Original Article

A biological foundation for spatial–numerical associations: the brain's asymmetric frequency tuning

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"Left" and "right" coordinates control our spatial behavior and even influence abstract thoughts. For number concepts, horizontal spatial–numerical associations (SNAs) have been widely documented: we associate few with left and many with right. Importantly, increments are universally coded on the right side even in preverbal humans and nonhuman animals, thus questioning the fundamental role of directional cultural habits, such as reading or finger counting. Here, we propose a biological, nonnumerical mechanism for the origin of SNAs on the basis of asymmetric tuning of animal brains for different spatial frequencies (SFs). The resulting selective visual processing predicts both universal SNAs and their context-dependence. We support our proposal by analyzing the stimuli used to document SNAs in newborns for their SF content. As predicted, the SFs contained in visual patterns with few versus many elements preferentially engage right versus left brain hemispheres, respectively, thus predicting left-versus rightward behavioral biases. Our "brain's asymmetric frequency tuning" hypothesis explains the perceptual origin of horizontal SNAs for nonsymbolic visual numerosities and might be extensible to the auditory domain.

Keywords: hemispheric asymmetry; numerical cognition; SNARC effect; spatial frequency tuning; spatial–numerical associations; spatial vision

Introduction

Across many domains of daily living, we find that numbers are systematically associated with space: on numbered artifacts, such as rulers, keyboards, graphs, and so on, small numbers (e.g., "1" or "2") tend to occur on the left side and larger numbers (e.g., "8" or "9") to their right. We henceforth refer to these ubiquitous associative patterns of "few–left" and "many–right" as spatial–numerical associations or SNAs. These pervasive SNAs have by now been studied in several hundred scientific publications; their origin is the focus of this contribution.

One popular method for measuring SNAs is to compare the speed of manual responses when peo-

ple classify numbers as "odd" or "even" with left- and right-side response buttons. Responses to small numbers are faster and more accurate with left-side buttons and responses to larger numbers are faster and more accurate with right-side buttons. SNAs can be found with many other tasks, such as magnitude classification (Is this number larger or smaller than the reference value?), magnitude comparison (Which of these two numbers is larger?), and with responses made by many different body parts, such as the eyes, one or both hands, the feet, and even by turning one's head or when choosing a walking direction (reviews in Refs. 1–3).

Interestingly, SNAs are range-dependent, such that numbers "4" and "5" are left-associated within the number set 4–9 but right-associated within the number set 0–5 (see Exp. 3 in Ref. 4 and Exp. 1 in Ref. 5). This context-dependence of SNAs is

[Correction added on November 3, 2020 after final online publication: Martin H. Fischer was designated as corresponding author.]

particularly challenging to explain and we will return to it repeatedly below, after briefly describing previous attempts to identify the origin of SNAs.

Searching for the origin of SNAs

Given that number symbols are a cultural invention and that they figure prominently on various artifacts, it is not surprising that the origin of SNAs was initially attributed to cultural techniques and their acquisition through schooling. These explanations included the acquisition of directional reading and writing skills,[6–8] directional finger counting habits,[9] and directional object counting preferences.[10–12] In conflict with such explanations of the origin of SNAs in sensory and motor habits, SNAs were subsequently discovered in preschoolers,[13] then in infants,[14] and recently even in newborn humans[15,16] and animals.[17,18] Of course, for uneducated minds, the number symbols were replaced with nonsymbolic numerosities to convey the intended magnitude meaning and to establish its spatial association. Moreover, SNA measurements were adapted to include habituation, preferential looking, or detection paradigms instead of speeded choice responses. We will describe two key studies in detail below.

One concern when using nonsymbolic numbers, such as visual dot patterns, is that the numerosity of elements is correlated with other physical variables, such as overall surface area, perimeter, density, and convex hull of the stimuli. Thus, it can be unclear whether responses are governed by number or other nonnumerical magnitudes unless control conditions are implemented. Much effort went into isolating the numerical dimension,[19] but this is never completely possible; it may even be ill-advised when aiming to understand how we comprehend the numerical sizes of sets in daily life.[20,21]

This brief history of research into the origin of SNAs raises a fundamental question: How do magnitudes become associated with space, regardless of their visual format? The initial studies with number symbols pointed to a culturally acquired origin of SNAs, while more recently discovered nonsymbolic SNAs in both human and nonhuman newborns demand a biological explanation.

De Hevia *et al.*[22,23] pointed out the presence of two factors: (1) a biological left-sided bias subject to right hemisphere specialization for visuospatial processing in general and maturational advantage,

and (2) a developmental preference for increasing numerical sequences. Together, these factors would support a preferred left-to-right scanning direction[24] and consequent association between few–left and many–right.

Alternatively, Rugani *et al.*[25] (see also Refs. 18 and 26) postulated that the right hemispheres of all vertebrate brains (including humans and birds) are tuned toward numerosity processing in general. Numerical test materials would then preferentially activate this hemisphere to induce attentional bias to the left side in all conditions.

More recently, Vallortigara[27] proposed a theory that relies on hemispheric specialization for emotional valence. In this view, a small/large number of items triggers negative/positive emotions, respectively, and this would preferentially engage the right/left hemisphere, thus leading to left-/rightward behavioral biases, respectively.

It is now clear that SNAs reflect multiple components: situated factors, such as the current number range; embodied experiences, such as sensorimotor habits; and grounding in biological constraints that were evolutionarily inherited. The hierarchical relationship between grounding, embodiment, and situatedness of number knowledge is elaborated elsewhere.[28–31]

So far, all biological explanations of SNAs ground on the association of numerosity with space. Here, we present a novel proposal that focuses on the association between nonnumerical visual-spatial frequency (SF) and space.[32] As we will later show, the *spatial frequency* features contained in any visual stimulus, including sets of dots, can serve as nonnumerical foundation for nonsymbolic SNAs.

The brain's asymmetric frequency tuning hypothesis

We present the *brain's asymmetric frequency tuning* (BAFT) hypothesis to explain how SNAs originate in all vertebrate brains. Our hypothesis relies on three arguments: (1) the SF decomposition of visual scenes; (2) the hemispheric specialization for different SF bands; and (3) the crossover of the optic fibers at the level of the optic chiasm. We introduce each argument in turn.

First, and in close analogy to the well-established auditory signal decomposition into power spectra (auditory Fourier analysis), the visual system also decomposes all scenes into power spectra over

SFs.[a] Such spectral decomposition is one of the earliest and most fundamental properties of human vision, beginning already at the retinal level and in the early visual cortex.[38–41] Human vision is organized into central foveal vision, specialized in processing high SFs for detailed inspections, and peripheral vision for orienting attention to new spatial goals defined by low SFs. This differential sensitivity to SFs across the visual field is the main reason for why we move our eyes, and thus strongly influences orienting behaviors.[42,43] Much of the early visual cortex performs SF analyses through specialized neuronal SF channels that can be selectively adapted.[44,45] SF analysis also informs the fundamental distinction between vision for perception and vision for action.[46]

SFs are defined as the number of dark-light cycles per degree of visual angle. Low SFs (few cycles per degree) capture the global distribution of light and dark across the entire scene; high SFs (many cycles per degree) instead code local changes from light to dark that correspond to smaller elements. Therefore, when a visual scene contains only a few coarse elements, this results in spectral decomposition of that scene with high power in the low SF range. Similarly, if there are many small elements present in the scene, this results in spectral decomposition of that scene with high power in the high SF range. Of course, there is no necessary correspondence between numerosity and SFs in a scene because it can also contain just a few tiny objects. Nevertheless, there is a plausible correlation that will be substantiated below. This insight constitutes the first argument of BAFT.

Second, there is considerable evidence that SF processing is lateralized in vertebrate brains: the

right hemisphere predominantly selects low SFs, while the left hemisphere predominantly selects high SFs (reviewed in Ref. 47). Evidence for this hemispheric SF specialization is wide-ranging: attending to global versus local object properties activates the right versus left hemisphere, respectively.[48,49] Moreover, hemispheric specialization for salient categories, such as letters versus faces, is governed by the SF characteristics of these materials.[50] Similarly, patients with left or right hemisphere lesions show impaired identification and recognition of local or global elements, respectively.[51] Asymmetric SF tuning of our brains constitutes the second argument of BAFT.

The third and final argument of BAFT refers to the well-established neuroanatomical fact that the fibers connecting eyes and brain cross at the optic chiasm (e.g., see Ref. 41, Chapter 9). This crossover provides each brain hemisphere with visual input from the contralateral hemifield: visual information from the left side of the current fixation point projects to the right hemisphere; conversely, visual information from the right-side projects to the left hemisphere. Together, these three components of BAFT explain the pervasive cognitive association of few items with left space and more items with right space (i.e., nonsymbolic SNAs) as resulting from the biological hemispheric asymmetry in SF selection. Figure 1 illustrates the key ideas behind BAFT.

Computational evidence for BAFT
Next, we document the feasibility of BAFT by applying SF analysis to the visual materials used by two key studies that reported nonsymbolic SNAs in 3-day-old chicks and newborn humans.[18,16] We begin by showing that the behavioral biases associated with few and many elements reported in these studies can be explained by systematic changes in the power spectra from their adaptation to their test materials. Then, we document how the presence of the range dependence of SNAs can also be explained by the same principle. Finally, we identify limitations of the control conditions offered in these studies. In the Discussion section, we describe possible extensions and implications of *BAFT*.

Materials and methods

In order to test whether hemispheric SF tuning explains the documented SNAs in human and nonhuman newborns, we decomposed the stimuli used by Rugani *et al.*[18] and Di Giorgio *et al.*[16] into

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[a]This is an oversimplification, but indeed the filter characteristic of many V1 simple cells has been found to be similar to Gabor filters,[33–36] which are optimal spatial frequency analyzers. A Gabor filter characteristic also emerges in the filters learned at the early hierarchical layers of deep convolutional neural networks (DCNN), and these networks can even be improved when Gabor filters are systematically introduced into these early layers, rather than learned.[37] V1 simple cell properties have been shaped by biological evolution, and Gabor-like properties in DCNN emerged from the training objective to categorize objects. This converging evidence makes it highly likely that spatial frequencies are a fundamental property of our visual environment that can be explored by biological or artificial vision.
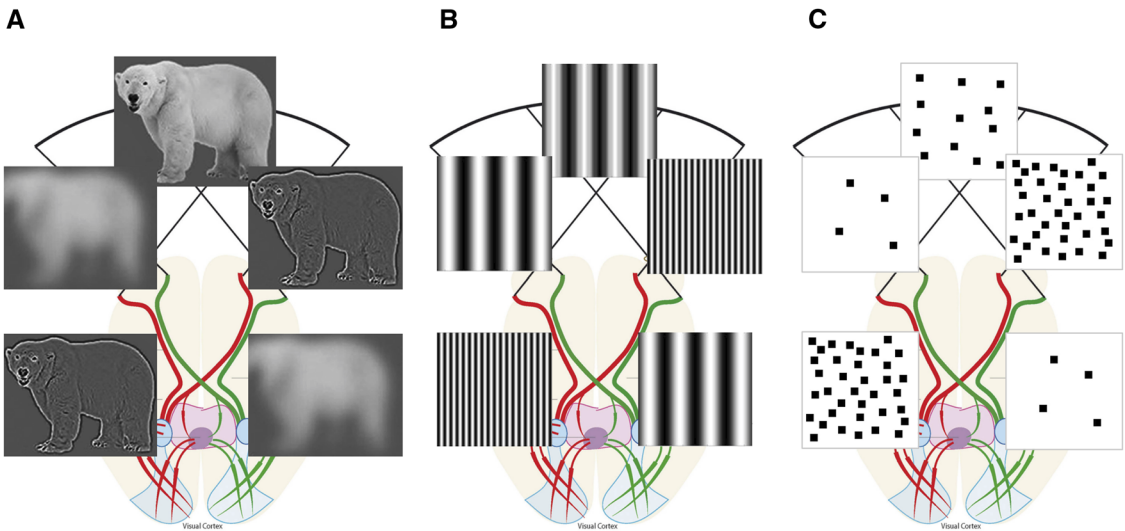
Figure 1. All panels illustrate how, with respect to a given visual scene characterized by middle SF range (top row), the left/right hemisphere preferentially filters higher/lower SF percepts, respectively (bottom row). As a consequence of the hemispheric predominance, attention is projected to the contralateral hemifield (middle row). (A) One everyday object is represented as coarse elements in the right hemisphere but as an assembly of details in the left hemisphere. (B) The general case, that is, processing of an SF-defined contrast grating. (C) The specific case, that is, processing SFs of square patterns used in the experiment by Di Giorgio and colleagues.[16] Within a given numerical range, any smaller/larger numerosity is represented by lower/higher spatial frequency ranges, respectively, compared with the middle spatial frequency range of the reference stimulus. The bottom row in panel C schematically indicates how decomposition of the difference between the adaptor and stimulus into low and high SFs is preferentially processed by the different hemispheres, resulting in the observed looking preference for contralateral space (middle row). The polar bear scenes of panel A are adapted from Figure 3 of Ref. 81, licensed under CC-BY, version 4.0. The anatomy of visual pathways is redrawn after Figure 1 of Ref. 82, licensed under CC-BY, version 4.0. Figure 1 is licensed under CC-BY, version 4.0 by Arianna Felisatti.

their SF content, using the fast Fourier transform algorithm.[52] Stimulus images were provided by the authors[b] or else extracted from or generated according to the published papers. We converted these images into the SF domain and computed their rotationally averaged power spectra with standard software (MATLAB®, R version 3.6.1; see Ref. 53). Next, for each experiment reported below, we subtracted the logarithm of the power spectrum of the habituation stimulus from that of the subsequent ("few" or "many") test stimulus, yielding relative power. Discrete data points were interpolated using a scatterplot smoother based on local polynomial regression fitting.[54]

Below, we plot relative power as a function of logarithmic SF. Specifically, we visualize changes in power of the current test stimulus relative to the standard stimulus (along the *y*-axis) against SF (along the *x*-axis). These plots summarize the purely physical stimulus conditions at the time of behavioral testing in the original studies to be reviewed. Each plot should be scrutinized by readers in four quadrants (Fig. 2); for example, the *upper left* quadrant identifies increases in power from the standard to the test stimulus for lower SF. According to BAFT, this is associated with increased right-hemispheric activity, which, in turn, induces a behavioral left-bias. Generally, those segments showing the largest deviations from the dashed zero-line represent the behaviorally relevant change in the respective testing conditions.

Results

Numerosity effect and range dependency
Let us first consider the study by Rugani and colleagues.[18] In their first experiment, they assessed the SNA in 3-day-old chicks with a habituation paradigm. After exposure to centrally presented
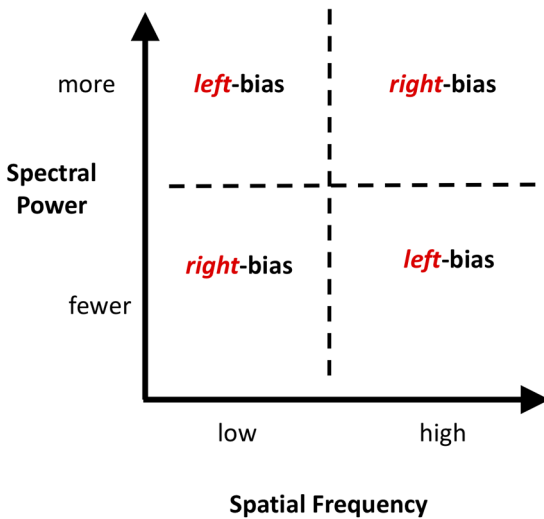
Figure 2. Schematic illustration of the relationship between physical stimulus attributes and resulting behavioral biases. Each panel of Figure 3 may be interpreted more easily by using this conceptual "overlay." For example, when the test stimulus has more power in the low spatial frequency spectrum than the habituation stimulus (top left quadrant), we expect the test stimulus to induce left-bias, owing to stronger engagement of the right than the left brain hemisphere.

square-patterns depicting five black squares, chicks were presented with two test situations: in one, they saw bilateral square-patterns displaying two identical squares and they preferred to explore the left-sided panel. In the other test, they saw bilateral square-patterns displaying eight identical squares and they preferred to explore the right-sided panel.

Panel A of Figure 3 shows the results of our computational analysis of this experiment. The largest deviations from the zero line occur in the high SF range, namely in the lower right quadrant of that panel. Specifically, the gray line depicts the fact that, when testing chicks with two squares after adapting them to five squares, this leads to a reduction in high SFs, thus inducing a behavioral left-bias according to BAFT. Similarly, the orange line depicts the fact that, when testing chicks with eight squares after adapting them to five squares, this leads to an increase in high SFs, thus inducing a behavioral right-bias, as explained by BAFT.

A similar analysis applies to the first experiment of Di Giorgio and colleagues.[16] They assessed the SNA in hour-old human newborns with a similar habituation paradigm. After exposure to centrally presented square-patterns depicting 12 black

squares, one group of newborns was presented with bilateral square-patterns displaying 4 identical squares; they looked longer at the left-sided panel. Another group of newborns was presented with bilateral square-patterns displaying 36 identical squares; they looked longer at the right-sided panel.

Panel B of Figure 3 shows the results of our analysis of this experiment. As before, the largest deviations from the zero line occur in the high SF range, with the gray line depicting a reduction in high SFs, thus inducing a left-bias. Similarly, the orange line depicts an increase in high SFs, thus inducing a right-bias. Both behavioral outcomes are explained by BAFT.

We now turn to an analysis of range dependence of SNAs. Rugani *et al.*[18] (Experiments 1 and 2) compared SNAs in two groups of 3-day-old chicks with identical test stimuli (8 squares) that followed habituation to either a small standard (5 squares; Experiment 1) or a large standard (20 squares; Experiment 2). Consistent with the range dependence of symbolic SNAs for humans (see above), Rugani *et al.*[18] reported a left-preference in exploratory behavior following the reduction and a right-preference following the increment in numerosity.

This range dependence of numerosity-related spatial exploration can also be explained by BAFT: testing chicks with 8 squares after adapting them to 20 squares (gray line in panel C of Fig. 3) leads to a strong reduction in high SFs, thus inducing a left-bias. Instead, testing chicks with eight squares after adapting them to five squares leads to an increase in high SFs, thus inducing a right-bias (see orange line of panel A).

A similar analysis applies to the range effect reported by Di Giorgio *et al.*[16] (Experiments 2a and 2b). They assessed SNAs in human newborns with identical test stimuli (12 squares) that followed habituation to either a large (36 squares) or a small (4 squares) standard. Again consistent with range-dependent SNAs, Di Giorgio *et al.*[16] reported a left-preference following the reduction and a right-preference following the increment in numerosity.

Panel A of Figure 4 shows the results of our combined analysis of these two experiments. In contrast with the previous analysis, the largest deviations from the zero line now occur in the low SF range, with the gray line depicting a strong increase
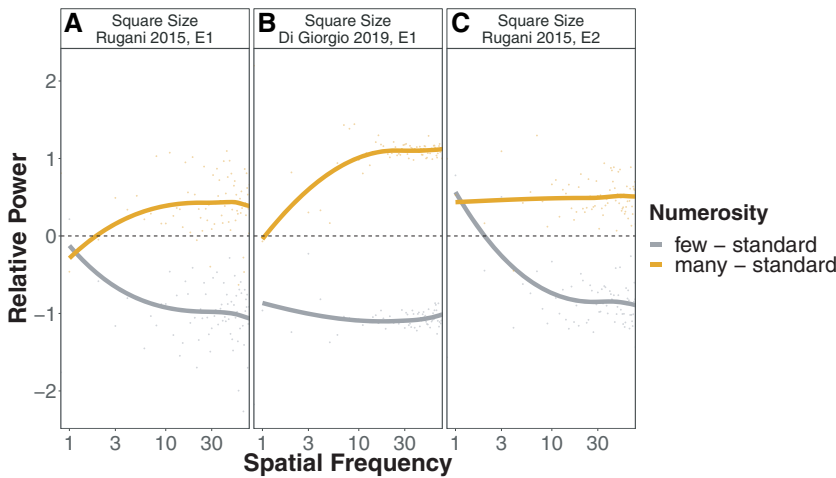
Figure 3. Relative power as a function of spatial frequency for the stimuli used by Rugani *et al.*[18] and Di Giorgio *et al.*[16] See Figure 2 for interpretation and the main text for details.

in low SFs, thus inducing a left-bias. Similarly, the orange line depicts a strong decrease in low SFs, thus inducing a right-bias. Again, both outcomes are explained by BAFT.

Other visual effects

Why does our computational analysis of the two range-related experiments by Rugani *et al.*[18] and Di Giorgio *et al.*[16] differ, with power changes in high SFs for Rugani *et al.*[18] and in low SFs for Di Giorgio *et al.*?[16] This apparent discrepancy is explained by the need to control for the correlation

of numerosity with different continuous visual features: in Experiments 1 and 2 of Rugani *et al.*,[18] numerosity was *positively* correlated with overall area and perimeter; instead, in Experiments 2a and 2b by Di Giorgio *et al.*,[16] numerosity was *negatively* correlated with overall area as the result of perimeter control. Our explanation was confirmed when we analyzed the third experiment of Rugani *et al.*[18] (Condition 3) where they replicated the range dependence of SNAs under perimeter control with identical numerosities. As can be seen in panel B of Figure 4, the deviations from zero now occur in the
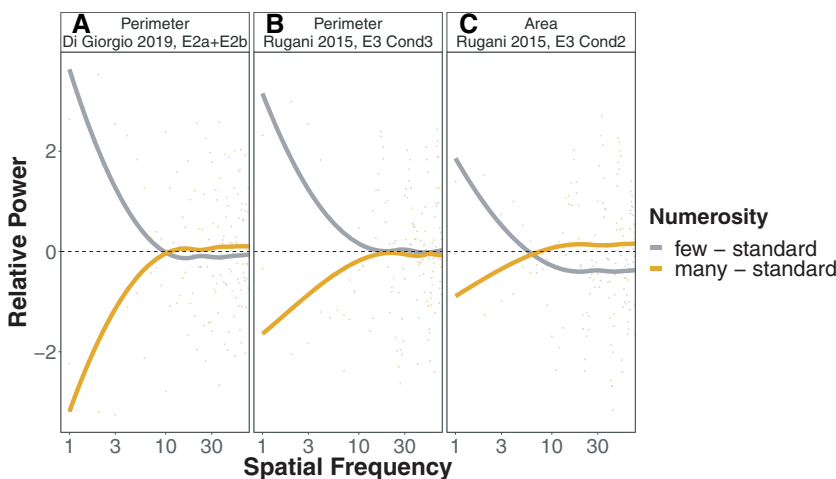

Figure 4. Relative power as a function of spatial frequency for the stimuli used by Rugani *et al.*[18] and Di Giorgio *et al.*[16] See Figure 2 for interpretation and the main text for details.

low SF range, as it did in the study of Di Giorgio *et al.*[16] (see panel C).

BAFT also explains the outcomes of other visual control conditions used by Rugani *et al.*[18] (Condition 2: area control). In this study, they again reported SNAs in 3-day-old chicks, which BAFT explains by comparing the changes in power spectra (see panel C of Fig. 4): the largest deviations from zero occur again in the low SF range, with the gray line depicting an increase in low SFs, thus inducing left-bias. Similarly, the orange line depicts a decrease in low SFs, thus inducing right-bias.

In summary, our computational analyses document a confound between numerosity and SF in two recent studies,[16,18] pointing to a biological, nonnumerical origin of SNAs. Our hypothesis of lateralized SF processing in the vertebrate brain,[55–57] therefore, argues that SF signals are used as proxy for numerosity-based behavioral decisions. We now discuss the wider implications of our findings.

Discussion

The present work was motivated by a long-standing search for the origin of SNAs, according to which small numbers and numerosities are associated with left space and larger numbers and numerosities are associated with right space.

This search for symbolic number–space associations in adult has previously pointed to nonnumerical and numerical culturally mediated influences, such as reading direction[58,59] or finger counting habits.[9,60–62] However, the nonsymbolic numerosity–space association found in human newborns[16] and 3-day-old chicks[18] was previously attributed to a biological mechanism of numerosity that is innately associated with space.

Here, we have presented a computational analysis of several visual materials that were recently used to document inborn SNAs. We were able to account for the reported behavioral biases in newborn humans and chicks by showing that they are systematically related to changes in the SF content of the test stimuli relative to the previously presented standard stimuli in all cases. This supported our novel, nonnumerical account for the origin of SNAs.

The BAFT hypothesis consists of three components: first, the vertebrate visual system decomposes visual input into SFs. This SF filtering represents global patterns, few or distributed elements in the

low SF range, and represents visual details, many and small objects in the high SF range. Second, left hemispheres of vertebrate brains prefer high SF content and right hemispheres prefer low SF content. And third, vertebrates' visual input is cross-lateralized to their brains, such that left-side stimuli engage the right hemisphere and vice versa.

On the basis of these established principles from vision science (e.g., see Ref. 41), BAFT offers a plausible biological mechanism for the origin of SNAs in the differential engagement of both hemispheres for those SF ranges that tend to co-occur with small and large numerosities. Clearly, we have discovered a previously overlooked visual feature that induces behavioral biases. However, BAFT goes well beyond merely identifying another potential confound when examining numerosity patterns. By bringing together three known facts about brain anatomy and neurophysiology, it localizes the origin of nonsymbolic SNAs without recourse to other cognitive principles. Moreover, BAFT is consistent with the strong impact of early visual experience on SNAs[63] and with the multifactorial nature of SNAs (e.g., see Ref. 28).

Importantly, our proposal substantially develops earlier suggestions about a functional role of brain asymmetries in SNAs.[22,25,64] While in early development, the right hemisphere dominates number processing, parietal areas of both hemispheres subsequently compute numerical information from sensory percepts,[65–67] presumably by filtering low/high SFs (reviewed in Ref. 68) and encoding numerosities.[69] Since parietal regions also guide spatial attention, their asymmetric activation favors attentional orienting toward the contralateral space.[70]

In summary, BAFT relies on the brain's asymmetric tuning for different SF bands with respect to the SF range contained in the scene. In tasks where higher cognitive functions are involved, such as discrimination and identification, the left (right) hemisphere would act as high-pass (low-pass) filter, allowing more efficient selection of many fine (few coarse) elements and thus avoiding redundant processing.[68,71] Experiencing a visual percept implies being exposed to SFs that act as a reference in the subsequent filtering process. As a consequence, SF selection depends on the overall SF range contained in the stimulus set, just like SNAs depend on the overall numerical range. Supporting

evidence comes from behavioral and neuropsychological studies: presenting a given stimulus in the right/left visual field yields a global/local processing advantage in neurologically normal participants;[72] presenting the same stimulus to right/left hemisphere patients results in deteriorated identification of global/local elements, respectively.[73] In habituation paradigms, the organism's perceptual adaptation to its recent visual experiences further enhances SF tuning by flexibly modulating the sensitivity profile of SF-selective neurons.[74] Whether this explanation of range effects is valid depends on further studies.

As mentioned in the introduction, not only visual but also auditory stimuli can be decomposed into their frequency components. This multimodal neural coding principle suggests extending BAFT to other perceptual domains:[71,75–78] indeed, the left hemisphere predominantly extracts signals from relatively high temporal frequency, while the right hemisphere extracts signals from relatively low temporal frequency.

We acknowledge that BAFT currently relies on computational analyses of materials from only a handful of experiments, although these are particularly diagnostic. BAFT may become part of a neuroscientifically grounded general theory of number knowledge[79,80] once the proposal has been supported by SF decomposition of other previously used SNA-inducing materials and by dedicated experiments.

Finally, a fundamental question to advance our knowledge about SNAs would be to ask whether the proposed role of SFs extends to ground the pervasive symbolic SNAs reviewed in the introduction. Establishing this link would have substantial educational and neuropsychological implications.

Author contributions

A.F. conceived and developed the BAFT hypothesis, contributed to data analyses, and drafted the first version of the manuscript. J.L. performed the data analysis and visualizations and contributed to the introduction, results, and discussion sections. S.S. contributed to the writing of the manuscript and restructuring the introduction and discussion sections. M.H.F. conceived of the idea and contributed to the writing of the manuscript.

Competing interests

The authors declare no competing interests.

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