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Numerosity and Cumulative Surface Area Are Perceived Holistically as Integral Dimensions

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Human and nonhuman animals have a remarkable capacity to rapidly estimate the quantity of objects in the environment. The dominant view of this ability posits an abstract numerosity code, uncontaminated by nonnumerical visual information. The present study provides novel evidence in contradiction to this view by demonstrating that number and cumulative surface area are perceived holistically, classically known as *integral dimensions*. Whether assessed explicitly (Experiment 1) or implicitly (Experiment 2), perceived similarity for dot arrays that varied parametrically in number and cumulative area was best modeled by Euclidean, as opposed to city-block, distance within the stimulus space, comparable to other integral dimensions (brightness/saturation and radial frequency components) but different from separable dimensions (shape/color and brightness/size). Moreover, Euclidean distance remained the best-performing model, even when compared to models that controlled for other magnitude properties (e.g., density) or image similarity. These findings suggest that numerosity perception entails the obligatory processing of nonnumerical magnitude.

Keywords: numerosity perception, approximate number system, analog magnitude system, integral and separable dimensions, multidimensional stimuli

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Accumulating evidence suggests the existence of an evolutionarily primitive mental system dedicated to the nonverbal representation of numerosity, known as the *approximate number system* (Nieder & Dehaene, 2009). This system, which is prevalent across the animal kingdom (Aulet et al., 2019; Dadda, Piffer, Agrillo, & Bisazza, 2009; Rugani, Vallortigara, & Regolin, 2013), allows for the rapid estimation of visual sets, an ability critical for decision making regarding quantity (e.g., foraging or group selection; Brannon, 2005). In humans, the ability to estimate numerosity is present from early in life (Izard, Sann, Spelke, & Streri, 2009) and has even been shown to predict later mathematical achievement, such that individuals with more precise acuity for numerosity likewise exhibit better performance on standardized math tests (Chen & Li, 2014).

Despite decades of investigation into the approximate number system, the nature of the underlying numerosity code remains hotly debated, pervading the fields of cognition (Leibovich, Katzin, Harel, & Henik, 2017), philosophy (Carey, 2009), neuroscience (Nieder & Dehaene, 2009), and computational modeling (Nasr, Viswanathan, & Nieder, 2019; Stoianov & Zorzi, 2012). Although the visual depiction of any set of objects is necessarily multidimensional (i.e., a set of objects may vary in size, shape, color, etc.) and numerosity is often correlated with other magnitude properties (e.g., area, density, etc.), it is commonly argued that the numerosity of objects is represented independently of other dimensions (Burr & Ross, 2008; Ferrigno, Jara-Ettinger, Piantadosi, & Cantlon, 2017). Specifically, the argument is that number is perceived directly, resulting in a representation of numerical quantity that is normalized over other properties (Dehaene & Changeux, 1993; Stoianov & Zorzi, 2012; Verguts & Fias, 2004).

Critically, nonnumerical cues such as cumulative surface area, density, and element size have been shown to influence numerical estimation (Gebuis & Reynvoet, 2012; Gilmore, Cragg, Hogan, & Inglis, 2016). An account of these interactions, which follows from the view that number is represented independently of other magnitudes, is that nonperceptual mechanisms mediate the interactions between numerical and nonnumerical magnitudes. During the process of explicit numerical estimation, number representations are then utilized by domain-general mechanisms, at which time numerical and nonnumerical dimensions are linked via linguistic (Winter, Marghetis, & Matlock, 2015), analogical (Cantlon, Platt, & Brannon, 2009; Holyoak, 1977), or decision processes (Cohen Kadosh, Gevers, & Notebaert, 2011).

An alternative to the dominant view argues for the existence of representational overlap between numerical and nonnumerical dimensions. Often, however, even proponents of this position posit magnitude dimensions that are initially independent and only later integrated

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within a general magnitude system (Lourenco & Aulet, 2019; Walsh, 2003), perhaps via Bayesian cue combination (Martin, Wiener, & van Wassenhove, 2017; Petzschner, Glasauer, & Stephan, 2015). A more provocative, although less frequently discussed, proposal is that the proposed overlap may be primary and perceptual in nature, such that number and nonnumerical magnitudes are perceived in a holistic manner. Although literate humans have access to symbolic numerals (e.g., Arabic digits and number words), which may allow for a truly abstract representation of number, it remains unclear whether the perception of numerosity is independent of other visual cues (Halberda, 2019). Such a possibility would be consistent with other evidence from human and nonhuman animals in which multidimensional stimuli are perceived holistically (Finkelstein, Ulanovsky, Tsodyks, & Aljadeff, 2018; Komorowski, Manns, & Eichenbaum, 2009). Specifically, the conjunctive coding of visual features is prevalent within human and nonhuman visual systems, potentially indicating a more robust and efficient method for representing multidimensional stimuli (Engel, 2005; Zohary, 1992).

In previous work, it has proven difficult to determine the mechanisms underlying the interactions between numerical and nonnumerical magnitudes because the various accounts of these interactions often make similar predictions. For example, on a magnitude-comparison task, in which participants make explicit judgments of relative numerosity, interference from nonnumerical dimensions could result either from a decision-stage conflict (akin to Stroop interference; Tzelgov, Meyer, & Henik, 1992; Yates, Loetscher, & Nicholls, 2012) or a perceptually integrated representation of numerical and nonnumerical magnitudes. That is, both accounts similarly predict that incongruent nonnumerical information leads to slower and less accurate numerical judgments.

The present study provides an approach for dissociating the two accounts. In particular, we asked whether the relation between number and nonnumerical magnitudes is best characterized by separable dimensions, consistent with the dominant view in the literature, or integral dimensions, contra this view. Separable dimensions are classically defined as pairs of dimensions for which a change in one dimension causes no perceived change in the other (Garner, 1974). By contrast, integral dimensions are pairs of dimensions for which a change in one dimension *does* cause a perceived change in the other. Moreover, whereas separable dimensions require independent processing of each component dimension, integral dimensions are perceived in a holistic or unitary fashion (Lockhead, 1972).

The central insight that guides the present approach is that separable and integral dimensions can be differentiated by the distance metric that governs their respective stimulus spaces (Garner, 1974; Shepard, 1964). In particular, perceived similarity for stimuli composed of separable dimensions is best explained by a city-block distance metric, whereas perceived similarity for stimuli composed of integral dimensions is best explained by a Euclidean distance metric (Garner & Felfoldy, 1970; Soto, Quintana, Pérez-Acosta, Ponce, & Vogel, 2015; Torgerson, 1958). Here, we focus specifically on the relations between number and cumulative surface area because of well-documented interactions between these two dimensions (Hurewitz, Gelman, & Schnitzer, 2006) and the involvement of cumulative area in early stages of computational models of number representation (Allïk & Tuulmets, 1991; Stoianov & Zorzi, 2012). By examining number and cumulative area within the framework of separable and integral dimensions, the dissociation between predicted distance metrics within the stimulus space allows for an unambiguous assessment of the underlying representations. If number and cumulative area are represented independently, then the relation between them will be best described as separable dimensions. As such, perceived similarity for dot arrays that vary parametrically in number and cumulative area will be best explained by the city-block distance metric. That is, the transition between any two stimuli will be well described by a (rectilinear) purely additive relation. Conversely, if number and cumulative area are integral, then the perceived similarity for these stimuli will be best explained by the Euclidean distance metric. That is, the transition between any two stimuli will be well described by a subadditive relation. Thus, the present approach allows for a clear and strong test of the dimensional status of number and cumulative area.

In Experiment 1, we collected explicit similarity judgments from participants using a categorization task in which city-block and Euclidean distances made divergent predictions regarding how stimuli are classified. In Experiment 2, we collected implicit similarity judgments, measured by the degree of distractor interference in a sequential match-to-sample task. In both experiments, similarity judgments for dot arrays that varied parametrically in number and cumulative area were compared to similarity judgments for stimuli previously suggested to be either separable (Experiment 1: shape/color; Experiment 2: brightness/size) or integral (Experiment 1: brightness/saturation; Experiment 2: brightness/saturation and radial frequency components). The present study provides the first direct test of the dimensional status of number and cumulative surface area and places these findings in relation to the perception of other multidimensional stimuli more generally.

Experiment 1: Are Similarity Judgments for Number and Cumulative Area Better Predicted by City-Block or Euclidean Distance?

In Experiment 1, we assessed whether similarity for dot arrays that vary in number and cumulative area, measured by explicit similarity judgments, is best explained by city-block distance, suggesting they are separable dimensions, or Euclidean distance, suggesting they are integral dimensions. Critically, we also assessed how similarity judgments for number and cumulative area compared to similarity judgments for dimensions previously shown to be separable (shape/color; Garner & Felfoldy, 1970) and integral (brightness/saturation; Gottwald & Garner, 1975).

Method

Participants. Sixty undergraduates (n = 20/condition,[1] mean $[M]_{\text{age}}$ = 19.51 years; 23 male) participated for course credit. All participants had normal or corrected-to-normal vision. Procedures were approved by the local Institutional Review Board (IRB). All participants provided informed consent in accordance with the relevant guidelines and regulations of the IRB.

Procedure and design. Participants completed a categorization task in which they were asked to select which of two stimulus choices was most similar to a target stimulus. The target stimulus was presented at the top center of the screen, and the two stimulus choices were presented on the bottom left and bottom right of the

[1] Although the sample size was not determined via pre hoc analyses, the sample size is consistent with that of recent work on integral/separable dimensions (n = 18; Op de Beeck, Wagemans, & Vogels, 2003).

screen. Participants were given unlimited time to respond, but the instructions emphasized speed and accuracy. Stimuli were drawn from a square stimulus space, comprising two primary dimensions: shape/color, brightness/saturation, or number/area. Stimuli for these conditions are described below:

Shape/Color (see Part A of Figure 1 in the online supplemental materials). Stimuli were 16 star shapes that varied in the number of points of the star (4, 5, 6, and 7) and hue (Drucker, Kerr, & Aguirre, 2009). Shapes were comparable in size and presented centrally on a solid black background (400 × 400 px). Color (hue) values in the hue, saturation, value (HSV) color space for shape/color stimuli were as follows: [5, 93, 62], [15, 93, 62], [25, 93, 62], and [35, 93, 62].

Brightness/Saturation (see Part B of Figure 1 in the online supplemental materials). Stimuli were 16 square images of solid Munsell colors (400 × 400 px). Stimuli were a constant hue of 5R (red). Stimuli varied in brightness (Munsell dimension values: 3, 4, 5, and 6) and saturation (4, 6, 8, and 10). The Munsell color system is perceptually normed such that equal distance in the stimulus space corresponds to equal discriminability (Munsell, 1919).

Number/Area. Stimuli were 64 dot arrays comprised of gray dots with a black background (400 × 400 px). Stimuli varied parametrically in number (8, 10, 12, 14, 16, 18, 20, and 22) and cumulative area (cm^2: 9, 12, 15, 18, 21, 24, 27, and 30), resulting in an 8 × 8 stimulus space[2] (see Figure 1). For each of the 64 dot arrays, five exemplars of each stimulus were used, resulting in 320 unique stimuli. Individual dot size was held constant within each stimulus. Dot placement varied randomly within each stimulus.

Stimulus values were selected to equate for discriminability, an important precondition when dissociating separable and integral dimensions (Melara & Mounts, 1993, 1994). Previous work suggests that when stimulus dimensions are not matched in perceptual discriminability, the more discriminable dimension can interfere

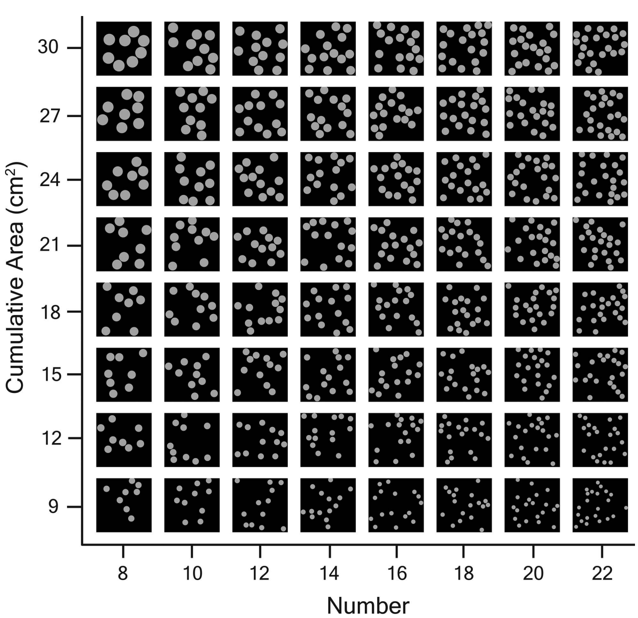

Figure 1. Number and cumulative-area stimulus space from Experiment 1. For each pair of number and cumulative-area values, five exemplars of each stimulus were created.

with judgments of the less discriminable dimension, regardless of whether those dimensions are separable or integral (Garner & Felfoldy, 1970; Melara & Mounts, 1993, 1994). Indeed, under such conditions, dimensional status is not straightforwardly interpreted because integral dimensions could appear separable simply because of differences in discriminability (Algom, Dekel, & Pansky, 1996). Thus, and crucially, stimuli were perceptually matched in the present study, such that each pair of adjacent stimulus values in one dimension was matched in discriminability to the corresponding pair of stimulus values in the other dimension. For example, the differences between first and second number values (8 and 10) and area values (9 and 12 cm^2) were equally discriminable (as indicated by accuracy in a separate group of participants; see the online supplemental materials), and this was true of all adjacent stimulus pairs (e.g., the discriminability of 20 and 22 in number was perceptually equivalent to the discriminability of 27 and 30 cm^2 in area).

Each condition comprised "correlated" and "conflict" trials. Correlated trials, although not the primary trials of interest, were included to first confirm that participants were sensitive to distance within each stimulus space. On correlated trials, both distance metrics predicted the same stimulus choice. In other words, one stimulus choice was closer in the stimulus space to the target stimulus, regardless of whether distance was assessed by city-block or Euclidean distance. Thus, on these trials, the closer stimulus should be judged as more similar to the target regardless of whether stimuli comprised separable or integral dimensions.

Conflict trials, which consisted of two types, were trials in which Euclidean and city-block distances made divergent predictions regarding stimulus choice. On these trials, one stimulus choice was closer to the target stimulus when distance was calculated according to the city-block distance metric, whereas the other stimulus choice was closer to the target stimulus when distance was calculated according to the Euclidean distance metric. Therefore, and critically, conflict trials predicted different patterns of results depending on whether stimuli comprised separable or integral dimensions.

As outlined previously, conflict trials were defined by the distance relations between the target and two stimulus choices (from here on referred to as SC_1 and SC_2). Thus, although trials were fully sampled throughout the stimulus space, Type 1 and Type 2 conflict trials always preserved the respective distance relations between target and choice stimuli. For Type 1 conflict trials (see, e.g., Part A in Figure 2), SC_1 (left square) was 3 city-block units from the target (triangle), whereas SC_2 (right square) was 4 city-block units away. Thus, if dimensions X and Y are separable dimensions, then participants should judge SC_1 as more similar to the target stimulus than SC_2. By contrast, SC_1 was 3 Euclidean units from the target, whereas SC_2 was 2.83 Euclidean units away. Thus, if dimensions X and Y are integral dimensions (and if .17 reflects a discriminable difference in the stimulus space), then participants should judge SC_2 as more similar to the target. Importantly, whether or not .17 is discriminable, if dimensions X and Y are integral, then, contra pre-

[2] An 8 × 8 stimulus space was used here for consistency with previous work (Ferrigno et al., 2017). However, separate participants (n = 11) completed the task with a 4 × 4 stimulus space, attained by subsampling the 8 × 8 space. The results corroborated the findings of Experiment 1 with the 8 × 8 space.

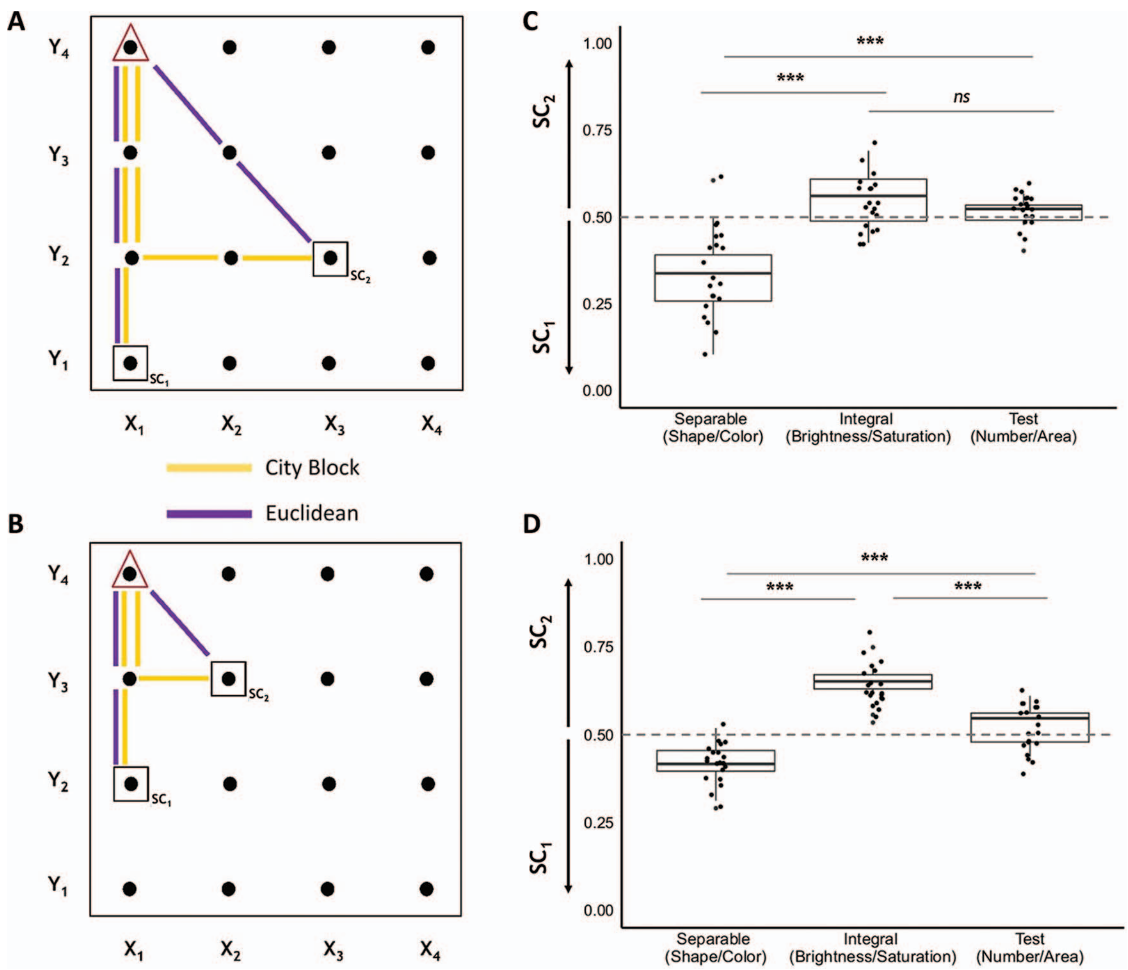

Figure 2. Example trial structure for Type 1 and Type 2 conflict trials (A and B respectively) and results for these trial types (C and D respectively). A and B: Generalized stimulus space comprising dimensions *X* and *Y*, where each black dot represents a stimulus. Conflict trials were sampled from across the stimulus space and refer to all trials in which the relations between the target and choice stimuli reflect the distance relations depicted here. For example, in B, SC_1 and SC_2 are both 2 units from the target in city-block distance; in contrast, whereas SC_1 is 2 units from the target in Euclidean distance, SC_2 is 1.41 units from the target in Euclidean distance. C and D: Box and whisker plots for each condition of Type 1 (C) and Type 2 (D) conflict trials. The *y*-axis represents the proportion of trials in which participants chose SC_2. Centerlines represent the median proportion. Data points represent individual participants' proportion choice. Asterisks above each bar represent pairwise group comparisons. *** $p < .001$. See the online article for the color version of this figure.

dictions for separable dimensions, participants should not judge SC_1 as more similar to the target stimulus.

For Type 2 conflict trials (see, e.g., Part B of Figure 2), SC_1 and SC_2 were both 2 city-block units from the target stimulus. Thus, if dimensions *X* and *Y* are separable dimensions, then participants should judge SC_1 and SC_2 as equally similar to the target, given they are equidistant to the target. However, in this case, it is also possible that SC_1 would be judged as more similar to the target because SC_1 and the target share attribute X_1. Importantly, in neither case would SC_2 be judged as more similar to the target if the dimensions are separable. By contrast, SC_1 is 2 Euclidean units away from the target, whereas SC_2 is 1.4 Euclidean units away. Thus, if dimensions *X* and *Y* are integral dimensions, then participants should judge SC_2 as more similar to the target.

Participants completed a total of 750 trials. For the shape/color and brightness/saturation conditions, which utilized a 4×4 stimulus space, trials were sampled randomly from all possible combinations of target and stimulus choices ($n = 3{,}360$). For the number/area condition, which utilized an 8×8 stimulus space, trials were sampled pseudorandomly from all possible combinations of target and stimulus choices ($n = 249{,}984$), in order to ensure an equivalent proportion of conflict and correlated trials as in the other two conditions.

The task was created and presented using PsychoPy software (Peirce et al., 2019). All trials were presented on a desktop computer with a 19-in. screen ($1{,}280 \times 1{,}024$ px). Participants sat at a distance of ~60 cm from the computer screen.

Results

To confirm that participants were sensitive to distance in each stimulus space, we assessed mean accuracy on correlated trials, in which both distance metrics predicted the same similarity judgments. The mean accuracy on correlated trials was significantly above chance (.50) in each condition ($ps < .001$, $ds > 1.87$; see Table 1). Moreover, the difference in distance between SC_1 and SC_2 to the target was significantly correlated with accuracy, shape/color: $r(33) = .679$; brightness/saturation: $r(33) = .723$; number/area: $r(90) = .674$. In other words, as the distance between SC_1 and SC_2 increased (i.e., as they became more dissimilar), participants more often chose the stimulus that was closer to the target. These effects confirm that participants' assessment of similarity corresponded to distance within the stimulus space.

Analysis of conflict trials revealed that for Type 1 conflict trials (see Part C of Figure 2), participants chose SC_1 significantly more often than chance in the shape/color condition, $t(19) = 6.48$, $p < .001$, $d = 1.45$, and chose SC_2 significantly more often than chance in the brightness/saturation condition, $t(19) = 2.93$, $p = .009$, $d = 0.66$. Critically, these results confirm the predictions for this trial type, given previous work that found shape/color and brightness/saturation to be separable and integral dimensions, respectively (Garner & Felfoldy, 1970; Gottwald & Garner, 1972). Although participants did not choose either SC_1 or SC_2 more often than chance in the number/area condition, $t(19) = 1.58$, $p = .131$, $d = 0.35$, this finding contradicts the prediction for separable dimensions. As noted previously, the lack of an SC_2 preference may reflect an inability to discriminate a difference of .17 for these dimensions.

To further characterize the relation between number and cumulative area, we compared results across conditions. A between-subjects analysis of variance (ANOVA) found that participants' choices differed significantly by condition, $F(2, 57) = 39.47$, $p < .001$, $\eta_p^2 = .581$, and crucially, post hoc group comparisons (Bonferroni corrected) revealed that the shape/color condition differed significantly from both the brightness/saturation, $t(38) = 7.02$, $p < .001$, $d = 1.89$, and number/area, $t(38) = 6.66$, $p < .001$, $d = 1.56$, conditions, whereas the brightness/saturation and number/area conditions did not differ significantly from each other, $t(38) = 1.99$, $p = .106$, $d = 0.63$. These findings are consistent with shape and color as separable dimensions and suggest that both brightness/saturation and number/area may be represented as integral dimensions.

For Type 2 conflict trials (see Part D of Figure 2), participants chose SC_1 significantly more often than chance in the shape/color condition, $t(19) = 6.21$, $p < .001$, $d = 1.39$, as predicted if shape and color are separable dimensions and participants preferred to match on the basis of a shared dimensional value (e.g., X_1). By contrast, participants chose SC_2 significantly more often than chance in the brightness/saturation condition, $t(19) = 14.36$, $p < .001$, $d = 3.21$, as predicted if brightness and saturation are integral dimensions. Participants also chose SC_2 significantly more often than chance in the number/area condition, $t(19) = 2.34$, $p = .031$, $d = 0.52$, as predicted if number and cumulative area are integral dimensions. A between-subjects ANOVA found that participants' choices differed significantly by condition, $F(2, 57) = 98.38$, $p < .001$, $\eta_p^2 = .775$. Post hoc group comparisons (Bonferroni corrected) revealed that the shape/color condition differed significantly from both the brightness/saturation, $t(38) = 13.87$, $p < .001$, $d = 3.27$, and number/area, $t(38) = 8.16$, $p < .001$, $d = 1.83$, conditions. The brightness/saturation and number/area conditions also differed significantly from each other, $t(38) = 8.08$, $p < .001$, $d = 2.46$.

Table 1
Descriptive Data for Experiments 1 and 2

Condition	Accuracy[a] *M* (*SD*)	RT (ms) *M* (*SD*)
Experiment 1		
Shape/color	.753 (.067)	1,230 (286)
Brightness/saturation	.697 (.050)	1,090 (307)
Number/area	.644 (.076)	1,260 (625)
Experiment 2		
Brightness/size	.914 (.040)	547 (91)
Brightness/saturation	.951 (.025)	475 (138)
Radial frequency components	.865 (.051)	927 (221)
Number/area	.973 (.016)	734 (254)

Note. RT = reaction time.
[a] Accuracy in each condition was significantly different from chance (.50), $ps < .001$.

Discussion

Taken together, the results of both conflict trial types confirm the status of shape and color as separable dimensions and of brightness and saturation as integral dimensions. Furthermore, similarity judgments for number/area stimuli were consistent with a Euclidean stimulus space, suggesting that number and cumulative area are represented as integral dimensions, although they may be less integral than brightness and saturation (cf. Smith & Kilroy, 1979; see General Discussion for further discussion).

But could participants have treated number and area independently, switching back and forth between the dimensions across the task? Note that participants were always presented with one stimulus choice that matched the target stimulus on one dimension (SC_1). If participants had a propensity to judge similarity on the basis of a single dimension, even if they switched dimensions across trials, they would have chosen SC_1 significantly more often than chance, contra our findings and bolstering the conclusion that number and area were represented holistically, as integral dimensions.

Nevertheless, the use of explicit similarity judgments in the categorization task leaves it uncertain whether the integralness of number and cumulative area resulted from higher-level cognitive processes rather than perceptual holistically dimensions (Cohen Kadosh, Lammertyn, & Izard, 2008; Van Opstal & Verguts, 2013). To address this concern, we used an implicit measure of perceptual similarity in Experiment 2. In particular, participants were given a sequential match-to-sample task in which they identified the target stimulus in the presence of a distractor stimulus. In this task, similarity was measured as the extent to which the distractor influenced participants' reaction times (RTs).

Moreover, another limitation of Experiment 1 was that the square stimulus space necessarily resulted in orthogonal axes (i.e., the axes oriented 45° to the primary axes) that exhibited greater variation than the primary axes (Drucker et al., 2009). That is, the distance between endpoints along the orthogonal axes was greater than the distance between endpoints along the primary axes. Most relevantly, previous research has shown that when participants are not instructed to attend to a specific dimension, they tend to categorize stimuli based on the most perceptually variable dimension (Jones & Goldstone, 2013). Thus, if greater distance in the square stimulus space corresponded to greater perceptual variability along the orthogonal axes, relative to the primary axes, then the use of a square grid could have unduly emphasized stimulus values along the orthogonal dimensions as opposed to the primary dimensions of interest (i.e., number and cumulative area). Although Experiment 1 nevertheless suggests that number and cumulative area may be integral dimensions, the ideal paradigm would equate perceptual variability across the primary and orthogonal axes by using a uniform space such as a dioctagon, as in the next experiment.

Experiment 2: Are Number and Cumulative Area Perceptually Integral Dimensions?

Using an implicit measure of perceptual similarity and a dioctagonal stimulus space, in Experiment 2 we further assessed whether perceived similarity for dot arrays that vary in number and cumulative area is best explained by city-block distance, suggesting they are separable dimensions, or Euclidean distance, suggesting they are integral dimensions. And to further generalize the results of Experiment 1, Experiment 2 examined a different set of separable (i.e., brightness and size; Garner, 1977) and integral (i.e., radial frequency components; Op de Beeck et al., 2003) dimensions than that of Experiment 1, in addition to brightness and saturation (used in both Experiments 1 and 2).

Method

Participants. Eighty undergraduates (n = 20/condition, M_{age} = 20.04 years; 29 male) participated in this experiment for course credit. All participants had normal or corrected-to-normal vision. Procedures were approved by the local IRB. All participants provided informed consent in accordance with the relevant guidelines and regulations of the IRB.

Procedure and design. In Experiment 2, we used dioctagonal, as opposed to square, stimulus spaces (Drucker et al., 2009; Shepard, 1964), comprising 16 unique stimuli, to ensure that distance (i.e., perceptual variability) was held constant across both primary and orthogonal axes (see Figure 3). This manipulation also ensured that stimulus changes along the primary axes were equally salient to changes along the orthogonal axes and, likewise, that changes along a single primary dimension were equally salient to changes along both primary dimensions.

For each of the four conditions, stimuli were drawn from a square stimulus space, comprising two primary dimensions: brightness/size, brightness/saturation, radial frequency components, or number/area. Stimuli for these conditions are described below:

Brightness/Size (see Figure 2 in the online supplemental materials). Stimuli were 14 solid circles created for the purpose of this experiment that varied in brightness and size, presented on a solid gray background (HSV [0, 0, 50]; 400 × 400 px). Brightness values ranged from HSV [0, 0, 42] to HSV [0, 0, 58]. Sizes

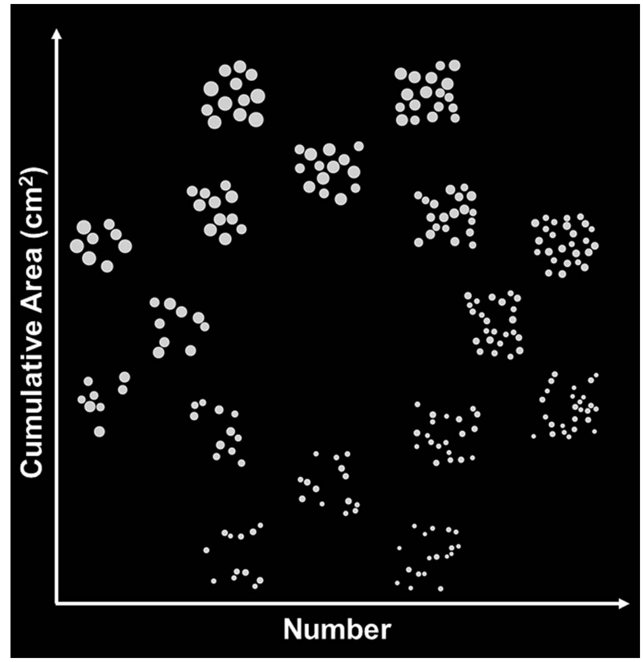

Figure 3. Number and cumulative-area stimulus space from Experiment 2. For each pair of number and cumulative-area values, five exemplars of each stimulus were created.

ranged from 100 to 175 px in diameter. Of the 16-point dioctagonal stimulus space used in the other conditions, stimuli corresponding to two of those points were removed from the present condition because the brightness values associated with those points were identical to the brightness of the background. Stimuli were perceptually matched such that brightness and size were equally discriminable (Melara & Mounts, 1993, 1994; see the online supplemental materials).

Brightness/Saturation. Stimuli were 16 square images of solid Munsell colors (400 × 400 px). Stimuli were a constant hue of 5R (red). Brightness and saturation values ranged from 2 to 8 in Munsell dimension values (see Table 2 in the online supplemental materials for stimulus values). The Munsell color system is perceptually normed such that equal distance in the stimulus system corresponds to equal discriminability (Munsell, 1919).

Radial frequency components. Stimuli were 16 solid black shapes determined by seven sinusoidal functions (radial frequency components [RFCs]), where each function comprised three parameters (frequency, phase, and amplitude). The stimuli used here shared five RFCs and varied in the amplitude of the remaining two RFCs, representing the two dimensions of the stimulus space (for additional stimulus details, see Op de Beeck et al., 2003). The dioctagonal stimulus space and corresponding stimuli were created by Drucker et al. (2009) and were obtained from GitHub (https://github.com/dmd/thesis/tree/master/ODB stims/images). RFCs were presented centrally on a solid white background (400 × 400 px) with the RFCs comprising ~15% of the stimulus. Stimuli were perceptually matched by Drucker et al. (2009).

Number/Area. Stimuli were 16 dot arrays comprising gray dots with a black background (400 × 400 px; see Figure 3 for stimulus values, as well as Table 4 in the online supplemental materials). For each of the 16 stimulus values, five exemplars of each stimulus were used, resulting in five unique stimulus sets/80 total unique stimuli. The stimulus set used was counterbalanced across participants (n = 4/set), ensuring that results were not unduly influenced by any particular dot array. Individual dot size varied up to 30% within each stimulus. Dot placement varied randomly within each stimulus. Stimuli were perceptually matched such that number and cumulative area were equally discriminable, and all equidistant stimulus pairs varied by a comparable ratio (see the online supplemental materials).

Participants completed a sequential match-to-sample task in which they were first shown a target stimulus, presented centrally for 1 s. Then, participants were shown two stimuli: the target stimulus and a distractor stimulus, presented at the center left and center right (side counterbalanced across trials). Participants were instructed to press the "q" key if the target was presented on the left and the "p" key if the target was presented on the right. Participants were given unlimited time to respond, but the instructions emphasized speed and accuracy. Participants completed 480 total trials, with each stimulus (n = 16) appearing with every other stimulus four times. For each possible stimulus pair (n = 120), each appeared twice as the target and twice as the distractor stimulus.

Perceived similarity was measured as the extent to which the distance between the target and distractor stimulus in the stimulus space affected participants' RTs. Specifically, we asked whether the city-block or Euclidean distance metric better predicted variation in RT as a function of the difference between target and distractor stimuli. Because all stimuli were perceptually matched within condition, such that all equal distances in the stimulus space were equally discriminable, distance predictors were calculated with respect to stimulus coordinates in a normed stimulus space that ranged from 0 to 100 on each axis (see Tables 2 and 4 in the online supplemental materials). For example, for brightness/saturation stimuli, axes ranged from 2 to 8 in Munsell dimension values; accordingly, similarity between stimuli with Munsell values [2, 2] and [8, 8] would be calculated with respect to their normed values, [0, 0] and [100, 100], resulting in a city-block distance of 200 and a Euclidean distance of 141.42.

All conditions were created and presented using PsychoPy software (Peirce et al., 2019). The task was presented on a desktop computer with a 19-in. screen (1,280 × 1,024 px). Participants sat at a distance of ~60 cm from the computer screen.

Results

The mean accuracy on the match-to-sample task was significantly above the chance level of .50 (ps < .001, ds > 7.16), confirming that participants successfully matched the target stimulus (see Table 1). Subsequent analyses were conducted on participants' mean RTs for each stimulus pair (correct trials only). Trials with RTs greater than 2.5 standard deviations (SD) from the participant's mean RT were excluded from the analyses (brightness/size = 2.50%, brightness/saturation = 2.83%, radial frequency components = 2.90%, number/area = 2.37%). For each condition, we used linear regression models[3] with the similarity metrics as predictors of RTs. Preliminary analyses confirmed that the model residuals were normally distributed, with skewness and kurtosis values within an acceptable range (Curran, West, & Finch, 1996; Tabachnick & Fidell, 2001). We then computed the Akaike information criterion (AIC) to compare the relative fits of the models (Akaike, 1974). A smaller AIC value indicates better relative model fit, with a difference greater than 10 denoting very strong support for the model with the smaller AIC value (Burnham & Anderson, 2004).

As noted previously, we included a different set of potentially separable and integral dimensions (brightness/size and radial frequency components) as a test of generalization, in addition to two sets of dimensions previously tested in Experiment 1 (brightness/saturation and number/area), to test for replication within a dioctagonal stimulus space. As predicted, city-block distance was a better predictor of RTs for the brightness/size condition, consistent with separable dimensions (see Table 2). Moreover, Euclidean distance was a better predictor of RTs for the brightness/saturation and radial frequency components conditions, consistent with integral dimensions (see Table 2).

We also found that Euclidean distance, compared with city-block distance, was a better predictor of RTs for dot arrays that varied in number and cumulative area, with the Euclidean model yielding a smaller AIC value and larger R^2, suggesting that number and cumulative area are integral dimensions. Given that the current task required the perceptual matching of stimuli, these findings provide more definitive evidence for the holistic representation of number and cumulative area that cannot be attributed to nonperceptual mechanisms such as linguistic or decision processes (Cohen Kadosh et al., 2007; Starr & Srinivasan, 2018).

However, a concern with these analyses might be that the better-fitting Euclidean distance metric for number and cumulative area could reflect misalignment of the primary axes in the stimulus space (Kemler Nelson, 1993). To address this concern, we calculated the city-block distances between stimuli given rotated axes (22.5° and 45°), following previous recommendations (Drucker et al., 2009; Foard & Kemler, 1984). We then compared the predictive power of these new distances to that of Euclidean distance (which remains constant under rotations). If the perceived similarity reflects true integrality of the primary dimensions, then Euclidean distance should remain a better predictor of RTs than city-block distance. However, if perceived similarity reflects separable dimensions that are misaligned to the assumed dimensional axes, then the city-block distances attained from the rotated coordinates should better predict RTs than Euclidean distance. To this end, we fit linear regression models to compare the relative fit of these rotated city-block models to the Euclidean model. We found that the rotated city-block models yielded larger AIC values and smaller R^2 values than that of the Euclidean model (see Table 2). Thus, Euclidean distance was a better predictor of RTs than the city-block distance, even when city-block distance was calculated relative to three unique pairs of axes (0°, 22.5°, and 45°), providing further support for the perceptual integrality of number and cumulative area.

[3] Due to high multicollinearity between the similarity metrics, we fit a linear regression model for each similarity metric and then compared the relative fit of each model (for a similar approach, see Blunden, Wang, Griffiths, & Little, [2015]).

Table 2
Linear Regression Model Fits and Comparisons for Each Condition in Experiment 2

Condition	Similarity metric	AIC	R^2
Brightness/size	City block	−300.38	.547
	Euclidean	−294.14	.515
Brightness/saturation	City block	−465.32	.612
	Euclidean	−470.34	.628
	City block (22.5°)	−462.71	.607
	City block (45°)	−448.27	.543
Radial frequency components	City block	−299.67	.587
	Euclidean	−331.41	.683
	City block (22.5°)	−313.52	.632
	City block (45°)	−319.82	.650
Number/area[a]	City block	−421.18	.573
	Euclidean	−435.38	.621
	City block (22.5°)	−418.65	.564
	City block (45°)	−423.32	.581
	Density/Average element size[b]	−407.08	.524
	Contour length	−324.77	.046
	Gabor-jet model	−319.87	.007

Note. AIC = Akaike information criterion.
[a] To rule out the possibility that changes in either number or cumulative area alone accounted for the perceived similarity of the dot arrays, we additionally examined models of each predictor individually. Of note, when considering only a single dimension, city-block and Euclidean distance are necessarily equivalent. Neither number nor cumulative area alone outperformed Euclidean distance in the number/area stimulus space as a predictor of reaction times (RTs; number: AIC = −332.57, R^2 = .106; cumulative area: AIC = −367.72, R^2 = .333). [b] We additionally examined models of density and average element size individually. Neither density nor average element size alone outperformed Euclidean distance as a predictor of RTs for number/area stimuli (density: AIC = −398.11, R^2 = .482; element size: AIC = −392.81, R^2 = .491).

Dot arrays, however, can vary in other magnitude dimensions, such as density and element size. Although these dimensions were not systematically manipulated in the present stimuli, we addressed this concern by first calculating the differences in density (calculated as the proportion of cumulative area to convex hull, M = 27.3%, range = 11.4–45.1%) and average element size; M = 1.48 cm^2; range = 0.410–3.19 cm^2 for each stimulus pair. We then fit a linear regression model with these values as predictors of RTs. We found that this model yielded a larger AIC and smaller R^2 than that of the Euclidean model (see Table 2), suggesting that perceived similarity was not based on density or element size.

Another dimension that has been shown to influence number discrimination is brightness (Cohen Kadosh, Cohen Kadosh, & Henik, 2008; de Hevia & Spelke, 2013). In the present stimuli, we held dot brightness constant, so as a result, cumulative area necessarily corresponded to the overall brightness of the stimulus (Purves, Williams, Nundy, & Lotto, 2004). Critically, cumulative area alone could not explain our results (see Table 2), and thus, neither can overall brightness. Nevertheless, it is still possible to consider the potential effect of brightness if it is indexed as the contrast between adjacent black and gray pixels. To this end, we calculated the proportion of adjacent black and gray pixels (background and dots, respectively) relative to the total number of pixels. We then calculated the difference in contrast for each stimulus pair and fit a linear regression model with these values as predictors of RTs. We found that, like density and average element size, this model yielded a larger AIC and smaller R^2 than that of the Euclidean model (see Table 2), further suggesting that perceived similarity cannot be attributed to brightness.

Yet another possibility is that perceived similarity was the result of overall image similarity, as determined by metric variation computed in early vision, namely, V1 simple and complex cell filtering. To address whether overall image similarity determined how participants completed the task, we calculated the difference in image similarity between each pair of number/area stimuli with the Gabor-jet model (GJM), which overlays a 10 × 10 grid of Gabor "jets," each comprising a set of Gabor filters at five scales and eight orientations, to construct a feature vector of the image (Margalit, Biederman, Herald, Yue, & von der Malsburg, 2016). When applied to the present stimuli, the GJM yielded an AIC value larger than that of the Euclidean model (see Table 2), suggesting that image similarity alone cannot account for the results obtained here.

General Discussion

The perceived similarity of visual arrays varying in number and cumulative area was best explained by Euclidean distance, suggesting that visual perception of numerosity is not independent from that of cumulative area (and vice versa). This finding challenges the dominant view of nonsymbolic number representation in which the claim is that of an abstract numerosity code, uncontaminated by other magnitudes, such as cumulative surface area. Indeed, well-known computational models of numerosity coding (Dehaene & Changeux, 1993; Stoianov & Zorzi, 2012) implement normalization over nonnumerical cues, such that the resulting number representation is wholly unrelated to these cues. Our results suggest that if the purpose of such models is to best approximate human perception, then they may benefit from maintaining cumulative-area processing in the resulting number representation.

Our findings also suggest that the well-documented behavioral interactions between numerical and nonnumerical magnitudes, in which participants are better at judging numerosity (or cumulative area) when cumulative area (or numerosity) is congruent and worse when it is incongruent (e.g., Hurewitz et al., 2006), may arise from an integral representation of numerosity and cumulative area. That is, congruity effects may reflect a perceptual interaction between numerical and nonnumerical dimensions, wherein the irrelevant dimension influences perception of the relevant dimension, making it difficult to attend to, and judge only, the relevant dimension. Importantly, such effects may also reflect discriminability of the dimensions (with more discriminable dimensions exerting greater influence over less discriminable dimensions), and there may also be entirely different magnitude interactions that arise via nonperceptual mechanisms (e.g., response stage; Picon, Dramkin, & Odic, 2019), such as when judgments of Arabic numerals are affected by the physical sizes of those numerals (e.g., Henik & Tzelgov, 1982). Future work will be needed to directly examine what mechanisms (perceptual vs. nonperceptual) underlie specific effects, such as congruency effects, on tasks of explicit magnitude comparison, given that the present work provides evidence for perceptual mechanisms underlying some magnitude interactions.

Classic work on area perception suggests that perceived area may not be sufficiently explained by the mathematical area of a stimulus (Stevens & Guirao, 1963; Teghtsoonian, 1965). More recently, Yousif and Keil (2019) suggested that judgments of cumulative area were better explained by "additive area" (i.e., the sum of the objects' dimensions) than mathematical area. Crucially, for the present work, cumulative-area (and number) values were perceptually matched, such that distances within the stimulus space were equally discriminable (see the online supplemental materials) and not determined a priori based on a particular mathematical computation of area. City-block and Euclidean distances were then calculated with respect to arbitrary normed units, as opposed to mathematical area values. Although the present work was not designed to determine which mathematical formula best characterizes perceived cumulative area, our finding that number and area are integral dimensions cannot be explained by a failure to properly measure perceived area.

In the present study, we found that density, average element size, and brightness could not account for participants' similarity judgments. However, these dimensions were not directly manipulated in our stimulus set. Future work will be needed to determine whether number and these other dimensions are also represented integrally. A systematic examination of the relations between number and different nonnumerical magnitudes, under conditions of equal perceptual discriminability, will be critical to determining their dimensional status. Much previous work has assessed interactions between numerical and nonnumerical dimensions, with the conclusion that despite the congruity effects, number is primary (Anobile, Cicchini, & Burr, 2016; Ferrigno et al., 2017; Piazza, De Feo, Panzeri, & Dehaene, 2018). However, it remains unclear whether the relative primacy of numerical, as opposed to nonnumerical, information reflects the nature of the number representation or a difference in perceptual discriminability (Castaldi, Piazza, Dehaene, Vignaud, & Eger, 2019; Melara & Mounts, 1993, 1994). Here, numerosity and cumulative area were matched for discriminability, and neither number nor cumulative area was represented at the exclusion of the other.

Studies using single-unit recordings in macaques (Tudusciuc & Nieder, 2009) and functional magnetic resonance imaging (fMRI) in human adults (Harvey, Fracasso, Petridou, & Dumoulin, 2015) have found overlapping representations of number and nonnumerical magnitudes. The results from both experiments in the present study corroborate these findings but raise questions about the nature of the overlap or what we have referred to as "integral" dimensions. Harvey et al. (2015) argued that the overlap arises from underlying independent representations of number and area because their results found differences in the tuning properties of the representations. However, it is unclear to what extent the tuning properties reflected the perceptual discriminability for the different displays (Castaldi et al., 2019).

We suggest an alternative possibility, which is that the relation between numerosity and cumulative surface area may reflect a process akin to dimensionality reduction in statistical methods. In this interpretation, correlated dimensions of magnitude are integrated in order to act as a low-dimensional summary of the multidimensional stimulus space (Austerweil & Griffiths, 2010). Such a representation would be commensurate with neuronal notions of "conjunctive" (or "conjoint") coding common to both human and nonhuman animals in several cortical regions (Engel, 2005; Finkelstein et al., 2018; Harper et al., 2016; Komorowski et al., 2009; Mazer, Vinje, McDermott, Schiller, & Gallant, 2002; Zohary, 1992). Integral dimensions of numerosity and cumulative area could result from a single population of neurons that code for the dimensions conjointly (i.e., exhibiting preferred stimulus values for both dimensions) in contrast to separable representations that would result from two populations of neurons coding for the dimensions independently (i.e., exhibiting preferred stimulus values for each dimension).

Nevertheless, one might ask whether the integralness of dimensions reflects task demands or a default representation that generalizes across context. Previous research suggests that task demands can serve to integrate dimensions that are not integral in the absence of those demands (Smith et al., 2012), and it has been shown that separable dimensions can appear integral in certain attentional or decisional contexts (Nosofsky, 1986). Is the integralness of number and area demonstrated here similarly the result of task demands or top-down effects? Critically, in neither Experiment 1 nor Experiment 2 were participants told the relevant stimulus dimensions, even when participants made explicit similarity judgments (Experiment 1). Moreover, the differences in task demands of Experiments 1 and 2 demonstrate effects that generalize relatively broadly, and although we do not dispute that attentional and decisional processes are involved in these tasks, it is unlikely that these processes remained consistent across experiments, which varied in task (explicit similarity judgment vs. implicit similarity judgment), presentation time (unlimited vs. 1 s), and dependent variable (accuracy vs. RT).

Following classic research, we emphasize that despite our claim that number and area are integral dimensions, integrality and separability do not constitute a strict dichotomy but, rather, may reflect an integral-to-separable continuum (Garner, 1974; Grau & Kemler Nelson, 1988; Melara & Marks, 1990; Shepard, 1964). Given the results of Experiment 1, in which number and cumulative area exhibited characteristics of integral dimensions but, nonetheless, appeared less integral than brightness and saturation, it is possible that number and cumulative area are not entirely lacking in perceivable dimensional structure (Lockhead, 1972; Smith & Kemler, 1978). Moreover, the Euclidean and city-block distance models in the present study assume a symmetric relation between dimensions, but it may be possible to formally test for a potential asymmetry whereby one dimension (i.e., number or cumulative area) contributes more heavily to the representation (Nosofsky, 1986; Soto et al., 2015; Tversky, 1977).

Notably, even for integral dimensions such as brightness and saturation, which have typically been regarded as one of the strongest examples of integral dimensions, participants can be trained to increase attention toward a particular dimension (Burns & Shepp, 1988; Goldstone, 1994). Indeed, if number and cumulative area retained some dimensional structure, then executive processes could allow for selective attention to numerosity, which could explain findings in which numerical estimation is possible in the presence of varying nonnumerical properties. We would contend that the ability to extract accurate numerical information likely arises via selective attention, without altering the underlying multidimensional representation. Indeed, a recent study using 7 Tesla fMRI revealed greater decoding accuracy along the dorsal stream when the task involved attending to numerosity (Castaldi et al., 2019), suggesting an important role for selective attention in focusing on the numerical, as opposed to nonnumerical, properties of a multidimensional stimulus set. The existence of congruency effects on, for example, magnitude-comparison tasks might reflect a failure of selective attention in this process. And if so, the prediction is that greater attention to the dimension of interest would reduce congruency effects. These findings are consistent with work outside of numerical cognition highlighting a key role of the frontoparietal network, specifically the prefrontal cortex, in selecting and amplifying task-relevant information (Mante, Sussillo, Shenoy, & Newsome, 2013; Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014).

Relatedly, recent work examining numerosity perception found that the ability to filter out nonnumerical information during numerical judgments improved with maturation and education (Piazza et al., 2018). In the present study, we found that on tasks in which participants did not attend to, or judge, numerical magnitude (or any other dimension), even college-educated adults exhibited integral representations of number and cumulative surface area. From this, a question naturally arises as to whether increased filtering observed over the course of development reflects a permanent representational change, or instead, an online ability to attend specifically to number in accordance with the demands of the task or internal goals. Critically, recent work suggests that it is possible for prefrontal networks to flexibly allocate attention toward a particular stimulus property in a goal-directed manner while retaining a stable stimulus representation (Birman & Gardner, 2019; Bugatus, Weiner, & Grill-Spector, 2017). Given our results, we suggest that filtering likely reflects an increased ability to selectively attend to numerosity, shifting one's decision boundary within a stimulus space without permanently modifying the integral representation of numerosity.

Context

The question of how multidimensional stimuli are perceived and represented has intrigued psychologists, philosophers, and neuroscientists alike. Classic work in psychophysics posits two kinds of dimension pairs: separable dimensions, which are perceived in terms of their component dimensions, and integral dimensions, which are perceived holistically. In the present study, we employed methods from the multidimensional scaling literature to provide insight into the nature of nonsymbolic number representations. Although it is well established that humans and other animals have the capacity for rapid, nonverbal estimation of numerosity, the mechanisms underlying number perception remain equivocal. The dominant view is that of numerosity representations as independent (i.e., separable) from other magnitudes, yet a direct test of separability has not been attempted. Here, we provide novel evidence that numerosity and cumulative surface area are represented not as separable but as integral dimensions, suggesting that the interactions between numerical and nonnumerical magnitudes observed across various tasks may be rooted in the holistic perception of magnitude.

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