) Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nat. Neurosci.* 10, 423–425
61. Mikellidou, K. et al. (2017) Spatiotopic coding during dynamic head tilt. *J. Neurophysiol.* 117, 808–817
62. Turi, M. and Burr, D. (2012) Spatiotopic perceptual maps in humans: evidence from motion adaptation. *Proc. Biol. Sci.* 279, 3091–3097
63. Zimmermann, E. et al. (2016) Spatiotopic adaptation in visual areas. *J. Neurosci.* 36, 9526–9534
64. Crespi, S. et al. (2011) Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS One* 6, e21661
65. Goodale, M.A. (2014) How (and why) the visual control of action differs from visual perception. *Proc. Biol. Sci.* 281, 20140337
66. Togoli, I. et al. (2020) The shared numerical representation for action and perception develops independently from vision. *Cortex* 129, 436–445
67. Müller, J.R. et al. (1999) Rapid adaptation in visual cortex to the structure of images. *Science* 285, 1405–1408
68. Solomon, S.G. and Kohn, A. (2014) Moving sensory adaptation beyond suppressive effects in single neurons. *Curr. Biol.* 24, R1012–R1022
69. Barlow, H.B. (1990) A theory about the functional role and synaptic mechanism of visual aftereffects. In *Vision: Coding and Efficiency* (Blakemore, C.B., ed.), pp. 363–375, Cambridge University Press
70. Gepshtein, S. et al. (2013) Sensory adaptation as optimal resource allocation. *Proc. Natl. Acad. Sci. U. S. A.* 110, 4368–4373
71. Morgan, M. et al. (2012) Observers can voluntarily shift their psychometric functions without losing sensitivity. *Atten. Percept. Psychophys.* 74, 185–193
72. Maldonado Moscoso, P.A. et al. (2020) Adaptation to hand-tapping affects sensory processing of numerosity directly: evidence from reaction times and confidence. *Proc. Biol. Sci.* 287, 20200801
73. Petrizzo, I. et al. (2020) Motor adaptation distorts visual space. *Vis. Res.* 171, 31–35
74. Halberda, J. et al. (2008) Individual differences in non-verbal number acuity correlate with maths achievement. *Nature* 455, 665–668
75. Piazza, M. (2010) Neurocognitive start-up tools for symbolic number representations. *Trends Cogn. Sci.* 14, 542–551
76. Westendorp, M. et al. (2011) The relationship between gross motor skills and academic achievement in children with learning disabilities. *Res. Dev. Disabil.* 32, 2773–2779
77. Visser, J. (2003) Developmental coordination disorder: a review of research on subtypes and comorbidities. *Hum. Mov. Sci.* 22, 479–993
78. Addams, R. (1834) An account of a peculiar optical phaenomenon seen after having looked at a moving body. *Lond. Edinb. Philos. Mag. J. Sci.* 5, 1
79. Barlow, H.B. (1990) Conditions for versatile learning, Helmholtz's unconscious inference, and the task of perception. *Vis. Res.* 30, 1561–1571
80. Webster, M.A. (2011) Adaptation and visual coding. *J. Vis.* 11, 3
81. Webster, M.A. (2015) Visual adaptation. *Annu. Rev. Vis. Sci.* 1, 547–567
82. Gallagher, R.M. et al. (2019) Confidence as a diagnostic tool for perceptual aftereffects. *Sci. Rep.* 9, 7124
83. Fischl, B. et al. (2004) Automatically parcellating the human cerebral cortex. *Cereb. Cortex* 14, 11–22
84. Wang, L. et al. (2015) Probabilistic maps of visual topography in human cortex. *Cereb. Cortex* 25, 3911–3931
85. Sereno, M.I. and Huang, R.S. (2014) Multisensory maps in parietal cortex. *Curr. Opin. Neurobiol.* 24, 39–46