Opinion

The role of neural tuning in quantity perception

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Perception of quantities, such as numerosity, timing, and size, is essential for behavior and cognition. Accumulating evidence demonstrates neurons processing quantities are tuned, that is, have a preferred quantity amount, not only for numerosity, but also other quantity dimensions and sensory modalities. We argue that quantity-tuned neurons are fundamental to understanding quantity perception. We illustrate how the properties of quantity-tuned neurons can underlie a range of perceptual phenomena. Furthermore, quantity-tuned neurons are organized in distinct but overlapping topographic maps. We suggest that this overlap in tuning provides the neural basis for perceptual interactions between different quantities, without the need for a common neural representational code.

Highlights

Humans and animals share a sense of quantities, such as numerosity, timing, and size, which underlies various cognitive functions.

Neural measurements reveal neurons with selective, tuned responses to specific quantities, organized in topographic maps.

The tuning properties of quantity-selective neurons link brain and behavior, both explaining and unifying distinct behavioral effects in quantity perception.

Traditionally discrete perceptual processes observed in subitizing and estimation numerosity ranges are united into a common framework based on similar neural tuning and neural adaptation effects within the same topographic maps.

Perceptual interactions between quantities may emerge from interactions between nearby neural populations, tuned to different quantities and modalities, without mapping these onto a single neural representation.

Neural tuning as the basis of quantity perception

Quantity perception refers to the ability to seemingly effortlessly sense the amount or quantity of sensory information. Both humans and animals can readily judge discrete quantities, such as numerosity, that is, the set size of a group of items, and use this information to make decisions, such as choosing the tree with the most fruit [1]. This ability is also present for continuous quantity dimensions, such as event timing and object size. This intuitive understanding of quantities is crucial for navigating the world, exploiting food sources and avoiding predation [2].

The neural and perceptual basis of quantity perception have been studied extensively in recent decades, using psychophysics, neuroimaging, and neurophysiology, in humans, nonhuman primates, birds, fish, and insects. In addition, many perceptual interactions between different dimensions of quantity and different sensory modalities have been demonstrated [3–9]. However, how the neural representation of quantities gives rise to perception remains elusive.

In this opinion article, we show that neural tuning is at the core of the neural representation of quantity and propose that this neural tuning is critical to understanding quantity perception. The idea that neural tuning is linked to perception is not new [10–14], and is well established in vision and perception in general. However, recent developments highlight the ubiquitous nature of neural tuning in quantity systems; for example, discoveries of neural tuning for different quantity dimensions and modalities, and the topographic organization of quantity-tuned neural populations. Guided by these new insights and the established links between neural tuning and perception in sensory cortices, we illustrate how neural tuning can account for various perceptual phenomena in quantity perception, including the numerical distance and size effect, the subitizing and estimation ranges, and adaptation effects. We further propose that perceptual interactions between different quantities and modalities result from interactions between spatially intermixed, topographically organized neural populations tuned to different quantities and modalities.

Neural tuning and perception

Neural tuning and topographic maps are fundamental properties of primary sensory and motor cortices. For example, the visual cortex projects the retinal image onto the cortical surface in visual

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field maps that contain neurons tuned to specific locations of the visual field constituting their receptive fields [15]. Likewise, the auditory cortex maps the cochlea's auditory frequency-specific responses (tonotopy), while somatosensory and motor cortices map the body's layout (somatotopy) [16].

Neural tuning and topographic organization of visual cortical neurons are closely linked to perception [16]. Damage or electrically stimulating specific parts of the early visual cortex causes blindness [17,18] or perceived flashes [19] respectively at the corresponding visual location. Furthermore, the properties of these maps match perception: in the visual cortex, more neurons, with sharper tuning, respond to a stimulus in the central than in the peripheral visual field, giving more detailed visual perception centrally [17,18]. Similar relationships occur in all other primary sensory and motor cortices [20,21].

Neural tuning is not limited to locations on sensory or motor organs, like retinal position. For example, visual neurons are also tuned to specific orientations [22], spatial frequencies [23] and motion directions [24]. Perception of these features depends on the activity of correspondingly tuned neurons, and stimulating these neurons biases perception towards their tuning preferences [25–28]. Thus, in sensory cortices, the proposal that neural tuning underlies perception is supported by extensive evidence collected over the past century.

Neural tuning in visual numerosity processing

Analogous to neurons in early sensory cortices, neurons exist that are tuned to quantities, such as visual numerosity [29]. The responses of numerosity-selective neurons peak when a specific numerosity is presented (the preferred numerosity), with different neurons exhibiting different preferred numerosities. Responses decrease with increasing difference between the presented and preferred numerosity, commonly modeled using a logarithmic Gaussian function [30–32] (Figure 1A,B). On a linear scale, numerosity tuning curves are asymmetrical, and increase in tuning width (the numerosity range to which these neurons respond) as the preferred numerosity increases (Figure 1A). On a logarithmic scale, numerosity tuning curves become symmetrical with constant tuning width across numerosities (Figure 1B).

The characterization of neurons tuned to visual numerosity was first made using single-cell recordings in nonhuman primates [29,32,33] (Figure 1C) and more recently in humans [34]. Human single-cell recordings are rare and converging evidence of neurons tuned to numerosity in humans has been provided using functional magnetic resonance imaging (fMRI). fMRI typically measures changes in blood flow and oxygenation that follow neural activity [35].

Numerosity tuning in humans was first shown using fMRI adaptation [36]. fMRI adaptation infers neural tuning is present because of decreased fMRI responses to a specific test numerosity after repeated presentation of another adapter numerosity. When the suppression of responses systematically decreases with the difference between adapter and test numerosity, this implies neural tuning (Figure 1D). In other words, adaptation affects neural populations depending on their numerosity tuning, where neural populations' responses are suppressed based on their shared response to the adapter and test numerosity.

Recently, visual numerosity tuning has also been measured by combining ultra-high-field fMRI [37–41] with biologically inspired neural model-based analyses [population receptive field (pRF) modeling] [42]. PRF modeling summarizes responses to many presented numerosities using tuning functions (Figure 1E) by comparing the prediction of how many candidate tuning functions would respond to the presented numerosities against the responses measured at each cortical
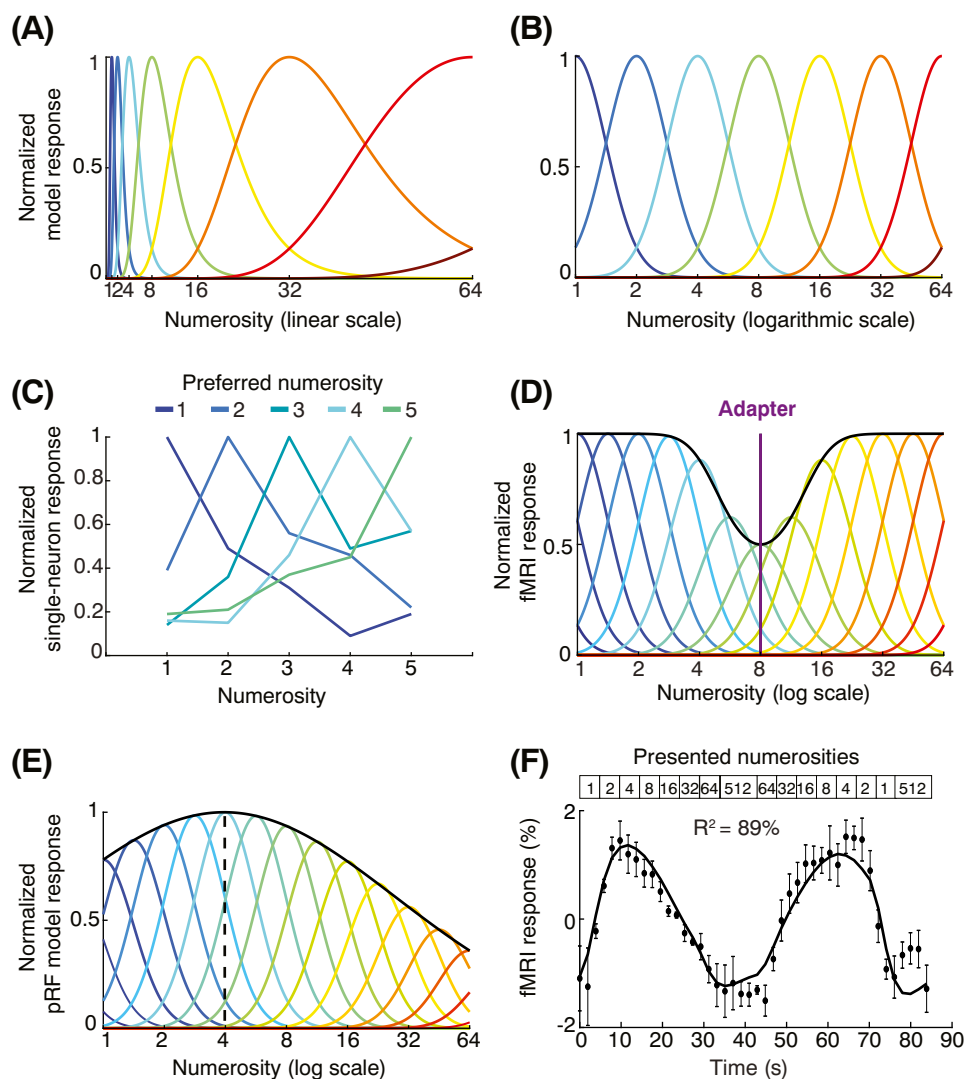
Figure 1. Characterizing numerosity-tuned neurons. (A) Numerosity-selective neurons are typically modeled as logarithmic Gaussian functions. The colors represent tuning curves with different preferred numerosities. On a linear scale, tuning curves are asymmetric and increase in width with preferred numerosity. (B) When plotted on a logarithmic scale, the model tuning curves become symmetric with a constant tuning width across different numerosities. (C) Single-neuron responses in macaque parietal cortex reveal that different neurons prefer, or are tuned to, different numerosities (drawn after [33]). (D) Functional magnetic resonance imaging (fMRI) responses are attenuated during fMRI adaptation, where fMRI response amplitudes are reduced depending on the distance between adapter and test stimuli (black line) (inspired by [36]). The colors indicate the hypothesized single-neuron tuning functions underlying the fMRI response. (E) Population receptive field (pRF) models summarize the aggregate responses of tuned neural populations within a cortical location (solid black line) [42]. The dashed line indicates the preferred numerosity of the neural population, whereas the colored lines indicate the hypothesized, underlying single-neuron contributions to the population responses. (F) Example of a parietal cortical location's fMRI time course (points: mean response amplitude; error bars: standard error over repeated measurements) elicited by viewing a sequence of numerosity stimuli (top) (data from [41]). The solid line shows the responses predicted by the pRF model from panel E. Here, the response amplitude peaks after the presentation of numerosity 4. These different approaches provide converging evidence that neurons are tuned to numerosity.

location (Figure 1F). The candidate tuning function that generates the prediction best correlated to a cortical location's measured response is taken as the tuning function of the neural population at that location. The studies using this method not only demonstrated neural tuning but uncovered the organization of tuned neural populations in networks of topographic maps, where preferred numerosity varies systematically across the cortex akin to a mental number line [38–40]. Many other neuroimaging studies are also consistent with the existence of topographically organized numerosity-tuned neurons, for example those using multivoxel pattern analysis [43–45] and representational similarity analysis [46]. These converging results suggest that topographic principles common in primary sensory and motor cortices are also an organizational principle of quantity mechanisms in the brain.

One alternative view proposes that numerosity tuning and perception reflect non-numerical image features that are often correlated with numerosity, such as density or surface area [47]. However, growing convergent evidence from psychophysical [48,49], neuroimaging and computational research [39,40,50] indicates numerosity itself is represented and perceived. This is further supported by recent computational research using neural network models which show numerosity-tuned responses [51,52] even in networks with no training [53,54]. Thus, a growing body of neuroscientific evidence supports the existence of a specialized neural system processing numerosity and that numerosity-tuned neurons are the core of this network.

Neural tuning underlies visual numerosity perception

Akin to the fact that neural tuning underlies primary sensory perception, established behavioral effects in numerosity perception can be explained by the properties of numerosity tuning functions. We highlight the tuning functions for numerosities 3, 4, 8, and 9, for illustration purposes (Figure 2A,B). Specifically, we discuss the numerical distance and size effects, subitizing and estimation, and adaptation.

Humans and animals show similar patterns of numerosity perception that obey Weber's law [55–57]. Specifically, behavioral discrimination improves with increasing numerical distance (numerical distance effect) and discrimination between two quantities with equal numerical distance deteriorates as their numerical size increases (numerical size effect) [58] (Figure 2C). Following Weber's law, the discrimination threshold between two numerical stimuli increases with numerosity of the stimuli: as numerosities increase, a larger difference between them is necessary for a fixed discrimination performance. This difference is proportional to the discriminated numerosities. Therefore, in the numerical distance effect, more numerically distant numerosities (e.g., 4 vs 8) are easier to discriminate than close numerosities (e.g., 8 vs 9). In the numerical size effect, two numerosities of a given numerical distance are easier to discriminate when the numerosities are lower (e.g., 3 vs 4) than when they are higher (e.g., 8 vs 9). Hence, in both the numerical distance and size effects behavioral discrimination performance will increase as a function of the ratio of compared numerosities [59] (Figure 2D).

Both numerical distance and size effects can be attributed to the response functions of the underlying numerosity-tuned neurons [13,60]. The response functions of neurons preferring 8 and 9 overlap more than those preferring 4 and 8, making these neural responses more similar and less discriminable, mirroring the numerical distance effect (Figure 2A,B). Moreover, numerosity response functions become progressively wider with increasing numerosity, so that the same numerical difference (a difference of 1; 3 vs 4 and 8 vs 9; Figure 2A,B) produces more overlapping response functions as numerosity increases. This reflects the numerical size effect. More generally, under the signal detection framework, the observer's discrimination performance depends on the degree of overlap between response functions. Therefore, in the numerical distance effect,
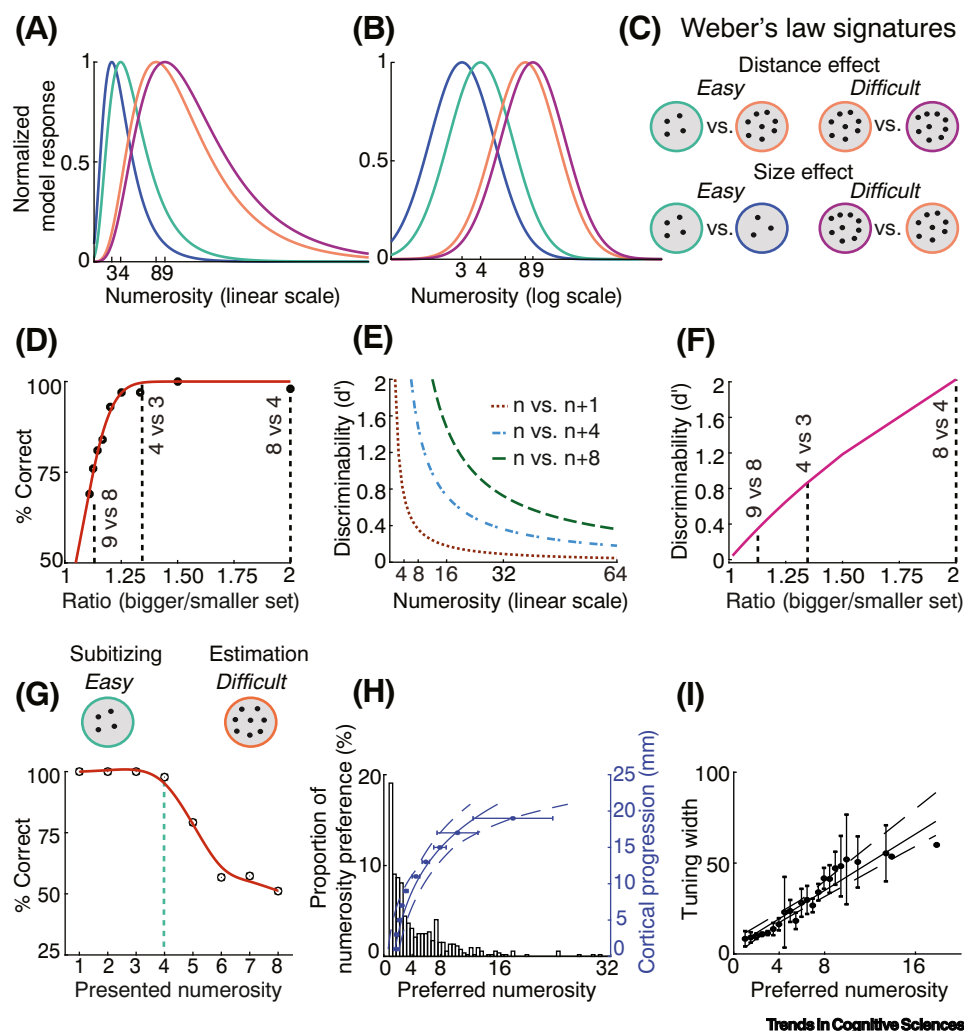
Figure 2. Numerosity tuning functions account for perceptual effects. (A) Idealized numerosity tuning functions with a preferred numerosity of 3, 4, 8, and 9 on a linear and (B) logarithmic scale. (C) Two numerosity perception effects reflecting Weber's law. The numerical distance effect: easier discrimination of distant numerosities (e.g., 4 vs 8) than closer numerosities (e.g. 8 vs 9). The numerical size effect: easier discrimination of low (e.g., 3 vs 4) than high numerosities (8 vs 9) at a given numerical distance (1 here). (D) In both effects, discrimination improves as the ratio of compared numerosities increases (drawn after [59]). (E) Using a signal detection framework, the discriminability index (d') is lower with more overlapping tuning functions. Discriminability is higher when any numerosity i is compared against a more different numerosity (n+8) than a more similar numerosity (n+1) (distance effect), and decreases with increasing numerosity (size effect). (F) In both the size and distance effect, discriminability increases following the ratio of compared numerosities. (G) Enumeration of up to four items (subitizing) is error free, while enumeration of higher numerosities (estimation) is error prone (drawn after [64]). This discrepancy between subitizing and estimation may reflect neural tuning properties (H, I). (H) Preferred numerosities progress continuously along the cortex covering both ranges, but more cortical area (blue) and more neural populations (black) respond to lower numerosities (data from [41]). Blue lines show logarithmic fit with 95% confidence intervals (dashed lines). (I) Neural tuning width increases with preferred numerosity (data from [41]). Points in (H) and (I) represent the mean and standard error of the mean.

the discriminability index (d') will be lower with a small numerical distance and more overlap between response functions (e.g., *n* versus *n* + 1; Figure 2E), and higher with a large numerical distance and less overlap between response functions (e.g. *n* vs *n* + 8; Figure 2E). Similarly, in the numerical size effect, for a fixed numerical distance, the discriminability index will be higher

at low numerosities and lower at high numerosities (Figure 2E). Uniting both effects, the discriminability index will increase as a function of the ratio of compared numerosities (Figure 2F), akin to behavioral observations [59] (Figure 2D).

Another well-documented behavioral phenomenon is the fast and error-free perception of very low numerosities (up to four items), known as subitizing [61]. The subitizing range is thought to be distinct from higher numerosities [61–63], primarily due to evidence for discontinuous behavioral performances observed in reaction time and accuracy [64] (Figure 2G). For example, response variability in numerosity judgements is much lower in the subitizing range [64]. The discontinuous behavioral performances are a violation of Weber's law [64]. Further evidence suggests that subitizing depends on attentional resources, more than estimation at higher numerosities [65,66]. Last, subitizing could also be a result of educational experience, which may explain why there is no apparent precision change in enumerating very low compared to higher numerosities in animals [10,55,56,67], and why innumerate adults have difficulty processing even set sizes smaller than three items on more cognitively demanding numerical tasks [68].

However, the notion of separate numerosity systems for subitizing and estimation is not universally accepted [57,69]. Studies examining numerosity tuning show that numerosity-selective neurons respond to low and high numerosities with similar tuning functions [10,36,56,67]. Furthermore, the effect of attention appears to be in proportion to the respective difficulty of enumerating both subitizing and estimation ranges, suggesting that subitizing and estimation are *equally* affected and may therefore still rely on a single mechanism [70]. Last, innumerate adults *can* subitize [68,71], arguing against a role of education in subitizing.

Recently, we demonstrated a continuous neural representation of subitizing and estimation range numerosity preferences within the same numerosity maps [41]. In other words, as one travels along the cortex, there is a progression of numerosity preferences that seamlessly traverses from subitizing to estimation ranges (Figure 2H). Consequently, we propose that a single neural mechanism underlies both subitizing and estimation ranges. Nevertheless, a single neural mechanism may still have distinct perceptual consequences in different numerosity ranges due to the logarithmic nature of numerosity tuning functions. First, within each numerosity map, a higher proportion of neurons prefer low numerosities, and thus, more cortical area [38,40,41] is devoted to lower than to higher numerosities (Figure 2H). Second, since tuning width increases with preferred numerosity [32,36,38,40,41] (Figure 2I), the precision of the numerosity representation decreases with increasing numerosity. As a result, the discriminability between a presented numerosity and its neighbor (n vs $n + 1$) is very high, up to four items, but decreases dramatically beyond four items (Figure 2E). Above a certain discriminability, discrimination performance reaches a ceiling, becoming error-free (Figure 2D,F). Based on these results, we suggest that differences in neural tuning properties, such as tuning width, proportion of neurons with a preference for low versus high numerosity, and cortical area underlie distinct behavioral performances when judging low and high numerosities. This is well established in vision and other sensory systems, where perceptual differences are related to a similar change in number of neurons and neural tuning widths [15,72]. For example, central vision has a higher resolution and uniquely supports tasks like reading, which is supported by both narrower tuning widths (receptive fields) and more neurons devoted to processing central vision.

Thus, we propose that differences in tuning properties and proportion of neurons can explain the different behavioral phenomena such as Weber's law, subitizing, and estimation. Extending the notion of neural tuning underlying behavioral phenomena, several reports indicate that numerical education and numerosity perception interact [73]. Therefore, we speculate that numerosity

tuning may be influenced by education, and that neural tuning may undergo further refinement during developmental stages.

Neural numerosity tuning can also account for the perceptual aftereffects produced by numerosity adaptation as measured using psychophysics. Psychophysical adaptation entails the repeated presentation of a particular adapter stimulus, which makes subsequently presented stimuli appear more different from the adapter than they are [74,75]. Numerosity perception is highly susceptible to adaptation: adapting to a low numerosity leads to an overestimation of a numerosity subsequently presented, whereas adapting to a high numerosity leads to an under-estimation [76–80] (Figure 3A).

A classic framework on the neural basis of adaptation after-effects views perception as the sum of responding neurons' preferred stimulus states, weighted by those neurons' response amplitude levels [81–84]. Repeated stimulation with a specific adapter stimulus leads to suppression of neurons' responses depending on how strongly they respond to that stimulus [85,86]. Using
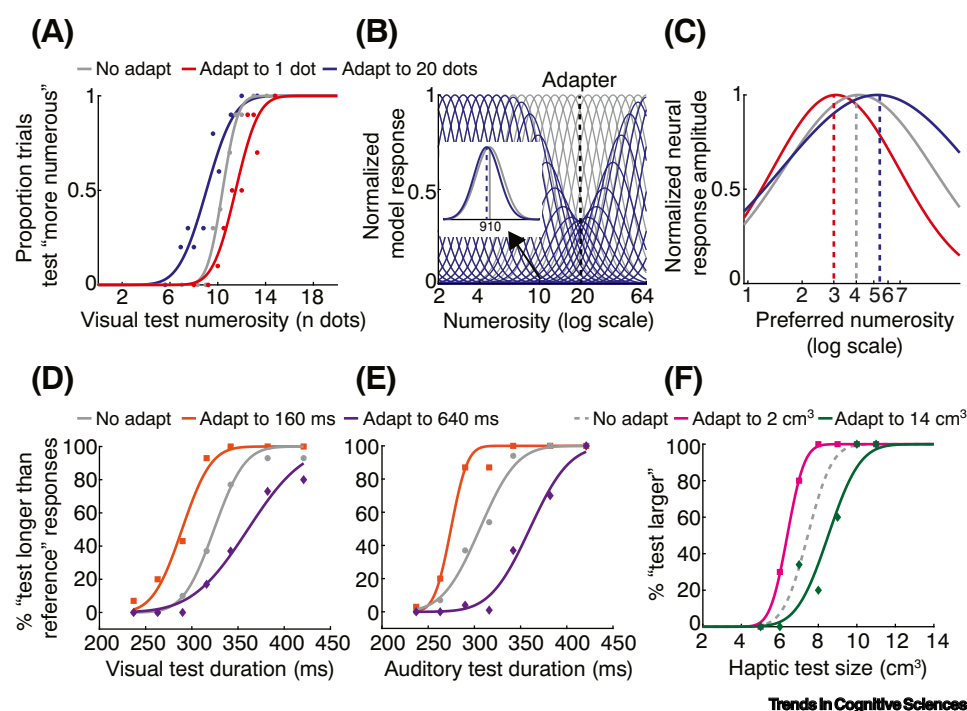
Figure 3. Adaptation aftereffects in different quantities and sensory modalities. (A) Adaptation to high (20) numerosity leads to underestimation of a subsequently presented low numerosity (reference stimulus), whereas adaptation to low (1) numerosity leads to an overestimation (data from: [80]). (B) These perceptual shifts can be explained by numerosity tuning, where repeated stimulation with a specific adapter stimulus suppresses the responses of neurons depending on the amplitude of their response to that stimulus. The population response to stimuli near the adapter will be biased away from the adapter, accounting for a repulsive perceptual shift. (C) Neural numerosity tuning within the subitizing range is altered by numerosity adaptation, with preferred numerosities being predominantly biased towards the numerosity of the adapter (data from [80]). Similar adaptation aftereffects have been found in (D) visual and (E) auditory duration perception, where adaptation to a long (640 ms) versus short (160 ms) duration leads to an under- versus overestimation of a test stimulus's duration (drawn after [82]). (F) Similarly, adaptation to a large (14 cm^3) versus small (2 cm^3) haptic object leads to repulsive changes in the perceived size of a test stimulus (drawn after [96]). Note that all psychometric curves presented in (A) and (D–F) show the same repulsive shift but differences in the direction of the curves (leftward versus rightward) are due to methodological differences [i.e., adaptation effect measured on the reference (A) or test stimulus (D–F)]. Thus, adaptation after-effects are also present in different quantity dimensions and sensory modalities, indicating similar mechanisms.

this framework, numerosity adaptation can be modeled as the summed responses of a population of neurons with logarithmic Gaussian tuning functions, which display maximum response suppression at the adapter numerosity (numerosity of 20; Figure 3B). After adaptation, the population response to a presented numerosity will have less contribution from the units with a preferred numerosity near the adapter numerosity, biasing the population response away from the adapter (Figure 3B inset). This model is appealing since the neural population response follows the same bias as perception.

Using a numerosity adaptation paradigm combined with fMRI, we recently showed that neural numerosity tuning within a network of topographic numerosity maps was systematically altered by adaptation [80]. Specifically, neural numerosity preferences were overall attracted to the adapter's numerosity (Figure 3C), with the extent of attraction increasing when the (unadapted) preferred numerosities were numerically further from the adapter's numerosity. When testing our fMRI adaptation paradigm psychophysically, we found repulsive perceptual aftereffects (Figure 3A), in agreement with other behavioral studies on numerosity adaptation.

The significance of our findings on neural numerosity adaptation is twofold. First, they underscore the relationship between neural tuning and perception, in particular since both are affected by adaptation. However, the direction of change in neural numerosity tuning does not match the predictions of the simple response–suppression models (Figure 3B), yet is consistent with our previous findings on changes in neural tuning and perception in the field of attention [87,88]. Second, our results highlight that neural populations whose numerosity preferences fall within the subitizing range are also affected by adaptation (Figure 3C). Typically, perception of the subitizing range is immune to adaptation except under conditions of high attentional load [76]. Hence, neural adaptation may seem inconsistent with the general absence of perceptual adaptation in the subitizing range. However, this difference can be explained by the properties of neural tuning. A small change in the response function of a population of neurons with a preference for a high numerosity can easily change its preferred numerosity by one or more (Figure 2B), so a different numerosity is perceived. We speculate that the same small change in the response function of a population of neurons with a preference for a very low numerosity may be insufficient to change its preferred numerosity by one (Figure 2B), so the perceived numerosity remains unchanged after adaptation. In other words, neural adaptation is likely too small to change the perceptual readout, since the perceptual readout is discrete. In summary, neural tuning unifies perceptual and neural effects of numerosity adaptation and further illustrates that subitizing and estimation perceptual ranges may be processed by a single neural mechanism.

Neural tuning underlies perception of other quantities and sensory modalities

Here, we consider other quantities and sensory modalities beyond visual numerosity. Like visual numerosity, we propose that neural tuning underlies the perception of other quantities and sensory modalities. We focus on perception of numerosity, object size, and timing in visual, auditory, and haptic modalities, whereas these mechanisms may well be absent in taste and smell.

Above, we explained how neural tuning may underlie adaptation of visual numerosity. Perceptual after-effects produced by adaptation also extend to other quantities, such as visual duration [82] (Figure 3D) and visual object size [89–91], and other sensory modalities, such as auditory numerosity [3] and auditory duration [82,92] (Figure 3E). In the haptic modality, there is evidence for adaptation after-effects for tactile numerosity [93], motor movement rate [94], tactile duration [95], and haptic object size [96] (Figure 3F). Similar to visual numerosity (Figure 3A–C), we propose that changes in the responses of neurons with different tuning functions mediate these changes in perception.

Indeed, neural tuning is not restricted to visual numerosity but is also present in different quantities and sensory modalities. Single-cell recordings have shown neurons tuned to visual event duration [97–99], visual line-length (a measure of object size) [100–102], auditory temporal numerosity [103,104], and auditory duration [105]. Although there is evidence for neural tuning to the number of self-produced actions [106] and for motor event timing [107,108], no study has examined neural tuning to haptic numerosity (e.g., number of hand-held objects) or tactile duration using single-cell recordings. There is some electrophysiological evidence for neural tuning to haptic object size in nonhuman primates, where neurons respond preferentially to specific sizes of grasped objects [109,110].

Human fMRI has contributed evidence of neural populations tuned to visual duration [111–113], visual object size [114], as well as visual line proportions (i.e., ratio of the length of two lines) [115]. No fMRI study to date has examined neural tuning to auditory numerosity (e.g., number of tones) or auditory duration. There is evidence for neural tuning to haptic numerosity [116,117], but neuroimaging evidence for neural tuning to haptic duration and haptic object size is lacking. Last, tuned responses to visual numerosity [38,40,41], visual event duration [111,113], visual object size [114], and haptic numerosity [116,117] have been investigated using pRF modeling, and in these cases, the quantity-tuned populations have shown topographic organization.

Collectively, these results strongly suggest that neural tuning is a general property of neural quantity processing and consequently may underlie quantity perception in general. Therefore, and although the evidence is not complete for all different quantities and modalities, especially in the haptic domain, we hypothesize that neural tuning, arranged in topographic maps, may be found for many quantities and modalities.

Known properties of neural tuning appear to account for Weber's law in other quantities. For example, tuning curves in early visual timing maps become increasingly wider with increasing preferred duration [111]. Similarly, neurons tuned to visual line length show wider response functions for longer preferred lengths, and their population responses become less able to discriminate between longer lines [101]. In line with this observation, Weber's law appears to hold not only for visual numerosity perception but also perception of visual duration [118,119], visual length [120,121], auditory numerosity [122,123], auditory duration [118,119,124–126], tactile numerosity [122], tactile duration [127,128], haptic size [129], and motor timing performance [107]. We therefore propose that properties consistent with Weber's law may be found in the neural tuning for many quantities and modalities.

However, systematic deviations from Weber's law have also been demonstrated [130–133]. We suggest that in the cases where quantity perception does not conform to Weber's law, the tuning profile of quantity-selective neural populations will reflect these perceptual effects. For example, perception of timing and object size are attracted to the middle of the presented range [134,135]; that is, the central tendency effect [136]. These bias effects may be accounted for by properties of neural tuning. Visual object size preferences are flexible with the range of presented object sizes [135], while visual timing tuning is finest in the middle of the presented range [111]. Therefore, although not all quantity perception follows Weber's law, systematic deviations from Weber's law may still reflect other properties of quantity-tuned neural populations.

Another deviation from Weber's law is subitizing. Separate subitizing and estimation mechanisms are also present in auditory [137] and haptic numerosity judgements [116,138–140] but not observed in other quantities. This can be explained by the discrete nature of numerosity compared to the continuous nature of other quantities.

Based on the above, we propose that tuned responses and topographic organization are common across quantity processing, but evidence of these properties is not complete for all quantities and modalities. Specifically, we hypothesize the presence of topographic maps for numerosity and timing in the auditory modality, and timing and object size in the haptic modality, and suggest that these maps may overlap with maps for other quantities. Additionally, the precise role of the distinct topographic maps in quantity perception is currently unclear. Moreover, a causal link between quantity tuning and quantity perception is highly plausible but remains to be established. We hypothesize that stimulation or manipulation of specific quantity-tuned neurons should alter quantity perception.

Neural tuning underlies interactions between different quantities

Given the evidence for the existence of neural populations tuned to different quantities and sensory modalities, and the role of neural tuning in quantity perception, we suggest that neural tuning is an invaluable mechanism for disentangling potential interactions between different quantities. A number of theories [4,6,8,9] postulate that different quantities might share computational and/or neural mechanisms. These theories are supported by neuroimaging findings showing overlapping brain activations during different quantity tasks [5,7,141] and perceptual interactions between quantity dimensions. However, overlapping brain activations do not necessarily imply a common neural code for different quantities, and recent behavioral studies examining the interaction of different quantities paint a more complex picture [78,142,143]. Furthermore, evidence from animal electrophysiology and human fMRI are not entirely consistent with the idea of a common neural mechanism
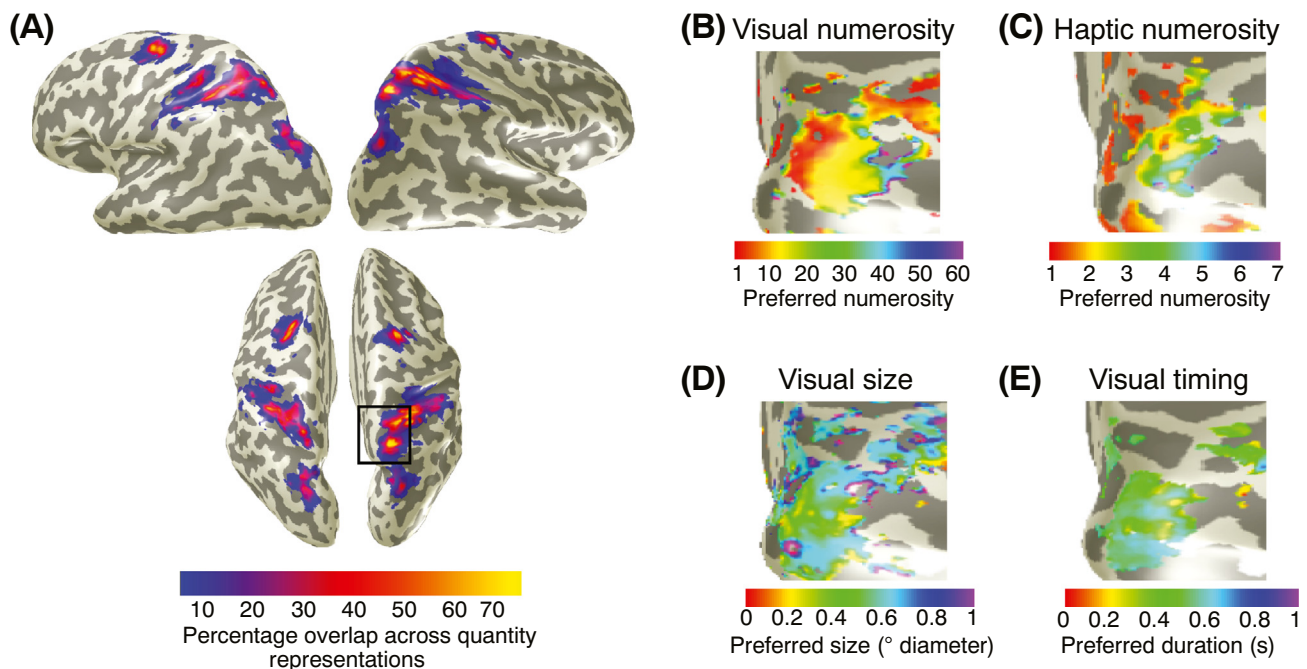
Figure 4. Topographic quantity maps. (A) The network of topographic maps of each quantity overlaps in the parietal and frontal lobes. The color map indicates the percentage of overlap between participants across four different quantity dimensions [individual participant maps of each quantity were transformed onto the N27 (Talairach) template's cortical surface]. The square highlights the region of the superior parietal lobule in which we show the four topographic maps in panels B–E for one participant. Selective responses to each quantity are organized into topographic maps, that is, regions where the preferred quantity changes gradually across the cortical surface. The topographic maps of (B) visual numerosity (data from [41]), (C) haptic numerosity (data from [116]), (D) object size (data from [114]) and (E) timing (data from [111]) overlap, but are distinct.

for different quantities. Single-cell recordings reveal that neurons responding to different quantities such as numerosity, size (line length), spatial frequency, duration and distance are anatomically intermingled, but most neurons encode only one type of quantity [100–102,144]. A minority of neurons are tuned to multiple quantities, but preferences for these different quantities are not correlated so their tuning functions appear independent. Nevertheless, small proportions of neurons are tuned to numerical quantity in the visual and auditory modality [103], and visual numerosity and visual line length [101]; therefore, we cannot exclude the possibility that a subpopulation of neurons might serve as abstract quantity detectors. Hence, further examining the tuning of single neurons to multiple quantities and their link to perception will be pivotal in elucidating whether related tuned responses are sufficient for generalized quantity processing.

In humans, we have revealed neural populations tuned to different quantities in nearby anatomical locations (Figure 4A), forming topographic maps of visual numerosity [38,40,41], haptic numerosity [116], visual object size [114], and visual timing [111] (Figure 4B–E). Moreover, these neural populations are not restricted to the cortex but also found in subcortical nuclei [117]. What do these tuned neural responses and topographic maps tell us about potential interactions between different quantities? When combining our individual findings on neural tuning to different quantities, we observe that neural responses to visual and haptic numerosity, object size and timing spatially overlap to a large extent. However, at a finer scale each quantity is processed by distinct topographic maps. For example, in the case of visual numerosity and haptic numerosity [116] or visual object size [114], we find neural selectivity in similar cortical regions but distinct maps, indicating that the responses of the underlying neural populations remain primarily quantity- and modality-specific (Figure 4B–D).

Based on all the above, we propose that observed commonalities in neural and behavioral representations between quantities are not accounted for by a common neural representational code across quantities, but by the interaction of spatially intermingled neural populations which are independently tuned to different quantities and modalities. The question then arises how these independently tuned neurons are organized and interact within the topographic maps. In primary cortices, these independently tuned neurons are organized in columnar and laminar structures within topographic maps. Recently, we suggested that laminar organization of numerosity maps follow that of primary cortices [145]. We speculate that a similar organization exists in quantity maps and may reveal the basis of their interaction [146].

Concluding remarks

The ability to perceive quantity information, such as numerosity, timing, and object size, is fundamental to cognition. In agreement with previous authors [13,14], we argue that neural tuning links perception to the brain's responses, serves as the neural basis underlying quantity processing, and can explain many behavioral effects in quantity perception, such as the numerical size and distance effects. In addition, recent neuroimaging studies show how neural tuning properties can also explain and unify the subitizing and estimation ranges, adaptation effects and interactions between quantities and sensory modalities. By endorsing the value of neural tuning in explaining the cognitive representations of quantities, new research avenues open up, ranging from neural quantity tuning in different developmental stages to the further exploration of the link between neural tuning, topographic quantity maps and quantity perception (see Outstanding questions).

Outstanding questions

Tuning has been found for many quantities, in some cases with topographic organization by preferred quantity. Do these principles apply to other quantities? We propose that tuned responses and topographic organization are common across quantity processing, but evidence of these properties is not complete for all quantities and modalities.

There are extensive networks of topographic maps representing many quantities. What is the role in quantity perception for the distinct maps within the network? In sensory systems, different topographic maps are often associated with different functions. Several maps have been found for each quantity, yet the links between different cognitive functions and different maps are unclear.

The link between neural tuning and perception is correlational – can we establish a causal link? We advocate for the role of neural tuning in perception, but this is not the only theory. Given our proposal, we hypothesize that stimulation or manipulation of specific quantity-tuned neurons should alter quantity perception.

How does neural tuning for quantities develop and is it altered as new skills are learned? Many behavioral developmental studies relate quantity perception to cognition in children. Yet, most neural studies, and in particular those studying quantity tuning, are in healthy adults.

How do differential attractive and repulsive changes in neural quantity tuning due to adaptation relate to perceptual changes? Adaptation produces both repulsive and attractive changes in neural tuning. Attraction of quantity preferences is not readily explained by simple response–suppression models. The perceptual effects of these changes in tuning are still poorly understood.

How is quantity tuning organized on the mesoscopic scale of the brain? In the visual cortex, at the mesoscopic scale, multiple features are organized in laminae and columns within the same topographic map. We speculate that neurons responding to different

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No interests are declared.

quantities and modalities may be held together in similar spatially distinct fine-scale neural structures.

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