

Relating magnitudes: the brain's code for proportions

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Whereas much is known about how we categorize and reason based on absolute quantity, data exploring ratios of quantities, as in proportions and fractions, are comparatively sparse. Until recently, it remained elusive whether these two representations of number are connected, how proportions are implemented by neurons and how language shapes this code. New data derived with complementary methods and from different model systems now shed light on the mechanisms of magnitude ratio representations. A coding scheme for proportions has emerged that is remarkably reminiscent of the representation of absolute number. These novel findings suggest a sense for ratios that grants the brain automatic access to proportions independently of language and the format of presentation.

Proportions are ubiquitous

We deliberate questions of ‘How much...?’ or ‘How many...?’ on a daily basis. Together with the invention of language, the human sense of magnitude and number has provided the foundation for arithmetic and mathematics and thus paved the way for major cultural advancements [1]. Until very recently, the main questions revolved around where and how the brain represents absolute magnitudes, such as the number of items in a set (discrete) or the length of a line (continuous). However, whereas simple quantification or enumeration (counting) is necessary, it is often not sufficient to govern behavioral decisions. We frequently need to explicitly relate two quantities to generate a more complex and comprehensive measure of magnitude: a proportion.

Comparatively little is known about the neural underpinnings of quantity ratios, although they are no doubt constructs we encounter as often as absolute numbers (Box 1). For example, one will strongly consider the purchase of an interesting item for 50% of the original price, whereas an advertisement for a new job offering 50% of one's current salary would hardly attract one's attention. In mathematics classes, students cringe when thinking about fractions and geometrical constructions, whereas at the same time they might relish the perfect proportions in the masterpieces of Leonardo da Vinci and Michelangelo. We are still far from grasping the neurophysiological effects that the aesthetic appeal of the ‘golden ratio’ or the physiognomy of David spark in the viewer [2]. Yet, on a more modest and elementary level, we might be on the verge of understanding how the brain comes to encode and process proportions.

Emerging evidence from several laboratories now suggests that this remarkable capacity may be independent of culture, chronological age and even species.

In this review on the cerebral representation of magnitude ratios, we synthesize experimental results from psychology, animal behavior, neuroimaging and neurophysiology. Focusing on both humans and non-human animals, we begin by highlighting important behavioral studies and then discuss in detail the first neuroimaging and neurophysiological experiments that address how the brain encodes proportions at the macroscopic (cortical) and microscopic (single cell) level. Detailed evidence for two fundamental questions will be presented. First, what are the differences and commonalities between the representation of absolute magnitude and magnitude ratios? Do they share neural substrates and coding schemes? Second, are proportions derived automatically (i.e. retrieved from memory by an autonomous quantity module) or are they actively constructed online using mental algorithms? How do task demands and strategic considerations shape the neuronal read-out for proportions? We conclude by providing a compilation of important open questions that, in our opinion, should form part of the research agenda in coming years.

Behavioral experiments: symbolic notation

On a conceptual level, significant differences exist between whole numbers and proportions. As opposed to the natural number system, the signature features of which have been extensively described (Box 2), there is no direct successor to a specific magnitude ratio (as an answer to the question ‘Which is the next one?’). In other words, proportions do not form a countable series. The interval between any two given magnitudes is infinitely divisible: there is an infinite number of other proportions between any two ratios.

At school, learning about fractions (specified by an integer numerator divided by an integer denominator) starts at around age eight (third or fourth grade). Already at these very early stages, substantial problems exist with this frequently encountered measure [3]. Various authors have argued that young children's understanding of fractions is hampered by prior knowledge of whole numbers (so-called whole-number bias or intrusions) [4–8]. For example, 1:56 is regarded as smaller than 1:75 because 56 is smaller than 75 [9].

Similar problems continue into adolescence [10] and adulthood [11]. It is possible that the difficulty in dealing with fractions lies in the fact that, to be able to name the

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Box 1. Proportions are ubiquitous

Mathematical theorems such as the intercept theorem (Figure 1a, top panel) constitute a basic concept in geometry. In construction analysis, these theorems are essential to erect robust buildings and, thus, 'surround' us every day. In mathematics, proportions are not only important in geometry, but also in analysis and algebra, where the ratio between the numerator and denominator forms a fraction. In a pie chart (Figure 1a, bottom panel), information is conveyed by the ratio of the different sectors to the full circle.

The golden ratio in Latin is called 'proportio divina', divine proportion. According to our idea of beauty, art and music masterpieces are

composed by using simple rules based on proportions (Figure 1b). Humans seem to have a sense for perfect compositions consisting of ratios.

Given that body proportions (Figure 1c, top panel) play a major role in social interactions, it is not surprising that the waist-to-hip ratio has been found to predict physical attractiveness in many societies. In field studies (Figure 1c, bottom panel) it has been shown that chimpanzees attack a group of conspecifics only if they outnumber their opponents by at least 1.5.

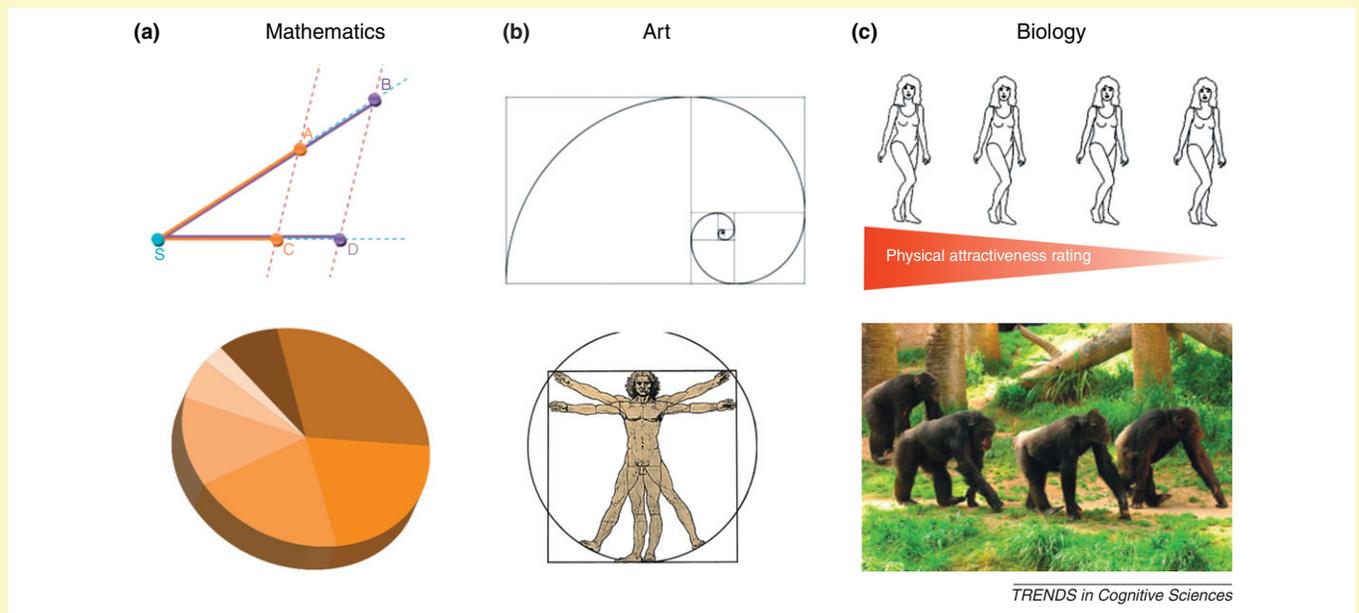


Figure 1. The ubiquity of proportions.

new magnitude, the whole-number numerator and denominator (acting as a reference) need to be merged. An interesting question that has been addressed in psychophysical experiments is therefore whether the brain encodes fractions by components (componential model) or by their actual numerical value (analog, integral or holistic model). A recent study investigated these hypotheses in skilled human adults with the help of the distance

and spatio-numerical association of response codes (SNARC) effect (Box 2) [11]. Participants were asked to compare two fractions or to compare a target fraction with various numerical references. The authors did not find a distance or SNARC effect for the real numerical value of the fractions, which suggested that it was not accessed to solve the task. Instead, distance effects were observed for numerical distances between numerators, denominators and reference numbers. Thus, in this study, fractions were processed by components and not by their true magnitude. Similar results, with strong effects of fraction components, were observed in experiments that failed to detect a size congruency effect, i.e. shorter response times and improved accuracy for 'congruent' trials in which the larger (smaller) fraction is also physically larger (smaller) [12].

However, recent studies have called these results into question, showing that fractions can indeed be encoded by numerical value [13–15]. If simple whole-number comparisons are made impossible by a balanced stimulus design in otherwise very similar experiments, both university and community college students show a strong distance effect for fraction magnitude and not for distance between numerator and denominator when comparing single and multi-digit fractions to a reference fraction [14]. Perhaps not surprisingly, university students are faster and more accurate at comparing fractions. However, this finding has never been reported for absolute magnitude comparisons. It is therefore

Box 2. Signature features of analog magnitude representation

Several psychophysical and neurophysiological findings are frequently reported in studies of absolute quantity. The 'distance effect' [53] refers to the fact that two quantities are more easily discriminated as the distance between them increases. For the 'size effect' [53], discriminability of two magnitudes spaced at equal distances increases as the numbers become smaller. The 'SNARC effect' [54] states that judgments about numbers are faster when the left hand is used to respond to small magnitudes and the right hand to large magnitudes. Absolute numerosity judgments are based on an analog magnitude representation that is logarithmically compressed, i.e. the behavioral peak functions remain symmetric for all numerosities on a logarithmic scale [55]. Neurons represent absolute quantities using the 'labeled-line code' (also termed 'place code') [56]. Stimulus magnitude is encoded by the maximum response rate of a particular neuron and the Gaussian tuning function is a peak function with the preferred magnitude represented at the maximum of discharge.

reasonable to assume that the subjects' strategy has a significant influence when accessing magnitude ratios. This hypothesis has been explicitly tested by providing fractions with common denominators that encourage the exclusive comparison of the numerator [16]. Indeed, in this situation participants rely on the numerators, although they access the whole fraction when the use of a componential strategy is made more difficult with a second stimulus set. Finally, when trained to map fractions to arbitrary visual shapes to prevent whole number symbols from interfering with the real numerical magnitude of the fraction, subjects represent the associated fraction values holistically [17].

Behavioral experiments: non-symbolic notation

In school children, one of the major obstacles to understanding fractions is notation [9]. To address the question of pre-verbal, non-symbolic representation of magnitude ratios, a number of behavioral studies have explored young children's ability to process proportions at an age when the acquisition of symbolic knowledge has not yet begun. For example, 4-year-olds already solve complex analogies in the form of $a:b:c:d$ to determine the relation between proportions [18], match the proportion of colored bricks in a test image to a sample stimulus [19] and can perform simple addition and subtraction tasks with spatial proportions, e.g. segments of a printed filled circle [20,21]. Finally, children of the same age are able to draw analogies between ratios of discrete and continuous magnitudes [22]: subjects observe a proportion of a continuous quantity being removed (e.g. a slice of pizza) and are then asked to take away the same proportion from a discrete quantity (e.g. a box of chocolates).

These findings strongly suggest that young children indeed have an understanding of the concept of proportionality. Further support for this notion comes from a more recent study that examined whether pre-verbal infants can process magnitude ratios [23]. In a preferential-looking protocol, the authors repeatedly presented 5- to 7-month-old infants with arrays of dots that depicted two groups by different item colors and shapes. Subjects were habituated to a specific ratio (i.e. looking time for a particular ratio progressively decreased) and were then shown arrays with differing proportions. The infants were able to detect ratios that deviated by a factor of 2, which was indicated by an increase in looking time.

The evolutionary advantage of detecting proportional magnitude

Proportions as communicative signals provide powerful information for humans and non-human animals alike and intuitively guide their behavior in social, foraging or mating situations. Physical attractiveness, for instance, often seems to rely on body proportions rather than absolute dimensions of body features. In humans, the proportions of body parts constitute powerful signals that have been repeatedly associated with high mate quality. Besides facial features, the effect of several non-facial bodily features on attractiveness, most notably female waist-to-hip ratio and male body type, have been studied in detail [24]. It has been suggested that, although preferences with respect to female body weights vary cross-culturally,

men universally prefer women with a low waist-to-hip ratio (WHR) [25]. Compared to a WHR mean in most populations of about 0.75 to 0.80, the WHR rated most attractive by men is typically approximately 0.70 (Box 1). Women, on the other hand, prefer men with broad shoulders relative to waist or hip size (i.e. a 'V-shaped' torso) and average WHRs. Women's ratings of male attractiveness can also be explained by other simple physical proportions, in particular the waist-chest ratio (WCR, a measure of upper body shape) [26]. Men with a small WCR (0.70) are rated significantly more attractive than men with a larger WCR (0.90).

Sexual selection might also favor the development of body proportions as fitness signals in animal species. So far, the focus of sexual selection research has been on absolute sizes of body features, such as tail length in barn swallows [27]. However, it might be the case that for some body signals proportional size is more important than absolute size.

Proportions are not only important for mate attractiveness but also in social interactions. Estimating the proportion between invader and combatant is an essential capacity for animals. Female lions extract from the roars of a rival group the number of lions in this group, relate it to the number of their own troops and only attack if the ratio of their group size compared to the opponents' is larger than a certain proportion [28]. Similar behavior has been observed in male chimpanzees: they only attack if the ratio of predominance is 1.5 [29].

Exploiting proportions is not limited to social situations. Foraging behavior in mallards gives rise to the assumption that ducks also successfully use ratios [30]. Mallards distribute themselves at different food patches depending on the profitability of the individual patches, i.e. more ducks flock to patches where more food is delivered.

It is parsimonious to assume that mating, hunting and foraging do not require an understanding of proportionality in the sense of high-level cognitive reasoning. A more basic, low-level sensory-driven process that triggers specific responses would be sufficient to explain the behavioral patterns observed in these field studies. Nevertheless, it is tempting to speculate that the underlying neural circuits could be the foundation for more sophisticated actions that involve a more thorough understanding of proportions. To this end, several controlled laboratory experiments have examined whether animals' use of magnitude ratios may extend beyond innate perceptual processing. Pigeons were trained to peck arrays consisting of equal numbers of two types of elements (e.g. red and blue dots) [31,32]. Prior to training, the birds had learned that one color (e.g. blue) was not rewarded when it was pecked. The birds were then tested with arrays in which the ratio of red and blue dots varied. In these tests the animals responded more frequently to arrays containing a greater proportion of rewarded elements (e.g. red dots) than they did to the originally rewarded array with its equal number of red and blue items. This peak shift effect still occurred when the total number of dots in the test arrays was increased (while the proportion of red to blue items was maintained). Similarly, pigeons can discriminate differences in color proportions within horizontal bars composed of continuous

blocks of color [32]. Thus, irrespective of whether the proportion is presented as a ratio of discrete items or a ratio of continuous features such as the length or area of an individual component, animals successfully solved the tasks, clearly demonstrating an understanding of magnitude ratios.

In one study that investigated animal reasoning with proportions, five chimpanzees were trained in a match-to-sample task [33]. The apes had to compare proportions specified with different items, e.g. a half-full glass of water matched half an apple. Remarkably, four animals failed and only one chimpanzee that had received extensive (sign) language-like training prior to this task passed the test. Thus, does the understanding of magnitude ratios depend on the ability to verbalize proportions? In the only comparative study to date, Vallentin and Nieder addressed this Whorfian conjecture by testing both rhesus monkeys and human adults on the same proportion discrimination task [34]. In a delayed match-to-sample protocol, non-symbolic spatial proportions were presented in the form of two horizontal lines (Figure 1a). The upper reference line and lower test line specified one of four proportions: 1:4, 2:4, 3:4 or 4:4. Stimulus presentation time was kept very short in order to prevent the human participants from verbalizing the proportions. Despite the seemingly easy task, performance levels for humans were not perfect (possibly because participants had not been informed about which ratios would be presented during the experiment) (Figure 1b). Upon completion of their training, animals reached very similar peak performance levels to humans (Figure 1c). Transfer trials with novel magnitudes demonstrated that the monkeys successfully generalized across proportions. Thus, symbolic labels are not required to derive quantity ratios. Interestingly, behavioral data from both animals and humans revealed the identical signature features of an analog magnitude representation (Box 2). Comparable to absolute number judgments, peaked behavioral tuning functions indicated that participants estimated proportions. A clear distance effect was observed for numerical value, which suggests that proportions were represented by their true (approximate) magnitude.

Neuroimaging: non-symbolic notation

Although much is known about the neurophysiological basis of absolute quantity and number [35,36], until recently there were no data concerning the neural representation of proportions. It was therefore unclear which cortical areas sustain the system for magnitude ratios and how the code is implemented by single neurons. Human neuroimaging studies exploring the neural circuits involved in mental calculation – including the arithmetic operation of division – have reported hemodynamic activity in a widespread network consisting of the inferior frontal gyrus, premotor cortex, presupplementary motor area and the intraparietal sulcus (IPS) [37,38]. However, these data do not lend themselves to clear-cut conclusions about the representation of individual operands (e.g. fractions), since the mathematical operations studied are complex and multi-layered, engaging numerous cognitive processes.

Recent functional magnetic resonance imaging (fMRI) experiments have now started to close this gap [39]. In a

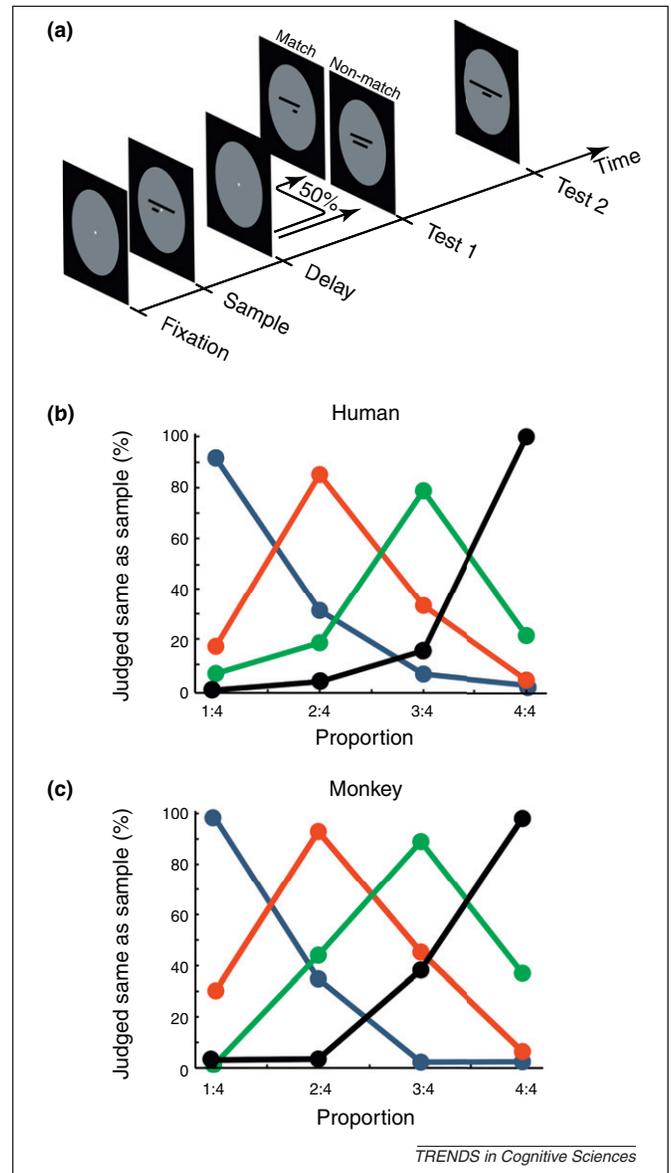


Figure 1. Spatial proportion discrimination task. (a) Proportions were specified by the ratio of the length of a reference line (top) and a test line (bottom). To start a trial, participants grasped a lever and maintained fixation. If the memorized sample and test display showed the same proportion, the lever had to be released (match; 50% of trials). Participants had to continue holding the lever until the second test appeared (which was always a match) if the sample and test display showed different proportions (non-match). (b) Behavioral performance of humans solving the proportion discrimination task. The behavioral curves are peak functions. The more distant the test proportions were compared to the sample stimulus, the easier it was for participants to solve the task (distance effect). (c) Monkey performance curves. Same layout as in (b). Reproduced, with permission, from [34].

passive viewing task, human adults were shown non-symbolic proportions that were specified either by the length of two horizontal bars (analogous to [34]) or by the number of dots in two differently colored groups [39]. Using an adaptation protocol inspired from previous work on the representation of absolute magnitude [40,41], participants were habituated to a given proportion (which was repeatedly presented) and then viewed abruptly deviating novel proportions (Figure 2a). Blood oxygenation level-dependent (BOLD) signal in the bilateral IPS and lateral prefrontal cortex (PFC) decreased during the adaptation period and

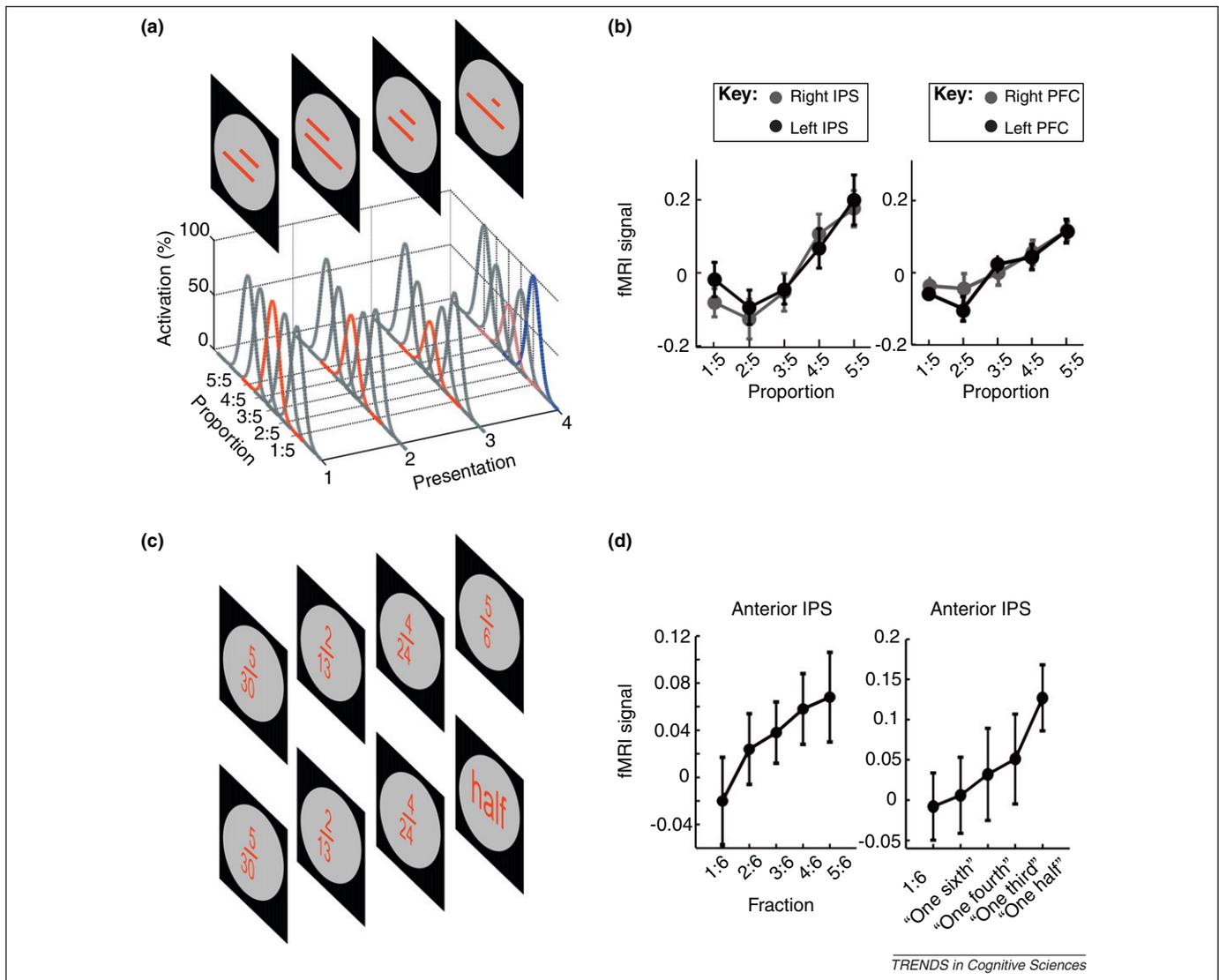


Figure 2. Functional MRI adaptation (fMRA) experiments for non-symbolic proportions and fractions. (a) Non-symbolic stimuli specified proportions by two horizontal lines. Proportions were shown repeatedly, leading to a decrease in BOLD signal activity for the presented ratio (schematic; red curve). Sudden introduction of a deviant proportion caused a rebound from adaptation, because a non-adapted neuronal population encodes this stimulus (blue curve). 3:5 was chosen as adaptation proportion for illustrative purposes only. Reproduced, with permission, from [39]. (b) Effect size of the BOLD signal change in the IPS and the PFC during the fMRA line proportion experiment. Rebound activity increases as the distance between the deviant and adapted proportion (1:5) grows larger. Reproduced, with permission, from [39]. (c) In the second adaptation experiment, subjects were adapted to fractions (approximately 1:6). Deviants were either also fraction numerals (top row) or fraction words (bottom row). Reproduced, with permission, from [50]. (d) Effect size of the BOLD signal rebound in anterior IPS. Recovery as a function of deviant distance from the adapted fraction is independent of the deviant's notation (numeral or word, left and right panel, respectively). Reproduced, with permission, from [50].

recovered as a function of the distance of the novel proportion from the adaptation stimulus (Figure 2b). Both the parietal cortex, in particular regions surrounding the IPS, and the lateral prefrontal cortex are key regions involved in the processing of numerical information, and many neuroimaging and electrophysiological studies have reported number-related activity in these high-level association cortices [36]. These results therefore suggest that the same regions that process absolute magnitude also encode magnitude ratios (Figure 3a). To directly test this hypothesis, the dot stimuli were rearranged to adapt participants to absolute number. Indeed, BOLD signal adaptation and subsequent recovery were observed in bilateral IPS and lateral PFC, and overlapped strongly with the regions identified in the proportion experiment (Figure 3a). In both proportion experiments, BOLD signal recovery

increased with the distance of the deviant from the adaptor stimulus. This implies that neuron populations are tuned to preferred proportions, because each deviant proportion activates a different, non-adapted set of neurons, causing an increase in signal [42], and also demonstrates that this coding scheme generalizes over the exact visual display (the same results were obtained whether proportions were specified by bars or dots). Since the same adaptation features are found for absolute magnitudes [40], it can be concluded that the analog magnitude code also applies to proportions. Supporting the behavioral data discussed above, the fact that participants were not instructed to perform a specific task hints at the possibility that the human brain is able to represent non-symbolic proportions in an automatic manner and need not intentionally construct magnitude ratios.

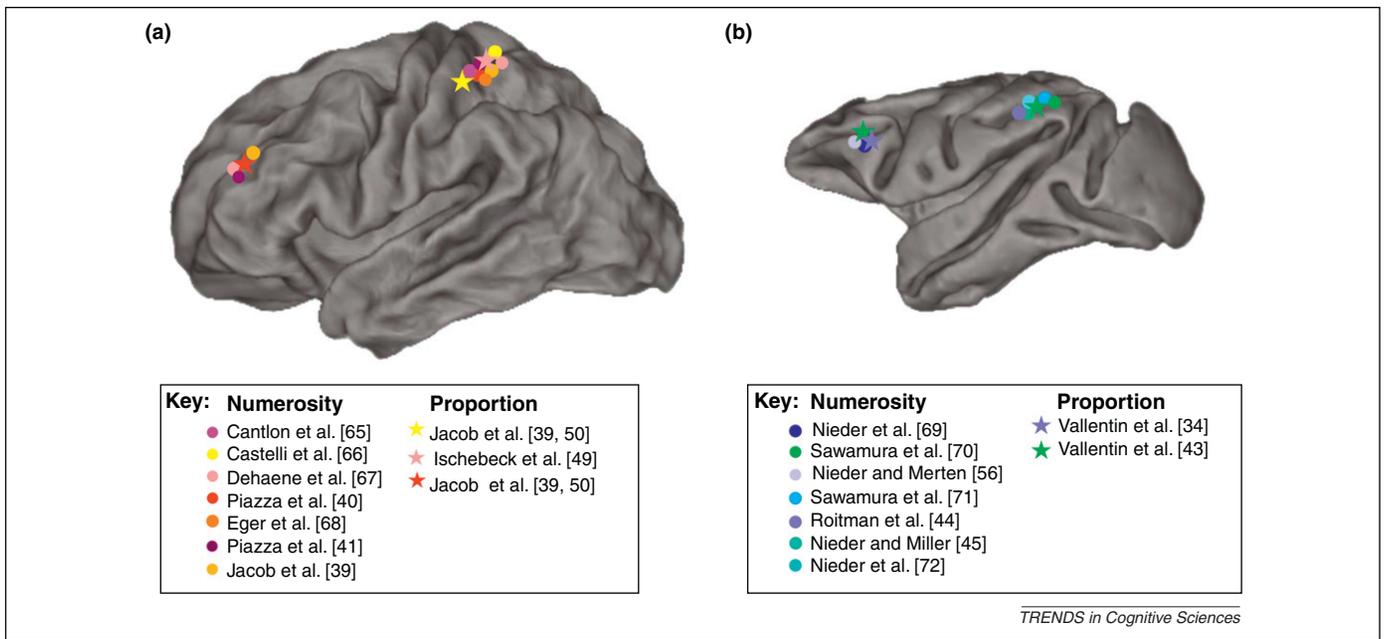


Figure 3. Comparative neuroanatomy (schematic) of the representation of absolute magnitude and magnitude ratios. (a) Lateral view of a human brain showing locations of peak fMRI activity for selected studies investigating numerosity and non-symbolic proportions or fractions (circles and stars, respectively). (b) Lateral view of a rhesus monkey brain depicting electrophysiological recording sites for studies investigating numerosity and proportions (circles and stars, respectively). The left hemisphere was selected for reasons of clarity only.

Single cell neurophysiology

To trace the neuronal code for magnitude ratios to the single cell level, electrophysiological recordings were obtained from the frontal and parietal cortex of behaving rhesus monkeys (Figure 3b) after training them on a delayed match-to-sample task (Figure 1a) [34,43]. In the PFC, approximately 30% of the neurons encoded one of the presented proportions. Neuronal activity was characterized by a peak firing rate for a specific proportion and decreased as the distance from this preferred proportion increased (Figure 4a and b). In other words, single neurons were tuned to specific ratios. Thus, the labeled line code (Box 2), which is frequently found for absolute magnitude (but see [44], discussed in [36]), also holds true for the representation of magnitude ratios. Discharge patterns of neurons in the inferior parietal cortex (area 7a) were very similar (Figure 4c and d). However, the overall number of proportion selective neurons was significantly smaller (approximately 16% of all recorded cells from this region). An error trial analysis revealed that the single cell activity in both prefrontal and parietal cortices is essential to successfully solve the task. When the neuronal activity did not reach maximum levels but decreased to 80%, the monkeys made mistakes. This result suggests that the neural network that includes the PFC and parietal cortex is required for the processing of proportions. Recording single unit activity in PFC and parietal cortex simultaneously provided the opportunity to directly compare the respective contributions of these areas [43]. Overall, neurons in the two regions shared many properties such as encoding strength and selectivity. There was also a tendency for parietal neurons to respond earlier than PFC neurons, which suggests that information could be relayed to the PFC after processing in the parietal cortex. A similar result was previously reported for the coding of discrete [45] as well as continuous magnitude [46].

Neuroimaging: symbolic notation

How does the use of symbolic labels transform the neuronal labeled-line code for proportions? Does the tuning to true numerical value break down in favor of isolated representation of the numerator and denominator? Studies of cerebral encoding of number symbols (numerals) predict that this need not be the case. In human neuroimaging experiments, the same BOLD signal adaptation phenomena can be elicited with both non-symbolic and symbolic numerosities [40,41]. In rhesus macaques trained to associate shapes of Arabic numerals with multiple-dot displays, PFC neurons are tuned to the numerical value the presented numeral signifies [47]. These association cells do not encode the visual shape *per se* but enable high-order associations to establish links between non-symbolic numerosities and arbitrary shapes [48]. Interestingly, for these neurons, distance effects are observed in both the non-symbolic dot protocol and the experiments using Arabic numerals.

In a recent fMRI study, adult participants were scanned while comparing two simple fractions, indicating with button press which fraction was larger (Figure 5a) [49]. The authors created four conditions with increasing task difficulty, assuming participants would use a componential processing strategy (i.e. treat numerator and denominator in separation): in the same denominator condition, comparison was easily achieved by selecting the larger numerator; for same numerators, participants had to select the smaller denominator; in the congruent condition, participants arrived at the same answer by comparing either the numerator or the denominator; finally, in the incongruent condition, both components had to be taken into account. Analysis of the behavioral data indeed showed an increase of reaction times and error rates for the four conditions, in accord with the results of previously discussed studies [11,16]. Differences in brain activation for the individual conditions most likely reflected increasing task difficulty.

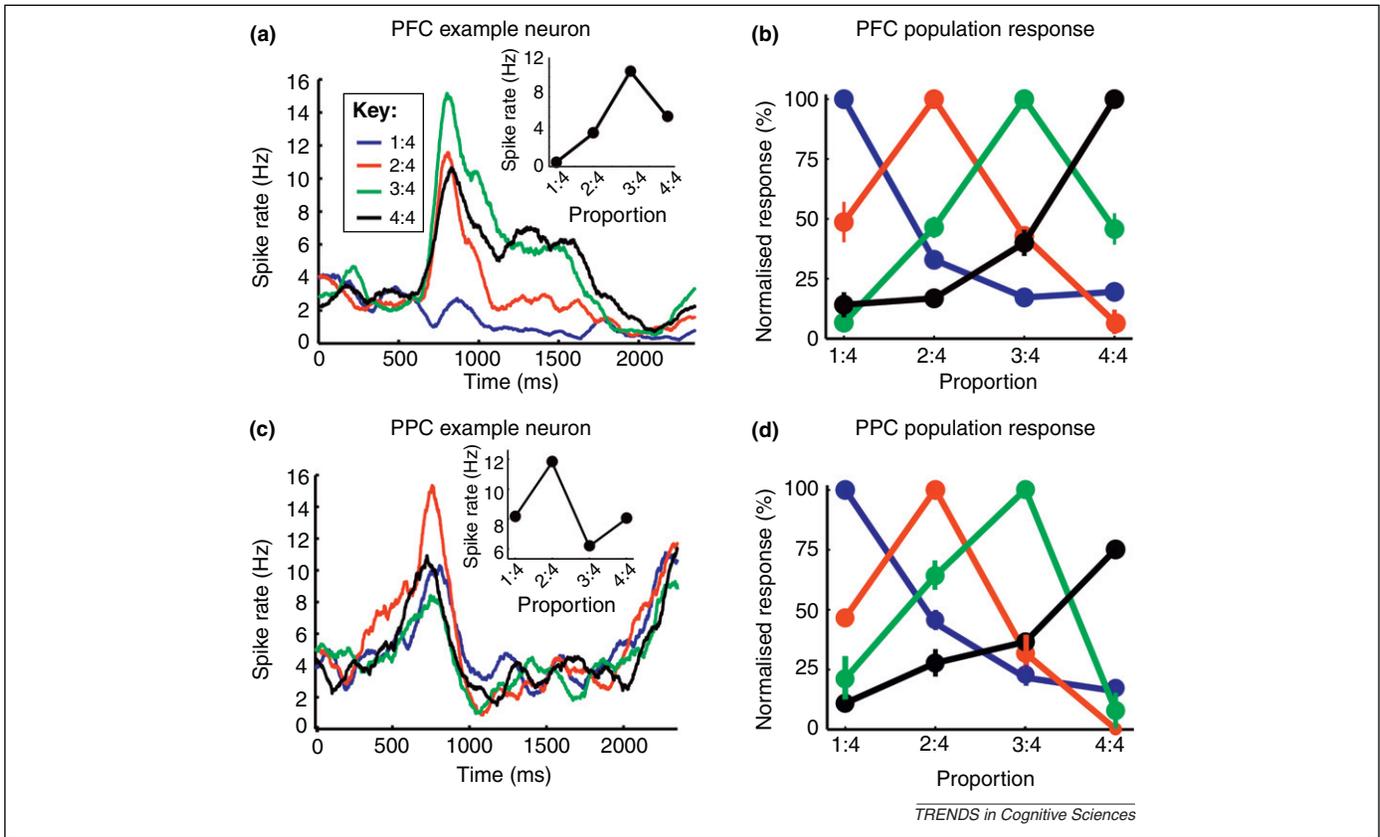


Figure 4. Neuronal responses to line proportions. (a) Peristimulus time histogram of a proportion-selective neuron from the monkey PFC. The inset shows the tuning curve of this example cell. The neuron was tuned to the proportion 3:4, i.e. it increased its firing rate maximally for this ratio. (b) PFC neuron population response to ratios. Neuronal tuning functions are symmetric and encode the distance effect, i.e. firing rates decrease as the sample proportion's numerical distance from the preferred proportion increases. (c) Proportion-selective example neuron from the monkey posterior parietal cortex (PPC). Same layout as in (a). (d) PPC neuron population response to ratios. Same layout as in (b). Reproduced, with permission, from [43].

Interestingly, however, although no brain region responded as a function of the numerical (partial) distance between the numerators or denominators (potentially arguing for componential processing), activity in the right IPS was modulated by total distance between the two presented fractions (Figure 5b). Although the subjects clearly adopted a componential processing strategy, the imaging results perhaps suggest that the human brain is indeed able to represent the real numerical value of fractions.

Following up on the fMRI adaptation study with non-symbolic proportions, Jacob and Nieder directly tested this

hypothesis [50]. The line and dot stimuli were replaced with single and multi-digit fractions (Figure 2c). In a first set of experiments, participants were adapted to number fractions (approximately 1:6 to avoid exact calculation) and saw deviants in the same notation. Despite the wide range of numerators and denominators for the adaptation stimuli, there was a robust BOLD signal decrease. As for non-symbolic ratios, the signal in bilateral IPS (and lateral PFC) recovered as a function of the deviating fraction (Figure 2d, left panel). Remarkably, this effect was independent of the deviants' notation: in further experiments,

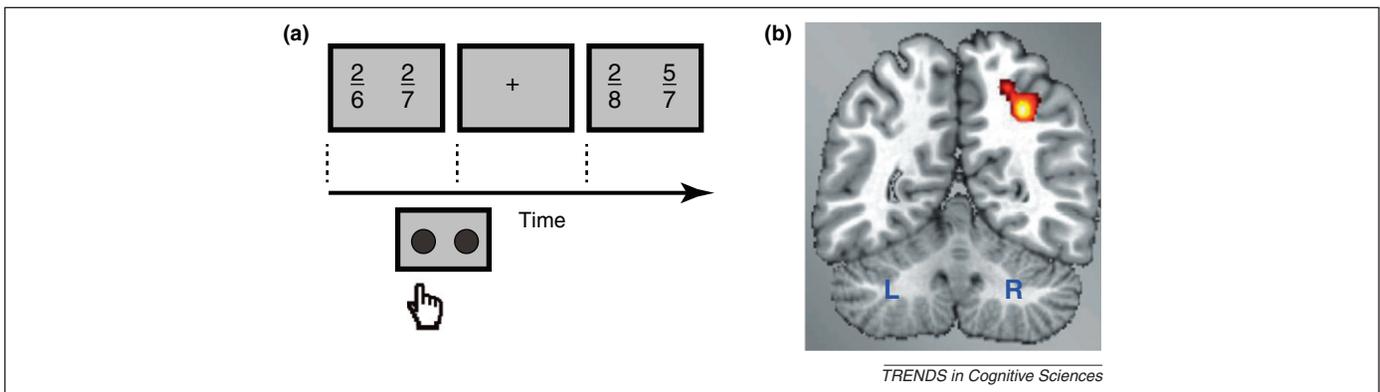


Figure 5. Task design and fMRI activity for comparison of fractions. (a). Participants indicated by button press which of two simultaneously presented fractions was larger. Two example trials are shown. (b) In the right IPS, fMRI activity correlated with total distance between the two fractions. Reproduced, with permission, from [49].

the fraction deviants were presented as words (although subjects were still adapted using numerals). BOLD signal recovery in frontoparietal cortex was identical to that seen for deviants presented as numbers (Figure 2d, right panel). This finding confirmed that there is cross-notation tuning to ratios and demonstrated that an analog code can be found even when ratios are processed as fractions with symbolic (verbal) labels.

Concluding remarks

The neuronal code for magnitude ratios is now slowly beginning to be understood. In this article, we have described experiments that have laid the foundations for a more thorough understanding of our remarkable sense of proportionality. The data address two central issues: first, how does the representation of proportions compare to its counterpart for absolute numbers, and second, in what way is the code shaped by specific task demands?

Converging evidence is suggesting that the brain uses an analog, labeled-line code to represent the true numerical value of quantity ratios. This coding scheme is highly reminiscent of absolute quantities (Box 2). Its behavioral and neurophysiological signatures are present even at early developmental stages and in different animal species. Single neurons in the prefrontal and parietal cortices are tuned to preferred proportions [34,43]. Several lines of evidence suggest that the code could be automatic, implemented by the brain even in the absence of a specific task, as well as independent of language and the format of presentation [39,50]. Proportions are represented bilaterally in the IPS and lateral PFC. Thus, both absolute quantity and quantity ratios are encoded in the same cortical regions (Figure 3). As classical association cortices guiding intelligent behavior, the parietal and frontal lobes represent late stages in the processing stream of lower-level sensory information. They are ideally suited to encode such a sophisticated measure as a proportion that requires the amalgamation of simpler, yet already abstract, absolute magnitudes.

The experimental data discussed in this review offer a tentative explanation to help resolve the controversy regarding componential versus analog (holistic) representation of magnitude ratios. This question can in fact be rephrased: how is the neuronal representation of proportions put to use by the active brain? How does a specific task change its read-out? The data presented here strongly argue that proportions can indeed be represented by their true numerical value. We hypothesize that only when strategic considerations come into play [15,16], e.g. when participants have to calculate with proportions or fractions, this code might be concealed. The question is thus one of passive representation, possibly by automatic retrieval of previously acquired numerical primitives from memory [51] versus active, intentional, goal-directed reasoning. When participants use componential strategies for exact calculation, isolated codes for the numerator and denominator could displace a holistic representation. By contrast, if calculation or verbalization is unfavorable or impossible and proportions have to be estimated, a clear analog code should emerge. This situation arises in all non-verbal animals or, in humans, when there is no explicit

task or no time to calculate, for example because stimuli are presented too rapidly. We propose that the outwardly contrasting coding schemes are therefore not mutually exclusive, but instead complement each other to facilitate behavior by giving rise to a single, most efficient code at any given time.

The highlighted experiments are clearly only scratching on the surface of the neural code for quantity ratios. As new research avenues are opening up, other important questions now await to be answered (Box 3). This review has focused on how animals and humans represent and process proportions and fractions. It will be a major challenge to determine how other numerical stimuli such as natural frequencies, decimal fractions or percentages are encoded. In decision making experiments, for example, single neurons in the lateral intraparietal cortex (LIP) increase their firing rate as a function of the likelihood of increase of certain outcomes, that is, they signal the probability associated with that particular event [52]. We do not know whether these neurons are embedded in the same networks as the cells described above, whether they are even

Box 3. Questions for future research

- How is the analog code for proportions constructed? Are the regions coding for the individual components (absolute magnitudes) different from the areas representing their ratio? Is there sequential processing from the frontal to the parietal cortex or vice versa? Do the same neurons encode both absolute number and proportions? Considering that proportions are represented at the apex of the processing hierarchy in the parietal and frontal cortex, we believe that such cells could indeed exist. For absolute magnitudes, some IPS and, in particular, PFC neurons generalize over non-symbolic and symbolic quantities [47] or over continuous and discrete quantities [57].
- What is the fate of the approximate representation of ratios in form of an analog code when exact manipulation (calculation) becomes necessary [49] or mathematical rules are applied [58]? Is this coding format still present or forfeited in favor of componential codes? Is there a division of labor between the left and right hemispheres for exact and approximate manipulation, respectively, as suggested for absolute number [59]?
- Is the network for representing ratios restricted to abstract numerical stimuli? For absolute quantity, a system is envisaged that processes magnitudes in the dimensions of space, time and number [60]. In a similar vein, one could think of the frontoparietal cortex as a general stimulus comparator or relator. Seen this manner, it might process ratios of different modalities such as tactile information or time intervals and even extra-dimensional, more complex analogies (e.g. glove:hand versus shoe:foot).
- Finally, there is hope that the basic research reviewed here will have implications and eventually translate into benefits for mathematical education. It might be possible to design teaching strategies that bias the understanding of proportions towards the brain's automatic, analog code in order to facilitate teaching of magnitude ratios [8]. Playing games can successfully convey the system of natural numbers to young school children [61,62]. An understanding of quantity ratios is traditionally even more demanding to achieve. Teaching is thought to be too formalized, stressing the concept of a fraction as a placeholder for the division of two whole numbers [3]. It has been advocated that mathematical education should aim to put less emphasis on exploiting previously acquired knowledge of natural numbers [7]. Teaching projects have already been devised to stress the conceptual meaning of fractions via physical world models, i.e. coming to view matter as continuous, non-symbolic representation (favoring semantic knowledge over syntactic knowledge) [63,64].

the same cells or whether they are part of very different routes of neural information flow. Nonetheless, given the behavioral relevance of quantity ratios, there will be much to gain by fostering research in this exciting new field of numerical cognition.

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