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Numerical discrimination is mediated by neural coding variation

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ABSTRACT

One foundation of numerical cognition is that discrimination accuracy depends on the proportional difference between compared values, closely following the Weber–Fechner discrimination law. Performance in non-symbolic numerical discrimination is used to calculate individual Weber fraction, a measure of relative acuity of the approximate number system (ANS). Individual Weber fraction is linked to symbolic arithmetic skills and long-term educational and economic outcomes. The present findings suggest that numerical discrimination performance depends on both the proportional difference and absolute value, deviating from the Weber–Fechner law. The effect of absolute value is predicted via computational model based on the neural correlates of numerical perception. Specifically, that the neural coding "noise" varies across corresponding numerosities. A computational model using firing rate variation based on neural data demonstrates a significant interaction between ratio difference and absolute value in predicting numerical discriminability. We find that both behavioral and computational data show an interaction between ratio difference and absolute value on numerical discrimination accuracy. These results further suggest a reexamination of the mechanisms involved in non-symbolic numerical discrimination, how researchers may measure individual performance, and what outcomes performance may predict.

1. Introduction

The most consistently observed effect in numerical cognition research is that the difficulty of numerical discrimination depends on the ratio difference between two values (e.g., Banks, Fujii, & Kayra-Stuart, 1976; Buckley & Gilman, 1974; Dehaene & Askhaven, 1995; Gibbon, 1977; Henik & Tzelgov, 1982; Hinrichs & Yurko, 1981; Moyer & Landauer, 1967; Parkman, 1971; Sekuler & Mierkiewicz, 1977). For example, discrimination of a 2:3 ratio is completed with the same speed and accuracy for sets of 20 and 30 objects or 40 and 60 objects. Performance in numerical discrimination tasks is used to assess the precision of individuals' approximate number system (ANS) via the calculated Weber Fraction. The Weber Fraction is calculated based on the ratios an individual successfully discriminates (e.g., Halberda & Feigenson, 2008; Halberda, Ly, Wilmer, Naiman, & Germine, 2012). Weber fractions has been shown to correlate with a variety of educational and economic outcomes (e.g., Halberda, Mazzocco, & Feigenson, 2008; Libertus, Feigenson, & Halberda, 2011; Libertus, Odic, & Halberda, 2012; Parsons & Bynner, 1997; for an alternate view see Gilmore et al., 2013; Inglis, Attridge, Batchelor, & Gilmore, 2011). Thus, it is important to examine the factors that drive performance in numerical discrimination. Recent work has detailed the possible additional factors that may contribute to performance, including inhibitory control (e.g., Cappelletti, Didino, Stoianov, & Zorzi, 2014; Gilmore

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et al., 2013) and perceptual factors such as area (e.g., Gebuis & Reynvoet, 2012a, 2012b) and density (Anobile, Cicchini, & Burr, 2014).

The present study investigates numerical discrimination behavior based on properties of the neural activity associated with perceiving numerosity, demonstrated via computational modeling. The specific prediction tested that neural coding of numerosity suggests discriminability is not independent of absolute value. While the ratio of the numerical difference is a major factor in performance we predict that for very close comparisons (e.g., <10:11) absolute value also affects discriminability. We use computational models to demonstrate that patterns of variation (e.g., noise) in the neural coding predict that the absolute value of the compared numerosities is a factor in the relative discriminability in addition to the proportional difference of the values.

1.1. Neural correlates of numerical perception

Research of the neural correlates of perceived numerosity includes data from both humans (e.g., Ansari & Dhital, 2006; Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Cantlon, Brannon, Carter, & Pelphrey, 2006; Dehaene, Piazza, Pinel, & Cohen, 2003) and nonhuman primates (e.g., Nieder, Freedman, & Miller, 2002; Nieder & Merten, 2007; Nieder & Miller, 2003; Sawamura, Shima, & Tanji, 2002). Numerical cognition has been explored in a variety of tasks, including numerical discrimination, arithmetic operations and even the perception of a digits (e.g., Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Holloway, Price, & Ansari, 2010). These studies suggest brain regions, including the intraparietal sulcus (IPS) and areas of prefrontal cortex are engaged in numerical processing. Number coding is these areas is graded; firing rate increases as the presented number magnitude increases or decreases (Roitman, Brannon, & Platt, 2007). There is also evidence of number specific activity in that the spiking rate of a given set of neurons is correlated maximally to a particular value N, and less so for $N + 1$, $N - 1$ and so on (Nieder et al., 2002; Nieder & Merten, 2007; Nieder & Miller, 2003; Sawamura et al., 2002). These properties of neural coding appear to hold across presentation formats (e.g., dot displays, written digits). Neural populations that employ number selective coding may be represented as a Gaussian-like tuning function that scales proportionally (Dehaene, 2007; Prather, 2012; see Fig. 1). By this representation of firing rate patterns, number magnitude is not coded exactly, but in a manner that is consistent with Weber–Fechner's law (Fechner, 1966 [1860]), that is, the mean activations as a function of increasing numerosity yield just noticeable differences that are a function of the proportional difference. This pattern has been seen with direct recording neural data, imaging data as well as behavioral data; the total pattern of results strongly implies a "representation" number in which proportional differences are important. The observed pattern of population codes also suggests that the tuning functions vary as a function of numerosity. Smaller numerical values are associated with more narrow tuning curves whereas larger numbers are associated with increasingly broader tuning curves. Thus the set of tuning curves associated with numerical perception resembles a set of Poisson distribution curves (see Fig. 1).

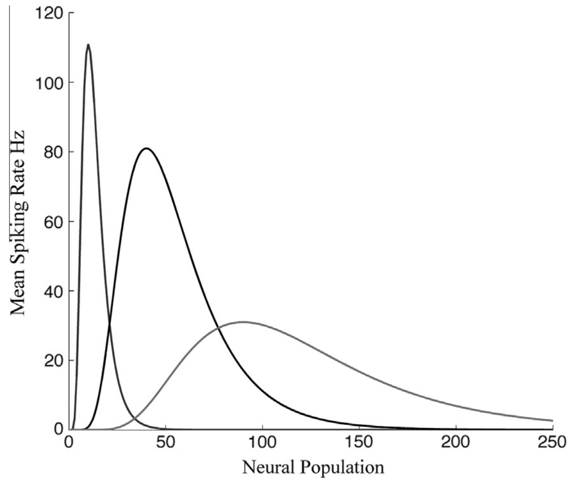

Fig. 1. Example tuning curves for numerical values. Each tuning curve includes the firing rate across many neural populations associated with a specific number. The index of the peak spiking rate corresponds to what number value the tuning curve is associated with. Small numbers are associated with high peak firing rates, while larger numbers with lower firing rates.

1.2. Current study

The current study employs a computational model based on properties of the neural coding to derive novel predictions about human number discrimination. Three details from the non-human primate data on neural coding of number are important with respect to the theoretical approach taken. First, the maximum firing rate correlates with the associated numerical value. Thus the tuning curves are represented as similar to Poisson distribution, where in addition to curve width that scales proportionally, the peak firing rate value declines (see Fig. 1). Second, though the mean firing rate is often reported it is important to consider the variability for these neural populations. The variability in the firing rates is not constant, recordings from monkey lateral intraparietal area (LIP) show that the coefficient of variation (standard deviation/mean) of neural activity changes with mean firing rate (Pearson, Roitman, Brannon, Platt, & Raghavachari, 2010; Roitman et al., 2007). Third, behavioral errors in numerical discrimination task are associated with neural coding "errors" (Nieder, Diester, & Tudusciuc, 2006; Nieder & Merten, 2007; Nieder & Miller, 2004; Nieder et al., 2002). For example, the neural population that responded maximally to the numerosity five showed reduced activation on trials in which five objects were presented and the subject made an error compared when the subject correctly responded. Using the characteristics of the neural coding to predict the types and relative frequency of errors has been used to provide mechanistic explanations of several behavioral phenomena observed in the numerical tasks (Prather, 2012). Two behavioral experiments and an accompanying computational model examine the effects of absolute value on number discrimination including a range of numerical ratio differences. Specifically the hypothesis that changes in noise predicts an effect of absolute value for discrimination of numerosity with very small differences. Thus only for a stimuli set with a range of comparisons including <10:11 ratios there will be a significant interaction between absolute value and numerical ratio difference, in addition to the main effect of numerical ratio difference.

2. Experiment 1

2.1. Method

2.1.1. Participants

Participants ($n = 46$) were adults (19–66 years, median 34). Recruitment and experimental sessions were via Amazon Mechanical Turk (see, Crump, McDonnell, & Gureckis, 2013). Participants received a small monetary compensation. Informed consent procedures were approved by the institutional IRB and were obtained from all participants.

2.1.2. Design

Participants completed a numerical discrimination task. Each trial included two sets of squares presented on screen simultaneously separated by a vertical line at midline (see Fig. 2). Participants were instructed to indicate which side had a greater number of objects via key press (LEFT or RIGHT). Comparisons included differences from as small as a 1.02 (50:51) ratio to as large as a 1.30 (40:52) ratio. Each ratio difference was presented at three different absolute values (e.g., 32:33, 64:66, 96:99). Participants each competed 90 comparisons total. There were 30 numerical ratio differences (see Appendix A). The total number of objects presented range from 61 to 231.

The stimuli were created such that for each comparison total area of squares on left and right sides equal and constant. The size of the largest and smallest squares was also equal for each comparison. Thus participants could not use simple heuristic of selecting the side with the largest shape. Item location was random within a window of the same size for all trials. Thus for any given comparison the side with the higher number of items also had a higher density.

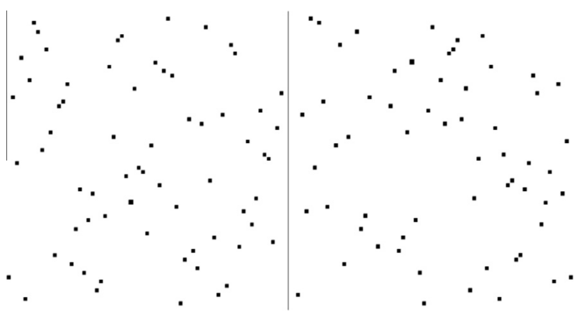

Fig. 2. Example stimulus. Participants were instructed to indicate if the left or right side of the mid-line had a higher number of objects. The sum area of items on both sides was equal. The size of the largest and smallest item on both sides was equal. Item location for each trial was random.

2.2. Results

Overall participant performance was $M = 68\%$ (see Fig. 3). We evaluated the factors predicting participants' performance in a group analysis. Logistic regression analyses were used to evaluate the likelihood of a correct response on each individual trial (4041 total). Each regression model included participant identity as a random factor in addition to the stated main factors. Ratio difference was log transformed and converted to standardized values, while absolute values were also converted to standardized values.

Regression analysis 1, a logistic regression with trial ratio difference as only factor, showed a significant effect ($B = 0.43$, $z = 12.17$, $p < 0.001$). As expected higher ratio differences were associated with a higher likelihood of trial correctness. Regression analysis 2, a logistic regression including ratio difference and absolute value, resulted in a significant effect of ratio difference ($B = 0.43$, $z = 12.16$, $p < 0.001$) but not absolute value ($B = 0.02$, $z = 0.68$, $p = 0.49$). Consistent with prior work, absolute value does not significantly contribute while increasing ratio difference is associated with increased likelihood of trial correctness. A comparison of regression analyses 1 and 2 showed no significant difference in the variance accounted for by the regression models ($\mathbf{X}^2 = 0.465$, $p = 0.497$).

Regression analysis 3 included ratio difference, absolute value and the interaction between ratio difference and absolute value. Regression results indicate that both ratio difference ($B = 0.43$, $z = 12.16$, $p < 0.001$) and the interaction of ratio difference and absolute value ($B = -0.09$, $z = 2.50$, $p = 0.012$) were significant predictors of trial correctness. Absolute value was not a significant predictor ($B = 0.0090$, $z = 0.282$, $p = 0.77$). Analysis 3 accounted for more variance than both analysis 1 ($\mathbf{X}^2 = 6.71$, $p = 0.034$), and analysis 2 ($\mathbf{X}^2 = 6.24$, $p = 0.012$).

2.3. Experiment 1 discussion

That numerosity ratio difference is a significant predictor of trial accuracy is consistent with prior research; larger ratio differences tend to be easier to discriminate. We also find that trial discriminability is predicted by the interaction of ratio difference and absolute value. Regression analysis that includes the interaction of ratio difference and absolute value accounts for participants' data significantly better than other regression models. The results suggest that for numerical discrimination tasks ratio difference is not the sole predictor of performance. The significant interaction suggests that the effect of ratio difference on discriminability may vary with absolute value.

The experiment 1 results may be due in part to the range of numerical comparisons used as stimuli. The range of absolute values and specifically the use of multiple absolute values per ratio difference is not typical in prior evaluations of numerical discrimination (see Table 1 for recent sample). The range of ratio differences evaluated in this experiment includes smaller ratios than often evaluated. It is possible that prior work simply did not contain the measurements necessary to detect the effects reported

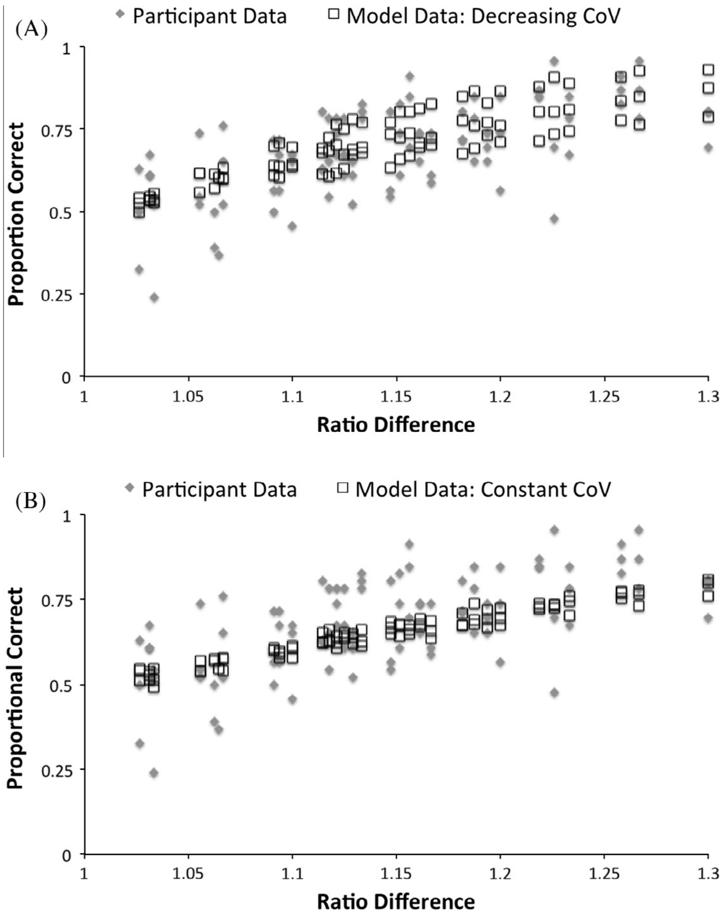

Fig. 3. Proportion correct for numerical discrimination trials. Horizontal axis indicates the ratio difference between the smaller and larger value. (A) Human results paired with results from a model instantiation with decreasing coefficient of variation in neural firing rate. (B) Human results with result from model instantiation with a constant coefficient of variation in neural firing rate. The effect of absolute value on performance is observed by the variation in proportion correct for trials of the same ratio-difference. This is shown by the characteristic horizontal spread of data points see for human data and decreasing coefficient of variation model that is not present in the constant coefficient of variation model.

Table 1
Difference ratios and absolute values used in a sample of recent work involving non-symbolic number discrimination. The current study is included for comparison. The current study also includes multiple versions of each ratio difference comparison at difference absolute values.

Study	Minimum ratio	Maximum ratio	Minimum value	Maximum value
Prather (in review)	1.03	1.18	30	117
Current experiment 1 and 2	1.02	1.3	30	117
Halberda and Feigenson (2008)	1.11	2	NR	NR
Libertus et al. (2012)	1.05	2.0	12	24
Libertus et al. (2011)	1.16	2.0	4	15
Mazzocco, Feigenson and Halberda (2011)	1.11	2.0	1	14
Fuhs and McNeil (2013)	1.11	2.0	1	30
Piazza et al. (2010)	1.06	1.25	12	40
Price, Palmer, Battista and Ansari (2012)	1.11	4.0	6	40
Inglis et al. (2011)	1.25	2	5	22
Odic, Libertus, Feigenson and Halberda (2012)	1.14	3.0	10	20
Halberda et al. (2008)	1.14	2.0	5	16
Bonny and Lourenco (2012)	1.13	2.0	4	12

NR = not reported.

here. To further examine if a measurable effect of absolute value depends on the ratio difference, Experiment 2 replicated Experiment 1, using a stimulus set with the same range of ratio differences (1.02–1.30) but with a larger representation of trials with less than a 1.10 difference. Prior reported behavioral data for numerical discrimination does not typically include either very small ratio differences or large variation in absolute value (Table 1).

3. Experiment 2

3.1. Method

3.1.1. Participants

Participants ($n = 33$) were adults (21–66 years, median 32). Recruitment and experimental sessions were via Amazon Mechanical Turk (Crump et al., 2013). Participants received a small monetary compensation.

3.1.2. Design

Individual stimulus construction was identical to Experiment 1. Comparisons included ratio differences from as small as 1.02 (50:51) to 1.30 (40:52) and a range of absolute values from 61 to 231 total items. Participants completed 132 trials, 66 of which were a ratio difference less than 1.10 (see Appendix A).

3.2. Results

3.2.1. Overall analysis

Overall participant performance was $M = 69\%$. We evaluated the factors predicting participants' performance in a group analysis. Logistic regression analyses were used to evaluate the likelihood of a correct response on each individual trial (4356 total). Each regression analysis included participant identity as a random factor in addition to the stated main factors. Ratio difference was log transformed and converted to standardized values, while absolute values were also converted to standardized values.

Regression analysis 1, a logistic regression with trial ratio difference as only factor showed a significant effect ($B = 0.45$, $z = 12.41$, $p < 0.001$). As expected higher ratio differences were associated with a higher likelihood of trial correctness. Regression analysis 2, a logistic regression with trial ratio difference and absolute value showed a significant effect of ratio difference ($B = 0.46$, $z = 12.44$, $p < 0.001$) and absolute value ($B = 0.10$, $z = 3.19$, $p = 0.001$). Comparison of the two regression models shows that analysis 2 accounted for more variance than the analysis 1 difference ($\mathbf{X}^2 = 10.14$, $p = 0.001$).

Regression analysis 3 included ratio difference, absolute value and the interaction between ratio difference and absolute value. The likelihood of trial correctness was predicted by ratio difference ($B = 0.46$, $z = 12.40$, $p < 0.001$), absolute value ($B = 0.095$, $z = 2.73$, $p = 0.006$) and the interaction there of ($B = -0.075$, $z = 2.03$, $p = 0.042$). Model comparison shows that analysis 3 accounts for more variation than both analysis 2 ($\mathbf{X}^2 = 4.11$, $p = 0.042$) and analysis 1 ($\mathbf{X}^2 = 14.26$, $p < 0.001$).

3.2.2. Analysis of smaller ratio differences

We also examined in a separate analyses, predictive factors for ratio differences either greater than 1.10 or less than 1.10. Ratio differences 1.10 and larger is a range more consistent with previous number discrimination experiments (see Table 1). For trials with ratio differences of smaller than 1.10 we used a series of logistic regression models that included subject identity as a random factor. Regression analysis 1, a logistic regression with trial ratio difference as only factor showed a significant effect ($B = 0.19$, $z = 4.20$, $p < 0.001$). As expected higher ratio differences were associated with a higher likelihood of trial correctness. Regression analysis 2, a logistic regression with trial ratio difference and absolute value showed a significant effect of ratio difference ($B = 0.19$, $z = 4.23$, $p < 0.001$) and absolute value ($B = 0.14$, $z = 3.16$, $p = 0.001$). Comparison of the two regression models shows that analysis 2 accounted for significantly more variance than the analysis 1 difference ($\mathbf{X}^2 = 10.03$, $p = 0.001$).

Regression analysis 3 was a logistic regression with ratio difference, absolute value and their interaction as predictors. The likelihood of trial correctness was predicted by ratio difference ($B = 0.19$, $z = 4.18$, $p < 0.001$), absolute value ($B = 0.14$, $z = 3.07$, $p = 0.002$) but not the interaction thereof ($B = -0.08$, $z = 1.79$, $p = 0.074$). Model comparison shows that analysis 3 accounts for significantly more variation than analysis 1 ($\mathbf{X}^2 = 13.20$, $p < 0.001$) but not analysis 2 ($\mathbf{X}^2 = 3.17$, $p = 0.074$). Thus for ratio differences of less than 1.10 the best model of the data includes a significant positive association between absolute value and trial correctness likelihood.

3.2.3. Analysis of larger ratio differences

For trials with ratio differences of 1.10 or larger we used a series of logistic regression models that included subject identity as a random factor. Regression analysis 1, a logistic regression with trial ratio difference as only factor showed a significant effect ($B = 0.31$, $z = 5.73$, $p < 0.001$). As expected higher ratio differences were associated with a higher likelihood of trial correctness. Regression analysis 2, a logistic regression with trial ratio difference and absolute value showed a significant effect of ratio difference ($B = 0.31$, $z = 5.73$, $p < 0.001$) but not absolute value ($B = 0.06$, $z = 1.19$, $p = 0.23$). Comparison of the two regression models shows no significant difference ($\mathbf{X}^2 = 1.42$, $p = 0.23$).

For regression analysis 3 only ratio difference was a significant predictor ($B = 0.31$, $z = 5.70$, $p < 0.001$), while absolute value ($B = 0.05$, $z = 1.01$, $p = 0.31$) and the interaction ratio difference and absolute value were not ($B = -0.061$, $z = 1.14$, $p = 0.26$). Model comparison shows that analysis 3 did not account for significantly more variation than analysis 1 ($\mathbf{X}^2 = 2.70$, $p = 0.26$) or analysis 2 ($\mathbf{X}^2 = 1.28$, $p = 0.26$). Thus for ratio differences of 1.10 or more the best model of the data includes only ratio difference as a significant predictor or trial correctness.

3.3. Discussion

In Experiment 2 we replicate the finding that participants' numerical discrimination performance is best predicted when taking into account the interaction of ratio difference and absolute value. When evaluating a ratio difference range consistent with prior work, greater than 1.10, we observe no effect of absolute value or the interaction of absolute value and ratio difference. It is only when ratio differences are near threshold, smaller than 1.10, that the effect of absolute value in addition to ratio difference is observed in discrimination judgments. For the smallest ratio differences absolute value increases are associated with increased likelihood of correct discrimination, larger values are easier to discriminate. The significant effect for absolute value for <1.10 ratio differences, along with the lack of effect for ratio differences >1.10 is consistent with the significant interaction when considering the entire range of ratio differences. This should not necessarily be taken an evidence that absolute value matters for only ratio differences less than 1.10 and not more than 1.10. The existence of a statistically significant effect for the smaller ratios but not the larger ratios does not mean that whatever underlying mechanism there may be suddenly stops once ratio differences are above 1.10. For any given ratio comparison, such as 9:10 it is not clear if which absolute value, 9:10, 18:20, 90:100, represents a "true" measure of individual numerical discrimination precision. It is unclear if stimuli with the same ratio-differences but difference absolute values would yield significantly difference estimates of individual acuity.

It is possible that on some trials participants used a strategy in which they choose based on detection of the most extreme values, the smallest and largest sets (e.g., Barth, Baron, Spelke, & Carey, 2009; Gilmore, Mccarthy, & Spelke, 2007; Mccrink & Spelke, 2010). To evaluate if participants used a range-based heuristic we evaluated performance when the most extreme values were present (30, 117). If participants used a strategy in which they selected based on the detection of the smallest or largest set, rather than by comparing the presented sets to each other we would expect the typical distance effect to be absent on these trials. Detection of the extreme value, and use of the heuristic, should not vary in difficulty based on the comparison value. To evaluate this we analyzed trials with an extreme value (30 or 117) in which participants may have used this heuristic. For these trials the correlation between proportion of correct trials and ratio difference was $R = 0.65$, $t(18) = 3.41$, $p = 0.003$. The larger the ratio difference the more likely participants were to respond correctly. The performance on this subset of trials was 74% correct, whereas performance on the total set was 69%. These results suggest that in the case of the extreme values the relative size of the to-be-compared to value affects participants performance in a manner consistent with numerical comparison, not range-based heuristics.

4. Computational models

We use computational models to evaluate the possibility that aspects of the neural correlates of number perception may account for the behavioral phenomena reported in experiments 1 and 2. The overall logic of this evaluation is that the pattern of errors observed in the computational model should mirror the behavioral data. Each model instantiation completed the same numerical discrimination trials as human participants in experiment 1. Several characteristics of the neural coding are integrated into the models; (1) larger numerical values are coded by proportionally broader neural tuning curves, (2) larger numerical values are associated with smaller maximum firing rates, (3) the coefficient of variation in neural firing varied with mean firing rate. All of these characteristics have been previously reported in direct neural recording studies of numerical perception using non-human primates. Accordingly, the implemented model coded number values via neural tuning curves that are probabilistic and the resulting pattern of neural coding "errors" was taken as predicting the pattern of behavioral errors (Nieder & Merten, 2007; Nieder & Miller, 2004; Nieder et al., 2002, 2006; Prather, 2012).

Two separate model instantiations were considered; a model with decreasing coefficient of variation, as seem in previous data (Pearson et al., 2010) and a model with constant coefficient of variation as a control. The purpose of the following simulations is to show that while both models will demonstrate a significant effect of ratio difference on numerical discrimination only a computational model with the specific assumption of varying "noise" will show an interaction between ratio difference and absolute value as seen in the behavioral data.

4.1. Design

Each model instantiation initiated with calculation of neural tuning curves corresponding to the set of numerical values to be compared. The tuning curve was constructed via a Gaussian curve equation where the width and height varied with the associated numerical value (see Fig. 1 and Appendix A). Random variation, i.e. noise, was added to each curve by changing the mean firing rate values by some percentage. The noise parameter was taken from a normal distribution such that the mean noise was 0% and the distribution of noise was proportional to the mean firing rate. The application of noise is used to define the coefficient of variation in the tuning curve values. To complete a numerical discrimination trial the model then translates the tuning curve into a numerical value by locating the peak activation value, and numerical value pairs are compared. This is iterated across all 90 trials and 1000 independent batches.

4.2. Results

4.2.1. Computational model with decreasing coefficient of variation

Overall performance of the decreasing coefficient of variation model was 71% correct. Model performance was evaluated using a linear regression analysis. The predicted variable was the proportion of correct responses for each trial (after an arc-sine transformation). Predictive factors ratio difference and absolute value were mean centered. First we evaluated the computational model instantiation with decreasing coefficient of variation. Regression analysis 1, a linear regression with ratio difference as the only predictive factor shown a significant ($B = 1.46$, $t = 15.69$, $p < 0.001$), $R^2 = 0.73$. Regression analysis 2, a linear regression with ratio difference and absolute value comparison significant effect of ratio difference ($B = 1.47$, $t = 28.09$, $p < 0.001$) and absolute value ($B = 0.0009$, $t = 13.82$, $p < 0.001$), $R^2 = 0.91$. Regression analysis comparison showed that analysis 2 accounted for significantly more variance than analysis 1, $F(1,87) = 191$ $p < 0.001$.

Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. For regression analysis 3, performance was significantly predicted by ratio difference ($B = 2.40$, $t = 27.92$, $p < 0.001$), absolute value ($B = 0.006$, $t = 10.26$, $p < 0.001$) and the interaction ($B = -0.006$, $t = 11.65$, $p < 0.0001$), $R^2 = 0.96$. Regression analysis comparison showed that analysis 3 accounted for significantly more variance than analysis 1, $F(1,86) = 135$, $p < 0.001$, and analysis 2 $F(1,87) = 255$, $p < 0.001$. For the computational model that included neural firing with an decreasing coefficient of variation data was best described by a regression including ratio difference, absolute value and their interaction. Similar to behavioral data in experiments 1 and 2 there is a significant effect of the interaction of ratio difference and absolute value.

4.2.2. Computational model with constant coefficient of variation

For the model instantiation with a constant coefficient of variation overall performance was 62%. Regression analysis 1, a linear regression with ratio difference as the only predictive factor shown a significant ($B = 1.06$, $t = 37.42$, $p < 0.001$), $R^2 = 0.94$. Regression analysis 2, a linear regression with ratio difference and absolute value comparison significant effect of ratio difference ($B = 1.06$, $t = 46.36$, $p < 0.001$) and absolute value ($B = 0.0002$, $t = 6.98$, $p < 0.0001$), $R^2 = 0.96$. Regression analysis 2 accounted for significantly more variance than analysis 1, $F(1,87) = 48.71$, $p < 0.0001$.

For regression analysis 3, performance was significantly predicted by ratio difference ($B = 1.00$, $t = 16.71$, $p < 0.001$), but not absolute value ($B = -0.0003$, $t = 0.68$, $p = 0.49$) or the interaction ($B = 0.0004$, $t = 1.12$, $p < 0.26$). Regression analysis 3 accounted for significantly more variance than analysis 1, $F(1,86) = 25.06$, $p < 0.0001$, but not analysis 2 $F(1,87) = 1.26$, $p = 0.26$. For the computational model that included neural firing with a constant coefficient of variation data the interaction of ratio difference and absolute value did not improve prediction of trial discriminability. Contrary to behavioral data in experiments 1 and 2 there was no significant effect of the interaction of ratio difference and absolute value.

4.3. Discussion

Using two different computational models of numerical discrimination we show decreasing coefficient of variation is associated with numerical discrimination results that mirror the behavioral data. Both model instantiation match the human data well in terms of overall performance and the effect of ratio difference on trial discriminability (Fig. 2). However, the novel finding of a significant interaction between ratio difference and absolute value is only present for the model instantiation with decreasing coefficient of variation. The computational model with decreasing coefficient of variation best matches both the neural data (see Pearson et al., 2010) the current behavioral data. The results suggest that the changing coefficient of variation in the neural populations that code for number is the mechanism that underlies the novel behavioral effect described in experiments 1 and 2: a significant interaction between ratio difference and absolute value.

5. General discussion

An important characteristic of human numerical judgment is that discrimination that fits Weber's law. This is reflected in human behavioral patterns and also in the neural activity associated with numerical perception. The present results show that another, subtler, property of population coding is also evident in human numerical judgments: judgment accuracy, or "noise", changes with the absolute values being compared. We show behavioral evidence of an interaction effect between ratio difference and absolute value in predicting discriminability. We also present a computational model that suggests the phenomenon is a consequence of the known specifications of neural coding associated with numerical perception. Though cognitive representation metaphors such as the mental number-line, may be consistent with behavior, evaluation of underlying neural mechanisms is necessary for a full characterization of behavioral phenomena. We show here that use of a computational model of known neural coding characteristics can develop predictions of behavior beyond the scope of representational metaphors. The neurocomputational analysis provides a baseline of expected behavioral patterns and a more mechanistic understanding of how these tasks are completed by participants.

5.1. What are the implications?

Implications of the results are that individual numerical discrimination performance can be situated across multiple factors, at the very least including ratio difference and absolute value. The current results add to questioning of the existence a 'pure' numeracy measure. The current data cannot fully address the debate, as a resolution will require significantly more behavioral and neural data. The current results do show that by simply considering the known characteristics of the neural coding of number, both numerical ratio difference and absolute value underlie numerical discriminability. It's possible that measures of numeracy may depend on the range of absolute values used in assessment. Measures of individual numeracy (e.g., Weber fraction) using a greater range in absolute value may show a stronger or weaker connection to educational outcomes. The relationship of non-symbolic numeracy to symbolic arithmetic and other outcomes is dependent on an accurate measure of non-symbolic numeracy. It is unclear if we currently have a full understanding of the mechanisms involved in, and factors influencing, non-symbolic numerical discrimination.

5.2. Caveats and limitations

It is possible that these observed patterns are not due to numerosity per se but other stimulus properties such as density, contour, individual item area, or total area (Gebuis & Reynvoet, 2012a, 2012b). Although researchers can typically control for some of the correlated cues such as and density, they cannot control for them all simultaneously because of their interdependency. Though sets of judgments can be created such that participants use of these cues can be evaluated. In the current stimulus set it is possible that participants attended to the relative item density of the displays in making discriminations. Recent work suggest that attending to density is associated with lower Weber fractions and that participants use density cues above a certain density threshold (Anobile et al., 2014). The results of experiment 2 suggest that use of density cues do not drive the interaction effect. The current "neural noise" hypothesis predicts the interaction to only be present when very small ratio differences are considered, exactly what the results of experiment 2 show. If use of density cues on high absolute value (and thus high density) trials accounted for the result then the "large ratio differences" analysis in experiment 2 should also show a significant interaction. The lack of interaction in this analysis is consistent with the current hypothesis: the effect of absolute value on numerical discrimination is only apparent when small ratio differences (less than 10:11) are included. Based on the current data we cannot assert that participants could not at any time attend to a non-numerical cue. Given that the computational results indicate that neural coding of number predicts the behavioral pattern observed it is unlikely that a non-numerical cue is responsible for the behavioral effect. Non-numerical cues were either controlled for, such as area, or correlated with ratio difference, such as density. The stimuli are controlled for total area and individual item area, thus are not a reliable cue. The "shape" of the item sets was randomized.

The general question of how perceptual (and non-perceptual) factors contribute to behavior on numerical tasks, and which neural mechanisms may be employed, is a question of great interest (e.g., Cappelletti et al., 2014; Gilmore et al., 2013). Particularly discriminability in cases where numerical and other perceptual cues are incongruent (e.g., Gebuis & Reynvoet, 2012a, 2012b). It is possible that these non-numerical perceptual cues contribute to the neural responses. Suggesting that neural correlates of number are not a response to "pure" numeracy per se, but a variety of characteristics that tend to correlate with number. That is entirely possible and cannot be addressed here. The assumption of this study is not that the task is purely numerical; it is that the neural responses associated with viewing numerical stimuli predict a novel pattern of behavior with regard to item discriminability.

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Appendix A

A.1. Model specifications

Simulations were evaluated using MATLAB (Mathworks) software. Neural tuning curves vectors were calculated for number pairs identical stimuli in the behavioral experiment. The initial vectors can be interpreted as idealized activation patterns to which some activation noise is added to determine the model output vectors. If the model produced vectors where the maximum value has the same index then the model correctly estimated that number value. Variation in spiking rate, e.g., noise, is calculated as a change in the vector values by some percent taken from a random distribution, where the mean noise is zero. The range of distribution is equivalent to the coefficient of variation. If the noise range is proportional to the spiking rate then the coefficient of variation is constant. If the noise range varies with the mean spiking rate then the coefficient of variation also varies. Model instantiations used either a constant coefficient of variation or a decreasing coefficient of variation. After the application of noise the vector output values were calculated, where the index of the maximum value of the vector equaled the output. The entire process of the application of random noise to the set of tuning functions was repeated 1000 times. As previously noted, prior work has shown that when behavioral errors occur the neural activity for the preferred quantity was significantly reduced compared to correct trials.

The following simulations use vectors to represent neural tuning functions. Each item in the vectors represents the relative activation level, in terms of spiking rate for a population of cortical neurons. Each simulation included one vector for each of the number magnitudes to be estimated. The values in each vector represent the relative activation (spiking rates) of number selective neurons. For example, the numerical value A was represented by the vector $A(n_1, n_2, \ldots n_{250})$, where the value for n_x is the spiking rate for the neurons selective for the number magnitude A. Vectors for values $A = 1$ through 100 were calculated and each vector contained 250 activation values. For example, the activation value at index 5 corresponds to the mean spiking rate the neural population that respond maximally to visual display of 5 items. Research suggests that the maximum spiking rate for large numbers is lower than for smaller numbers. Activation values for each vector were calculated using a modified Gaussian distribution function (shown below). This a general function that defines a variety of Gaussian distributions. Similar equations have been used in prior computational work (Dehaene, 2007; Prather, 2012). The method of using logarithmic differences results in Gaussian functions that are symmetric on a log scale and of identical width (see Fig. 1). On a linear scale the functions vary in width and positive skew (skew merely refers to the fact that the function is not symmetric about the mean). Smaller values are both narrower and more skewed. This is simply the consequence of transforming a Gaussian curve that is symmetric on a log scale to a linear scale.

$$f(x) = he^{\frac{-(x-m)^2}{2s^2}}$$

Activation values for each vector were calculated using a modified Gaussian distribution function that varies in height similar to a Poisson distribution (see Fig. 1). The maximum vale of the tuning curve h, varies with the numerical value (y), such that $h = (121 - y)$. The relative width of the calculated curves varied with the value of S (in all current simulations $S = 0.7$). The mean of the distribution, m is a constant set to 0. The distance between the target numerical value (T) and the current vector index (V) is defined as $X = \log_{20}T - \log_{20}V$. The method of defining X by logarithmic differences results in Gaussian functions that are symmetric on a log scale and of identical width.

A.2. Stimulus list

Experiment 1

117–105	117–90	117–102	111–99	117–99	64–60	114–93	114–90	38–34
72–60	78–64	78–76	114–99	99–90	117–93	35–32	111–93	32–30
33–32	39–31	36–32	38–30	38–32	39–32	38–31	72–64	99–96
68–60	66–60	74–62	76–62	117–114	36–31	74–60	37–32	62–60
72–62	37–30	105–90	78–66	114–108	108–90	66–64	33–31	34–30
35–31	39–35	37–31	105–93	76–68	38–36	78–60	114–102	111–90
66–62	72–66	108–99	78–68	78–70	31–30	33–30	102–90	93–90
39–38	37–33	70–64	35–30	117–96	76–72	39–34	38–33	105–96
114–96	39–33	76–64	70–60	39–30	99–93	74–64	76–66	111–96
78–62	96–90	36–30	108–96	76–60	108–93	74–66	36–33	70–62

Experiment 2

34–31	68–66	117–105	117–90	117–102	111–99	117–99	64–60	102–93
114–93	114–90	38–34	72–60	78–64	78–76	37–35	38–35	114–99
74–68	99–90	117–93	35–32	38–37	68–62	111–93	32–30	33–32
39–31	36–32	38–30	111–102	38–32	74–72	37–34	39–32	38–31
72–64	99–96	68–60	105–102	66–60	74–62	76–62	114–105	117–114
76–74	36–31	78–74	74–60	37–32	62–60	96–93	72–62	37–30
105–90	78–66	114–108	39–37	111–108	108–90	111–105	64–62	66–64
33–31	34–30	35–31	34–32	39–35	114–111	35–33	37–31	34–33
105–93	66–62	76–68	38–36	78–60	39–36	114–102	111–90	68–64
72–66	36–34	108–99	78–68	78–70	31–30	76–70	99–93	78–72
33–30	105–99	102–90	93–90	39–38	37–33	70–64	35–30	117–96
32–31	76–72	39–34	38–33	105–96	114–96	39–33	102–99	70–68
76–64	70–66	70–60	39–30	35–34	102–96	74–64	76–66	111–96
78–62	96–90	37–36	36–30	108–96	117–111	76–60	108–93	74–66
36–33	74–70	72–68	70–62	117–108	108–102			

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