Mathematical Model of Developmental Changes in Number Cognition

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Introduction

The acuity of individuals’ approximate number system (ANS) is measured using a non-symbolic numerical discrimination task (e.g., Halberda & Feigenson, 2008) which is encapsulated by the Weber Fraction measure (Piazza & Dehaene, 2004). Children’s performance on this task is linked to symbolic arithmetic skills, standardized test scores and other long-term outcomes (e.g., Beddington et al., 2008; Libertus, Odic, & Halberda, 2012; Parsons & Bynner, 1997). To complete this task individuals must perceive relative quantity of non-symbolic numerosity and indicate their relative values. Numerosity is typically presented visually as sets of objects, though other modalities such as sound have been used (e.g., Jordan & Brannon, 2006). Discriminability of numerical stimuli is thought to depend solely on the ratio-difference between values being compared if other perceptual factors are controlled for. Thus comparison of the same ratio difference, such as 20:25 and 40:50 are equally discriminable and absolute value is not relevant. Thus individual performance on numerical discrimination in terms of accuracy and reaction time varies with the ratio differences and is independent of absolute value. This has been shown in a range of behavioral and neural data with adults (e.g., Barth, Kanwisher, & Spelke, 2003), children (e.g., Barth, Mont, Lipton, & Spelke, 2005) and non-human primates (e.g., Nieder & Miller, 2004).

Research with adults contradicts the account that ratio is the sole predictor of discriminability in number comparison task. Though absolute value does not predict discriminability, the interaction of ratio difference and absolute value does (Prather, 2014). The interaction between absolute value is not typically reported because data including comparisons with small ratio differences and variations in absolute value are needed to clearly show the effect.

Though there is initial evidence of the effect of absolute value on numerical discrimination it is unclear if such an effect would be present with children, and if the effect varies across development. The consequences of such an effect in children are directly relevant to measures of numerical acuity. Measures of numerical acuity are used to evaluate a correlation to performance on symbolic, and other educational outcomes. If children’s performance varies across absolute value, which is not typically accounted for, then it is unclear the reported numerical acuity is the “true” measure of participants’ accuracy. Inclusion of varying absolute values may change the degree to which non-symbolic discrimination predicts other outcomes.

The current study employs behavioral experimentation and computational modeling to address the following questions: 1) is children’s numerical discrimination solely dependent on ratio difference or also an interaction between ratio difference and absolute value, 2) do the factors contributing to children’s numerical discrimination difficulty change with development, 3) how might the neural coding involved numerical perception account for these behavioral effects?

Experiment 1

Method

Participants
Participants were children (n = 51) between ages of 5:5 and 8:11 (median 7.5). A small group (n = 4) of participants were not included in the analysis due to selection bias on the numerical comparison task, indicated by selection of one side (left or right) on >80% of trials. Participants completed two tasks, a non-symbolic numerical discrimination task and a symbolic number-line estimation task. Task order was counter-balanced across participants. The experiment comprised of a single laboratory session of approximately 30 minutes. Experimental design was approved through the Indiana University Internal Review Board.

Non-symbolic numerical comparison.
Each participant completed 51 trials of a forced choice comparison between pairs of sets of shapes presented simultaneously. The sets were comprised of squares that varied in area such that the two sets were matched in overall area, area of largest shape and area of smallest shape. Stimuli were presented to participants on laminated cards (8.5 x 11 inches). Participants were not given a time limit but were instructed to answer as quickly as they could. Stimuli were presented in a randomized order. Stimuli were comprised of 17 ratio differences from 1.03 to 1.18, and 3 absolute value sizes for each ratio difference. For example for the ratio 1.04 the comparisons 25:26, 50:52 and 75:78 would be used. The location (left or right) of the larger value was counter balanced. Participants responded by pointing to which set they thought had a larger number of objects.
Results

Overall participants’ performance on the numerical discrimination task was M = 60%. We evaluated participants’ performance on the numerical comparison task using a series of logistic regression analyses. The correctness of each trial was predicted by the trial ratio difference, absolute value and their interaction. In each analysis we evaluate which set of factors best predict trial correctness. All regression analyses included participant identity and participant age as random factors. Each regression analysis includes 51 data points per subject.

All Participants

First we examined which factors predicted performance on the numerical discrimination task for all participants as a group. Regression analysis 1 included only ratio difference as a predictor of trial correctness. Ratio difference was a significant predictor (b = 3.10, z = 3.19, p = 0.001). As expected larger ratio differences were associated with increased likelihood of a correct response. Regression analysis 2 included ratio difference and absolute value as predictors of trial correctness. Ratio difference (b = 3.12, z = 3.20, p = 0.001) was a significant predictor while absolute value (b = -0.0002, z = 0.29, p = 0.76) was not. A comparison of regression analyses indicated that analysis 2 did not account for more variance than analysis 1, $\chi^2 = 0.08$, p = 0.76.

Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Ratio difference (b = 0.09, Z = 3.34, p < 0.001), absolute value (b = 0.049, Z = 2.51, p = 0.012) and their interaction (b = -0.045, Z = 2.52, p = 0.011) were significant predictors of trial correctness. A comparison of regression analyses indicated that analysis 3 accounted for more variance than both analysis 1, $\chi^2 = 6.44$, p = 0.001 and analysis 2 $\chi^2 = 6.35$, p = 0.01. Thus for the total set of participants performance is best described by the regression analysis that includes ratio difference, absolute value, and their interaction as significant predictors.

Participants grouped by numerical discrimination performance

We then evaluated how predictors of participants’ numerical comparison score may vary based on their numerical discrimination score. Participants were split into three groups based on their overall numerical discrimination score, best performers, middle performers and worst performers. Participant age was positively correlated with numerical comparison performance, r = .49, t(45) = 3.77 p < 0.001. Thus participants in the best scoring tertile tended to be older than those in the middle and worst tertiles. We use discrimination task score to evaluate the effect of development, as it is a more theoretically motivated selection variable than age per se.

For participants in the best performing tertile (n = 16, median age = 8:1 years, 816 total trials) overall performance on the numerical comparison task was M = 68.7%. Regression analysis 1 included only ratio difference as a predictor. Ratio difference was a significant predictor (b = 5.76, z = 3.30, p < 0.001) or trial correctness. Regression analysis 2 included ratio difference and absolute value as predictors of trial correctness. Ratio difference (b = 5.67, z = 3.24, p = 0.001) was a significant predictor while absolute value (b = 0.001, z = 1.06, p = 0.28) was not. A regression analysis comparison indicated that analysis 2 did not account for more variance than analysis 1, $\chi^2 = 1.14$, p = 0.28.

Regression analysis 3 included ratio difference, absolute value and their interaction as predictors of trial correctness. Ratio difference (b = 12.86, z = 2.80, p = 0.005) was the only significant predictor. Absolute value (b = 0.06, Z = 1.74, p = 0.082) and the interaction of ratio difference and absolute value (b = -0.05, Z = 1.70, p = 0.087) were not significant predictors. A regression comparison indicated that analysis 3 did not account for more variance than analysis 2 ($\chi^2 = 2.92$, p = 0.08) or analysis 1 ($\chi^2 = 4.06$, p = 0.13).

For participants in the middle tertile (n = 15, median age 7:7 years, 765 total trials) overall performance on the numerical comparison task was M = 61.2%. Regression Analysis 1 included only ratio difference as a predictor. Ratio difference was not a significant predictor (b = 0.64 z = 0.37, p = 0.70). Regression analysis 2 included ratio difference and absolute value. Neither ratio difference (b = 0.68, z = 0.40, p = 0.69) nor absolute value (b = -0.0006, z = 0.52, p = 0.60) were significant predictors of trial correctness. A regression analysis comparison indicated that analysis 2 did not account for significantly more variation than analysis 1, $\chi^2 = 0.27$ p = 0.60.

Regression analysis 3 included ratio difference, absolute value and their interaction as predictors of trial correctness. Ratio difference (b = 9.38, z = 2.08, p = 0.03) absolute value (b = 0.07, Z = 2.06, p = 0.039) and their interaction (b = -0.06, Z = 2.08, p = 0.037) were significant predictors. A regression analysis comparison indicated that analysis 3 accounted for significantly more variance than analysis 2, $\chi^2 = 4.36$ p = 0.03 but not analysis 1 $\chi^2 = 4.63$ p = 0.09.

For participants in the worst performing tertile (n = 16, median age = 6:5 years, 816 total trials) overall performance on the numerical comparison task was M = 50.6%. Regression Analysis 1 included only ratio difference as a predictor. Ratio difference was not a significant predictor of trial correctness (b = 3.05, z = 1.86, p = 0.06). Regression analysis 2 included ratio difference and absolute value as predictors. Ratio difference (b = 3.14, z = 1.91, p = 0.05) was a significant predictor while absolute value (b = 0.07, z = 0.99, p = 0.32) was not. A regression analysis comparison indicated that analysis 2 did not account for more variance than analysis 1, $\chi^2 = 0.98$, p = 0.32.

Regression analysis 3 included ratio difference, absolute value and their interaction as predictors of trial correctness. Neither ratio difference (b = 3.10, Z = 1.88, p = 0.48), absolute value (b = 0.95, Z = 0.51, p = 0.61) or their
The significant contribution of ratio difference in predicting children’s numerical discrimination performance is consistent with prior research; larger ratio differences tend to be easier to discriminate. We also find that overall, participant performance is predicted by the interaction of ratio difference and absolute size. Regression analyses that include the interaction of ratio difference and absolute value account for more variance in participants’ data than other analyses. Simply, the results suggest that for numerical discrimination tasks ratio difference is not the sole predictor of performance, similar to recent findings with adult participants (Prather, 2014).

We also examined how the interaction between ratio difference and absolute value varies with development by reevaluating participant data when grouped by performance. Participants in this experiment were a heterogeneous group, with ages ranging from 5:5 to 8:11 and discrimination scores ranging from chance to over 75%. We use a tertile split in performance to balance having sufficient data points in each analysis and also evaluating participant groups that performed differently. The results suggest that the predictors of numerical comparison scores vary with participants’ skill level. Participants in the best and worst performing tertiles did not show a significant interaction between ratio difference and absolute value. Only participants in the middle group showed a significant effect of the interaction of ratio difference and absolute value.

The conclusion from these results is that there is a behaviorally measurable effect of absolute value in numerical discrimination, which is present when considering all participants, is not present for all participant groups. The current results we suggest that the influence of absolute value varies across development, roughly following a U-shaped curve. This is demonstrated by the presence of the interaction effect in the middle tertile group but not best or worst tertiles. To examine if there is a principled reason to expect this effect we consider developmental change in the neural mechanisms involved in numerical perception in experiment 2.

**Experiment 2**

The following series of computational models demonstrate how developmental changes in the neural coding of number is the underlying mechanism of the behavioral effects reported in Experiment 1. Behavioral data shows the predictors of numerical discrimination scores vary with participants’ numerical discrimination skill. The interaction of absolute value and ratio difference was a significant predictor of numerical discrimination only for participants in the middle tertile. We demonstrate here that known characteristics of the neural coding of numerical perception, and how it changes with development, lead to this exact prediction.

The logic of these computational models is that behavioral errors, and neural coding “errors” are associated (Nieder & Merten, 2007). This is not to suggest that participants’ behavior is solely dependent on variations in these neural populations, but that it forms the basis for the patterns of behavior. A range of behavioral phenomena have been shown to be predicted by neural coding including the ratio distance effect, number-line estimation and operational momentum effects (Nieder & Dehaene, 2009; Prather, 2012).

The characteristics of the neural coding of numerical perception have been described via both human neuroimaging studies and non-human primate direct recording (e.g., Nieder & Dehaene, 2009; Nieder & Merten, 2007). The important characteristic for the current model is the “noise” associated with neural coding. Neural activity is typically reported through the mean spiking rate across some amount of time. For any neural population in addition to mean spiking rates that may be associated with numerical stimuli there is also variation in spiking rate. A neural population that fires at an average of 50Hz has an associated variation in the moment-to-moment firing rate. This noise around a given mean firing rate is illustrated by the coefficient of variation: standard deviation / mean. The coefficient of variation (CoV) for the neural populations that code for number varies with firing rate (Pearson, Roitman, Brannon, Platt, & Raghavachari, 2010; Roitman, Brannon, & Platt, 2007). Thus, the neural coding for larger numbers tends to have less “noise” than those for smaller numbers. The following computational investigation evaluates how neural coding of number with either a constant or changing CV may predict the behavioral results reported in experiment 1.

**Method**

Computational model versions included experimental and control conditions each with three instantiations corresponding to the participant tertiles in experiment 1 for a total of 6 separate models. The model simulated neural coding associated with numerical stimuli using probabilistic tuning curves that were then applied to the numerical discrimination task. The model evaluated the same stimuli as seen by participants in experiment 1. Developmental change was modeled through the coefficient corresponding to the relative width of the neural tuning
curves. Narrow tuning curves have been shown to be necessary for accurate coding of number (Diester & Nieder, 2008). Narrowing of the tuning curves increases precision and is generally associated with neurocognitive development. This has been illustrated in computational work in which narrowing of tuning functions of neurons contributes to modeling developmental changes in cognition (Schutte, Spencer, & Schöner, 2011; Simmering, Schutte, & Spencer, 2007).

**Modeling specifications**

Simulations were evaluated using MATLAB (Mathworks) software. Neural tuning curves vectors were calculated for number values identical stimuli in the behavioral experiment. The initial vectors can be interpreted as idealized activation patterns to which some noise is added to determine the model output vectors. The index of the maximum value corresponded to the perceived 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 noise distribution is equivalent to the coefficient of variation. The noise range varies with the mean spiking rate and the coefficient of variation (standard deviation/mean) also varies. Model instantiations used a coefficient of variation that was either constant or increased with firing rate. Neural data with non-human primates shows that the coefficient of variation increases with firing rate (Pearson et al 2010; Roitman et al., 2007). 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 per model instantiation.

Simulations used vectors to represent spiking rates for neural populations that comprise the 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 1 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 $x$. 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.

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

Activation values for each vector were calculated using a modified Gaussian distribution function that varies in height similar to a Poisson distribution. The maximum value of the tuning curve $h$, varies with the numerical value $y$, such that $h = (121 - y)$. The relative width of the calculated curve varied with the value of $s$. 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. 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. The maximum spiking rate for large numbers is lower than for smaller numbers (e.g. Nieder & Dehaene, 2009). Similar equations have been used in prior computational work (Dehaene, 2007; Prather, 2012).

The model instantiation with broad tuning curves ($S = 1.5$) corresponded to the low scoring numerical discrimination participant group. The model instantiation with medium tuning curves ($S = 0.5$) corresponded to the high scoring numerical discrimination participant group. The model instantiation with narrow tuning curves ($S = 0.3$) corresponded to the high scoring numerical discrimination participant group. Each model instantiation result is based on 1000 independent run-throughs of the model.

**Results**

**Model versions with varying coefficient of variation**

For the narrow tuning curve model numerical discrimination performance was $M = 83\%$. Performance was evaluated with a linear regression using ratio difference and absolute value as predictors for the percent correct for each trial (51 in total). Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, $b = 3.33$, $t = 7.59$, $p < 0.001$. Regression analysis 2 included ratio difference and absolute value as predictors of model performance. Both ratio difference, $b = 2.92$, $t = 20.05$, $p < .001$ and absolute value $b = 0.002$, $t = 20.19$, $p < .001$ were significant predictors of model performance. Regression analysis 2 accounted for more variance than model 1, $F(1,48) = 407.73$, $p < 0.001$. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference ($b = 2.33$, $t = 6.42$, $p < .001$), but not by absolute value ($B = -0.002$, $t = 0.98$, $p = 0.33$) or their interaction ($b = 0.004$, $t = 1.76$, $p = 0.084$). Regression analysis 3 accounted for more variance than analysis 1 $F(1,47) = 214.39$, $p < 0.001$ but not analysis 2 $F(1,47) = 7.59$, $p = 0.084$.

The medium tuning curve model overall performance was $M = 74\%$. Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, $b = 2.52$, $t = 7.41$, $p < 0.001$. Regression analysis 2 included ratio difference and absolute value as predictors of model
performance. Both ratio difference, b = 2.21, t = 15.40, p < .001 and absolute value b = 0.001 t = 15.24, p < 0.001 were significant predictors of model performance. Regression analysis 2 accounted for more variance than model 1, F(1,48) = 232.38, p < 0.001. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference (b = 1.07 , t = 3.32 , p < .001), absolute value (b = -0.007 , t = 3.18 , p = 0.002) or their interaction (b = 0.007 , t = 3.83 , p < 0.001). Regression analysis 3 accounted for more variance than both analysis 2 F(1,47) = 14.71, p < 0.001 and analysis 1 F(1,47) = 156.75, p < 0.001.

The broad tuning curve model overall performance was M = 60% (Figure 3). Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, b = 0.86, t = 7.46, p < 0.001. Regression analysis 2 included ratio difference and absolute value as predictors of model performance. Both ratio difference, b = 0.77, t = 9.86, p < .001 and absolute value b = 0.0004 t = 7.74, p < 0.001 were significant predictors of model performance. Regression analysis 2 accounted for more variance than model 1, F(1,48) = 59.89, p < 0.001. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference (b = 0.57 , t = 2.85 , p = .006), but not absolute value (b = -0.001, t = 0.82 , p = 0.41) or their interaction (B = 0.001 , t = 1.12 , p = 0.26). Regression analysis 3 accounted for more variance than analysis 1 F(1,47) = 30.73, p < 0.001 but not analysis 1 F(1,47) = 1.25, p = 0.26.

For the computational model instantiations with varying coefficient of variation results demonstrate that the significant interaction between ratio difference and absolute value is only present of the middle-performing model. The best and worst performing model instantiations do not show significant interactions.

Model versions with constant coefficient of variation

For the narrow tuning curve model numerical discrimination performance was M = 80% (Figure 4-A). Performance was evaluated with a linear regression using ratio difference and absolute value as predictors for the percent correct for each trial (51 in total). Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, b = 2.99, t = 25.62, p < 0.001. Regression analysis 2 included ratio difference and absolute value as predictors of model performance. Both ratio difference, b = 2.91, t = 36.12, p < .001 and absolute value b = 0.0004 t = 7.57, p < 0.001 were significant predictors of model performance. Regression analysis 2 accounted for more variance than model 1, F(1,48) = 57.38, p < 0.001. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference (b = 3.00 , t = 14.53 , p < .001), but not by absolute value (b = 0.001, t = 0.79 , p = 0.43) or their interaction (b = 0.0006 , t = 0.51 , p = 0.61). Regression analysis 3 accounted for more variance than analysis 1 F(1,48) = 28.38 p < 0.001 but not analysis 2 F(1,47) = 0.26, p = 0.61.

The medium tuning curve model performance was M = 71% (Figure 4-B). Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, b = 2.01, t = 24.79, p < 0.001. Regression analysis 2 included ratio difference and absolute value as predictors of model performance. Both ratio difference, b = 1.97, t = 26.18, p < .001 and absolute value b = 0.0001 t = 3.11, p = 0.003 were significant predictors of model performance. Regression analysis 2 accounted for more variance than model 1, F(1,48) = 9.69, p = 0.003. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference (b = 2.03 , t = 10.46 , p < .001), but not absolute value (b = 0.0005, t = 0.42 , p = 0.67) or their interaction (B = -0.0003 , t = 0.31 , p = 0.75). Regression analysis 3 accounted for more variance than analysis 1 F (1,47) = 4.80, p = 0.01 but not analysis 2 F(1,47) = 0.09, p = 0.75.

The broad tuning curve model performance was M = 58% (Figure 4-C). Regression analysis 1 included ratio difference as a predictor. Ratio difference was a significant predictor of model performance, b = 0.77, t = 9.93, p < 0.001. Regression analysis 2 included ratio difference and absolute value as predictors of model performance. Ratio difference, b = 0.76, t = 9.70, p < .001 was a significant predictor while absolute value b = 0.0005 t = 1.08, p =0.28 was not. Regression analysis 2 did not account for more variance than model 1, F(1,48) = 1.18, p = 0.28. Regression analysis 3 included ratio difference, absolute value and their interaction as predictors. Model performance was significantly predicted by ratio difference (b = 0.85 , t = 4.20 , p = .001), but not absolute value (b = 0.0007, t = 0.50 , p = 0.61) or their interaction (b = -0.0006 , t = 0.46 , p = 0.64). Regression analysis 3 did not account for more variance than analysis 1 F(1,47) = 0.69, p=0.50 or analysis 1 F(1,47) = 0.21, p = 0.64.

For the computational model instantiations with constant coefficient of variation results do not show significant interaction between absolute value and ratio difference for any of the model versions. Model tuning curve width and performance was not associated with a change in significant predictors of performance. For each model instantiation ratio difference was the sole predictor of performance.

Experiment 2 Discussion

When the coefficient of variation (CoV) in neural firing increases with mean firing rate matches neural data computational results match the behavioral results in Experiment 1. For the changing CoV model a significant interaction of ratio difference and absolute value is present for the “middle tertile” instantiation and not the best or worst performing instantiations. The constant CoV models
performance were predicted by ratio difference only in all cases. These results suggest that the coefficient of variation in neural firing is a key aspect of the mechanism underlying the interaction of absolute value and ratio difference. The characteristics of the neural tuning curves for the model version that best fits the behavioral data is consistent prior neural data (Pearson et al., 2010; Roitman et al., 2007) and consistent with recent adult data showing that increasing CoV models better account for performance on numerical discrimination task (Prather, in review). In sum, if we take into account all of the known characteristics of the neural coding of numerical perception the effects reported in experiment 1 are a logical consequence. Additionally both model versions demonstrate that narrower neural tuning curves are associated with better numerical discrimination as expect based on prior work (e.g., Nieder & Dehaene, 2009; Prather, 2012). This suggests that the differences in behavior between participant tertiles may be due to differences in neural tuning curves.

**General Discussion**

We show using a series of computational models that the changing precision of neural tuning curves and neural firing variation predicts the pattern of results reported in the behavioral data. Simply, if we assume neural coding that is consistent with neural data (Pearson et al., 2010; Roitman et al., 2007) the behavioral effects reported in experiment 1 or a logical consequence. Though the cognitive representation metaphors may be consistent with behavior, evaluation of underlying neural mechanisms is necessary for a full characterization of behavioral phenomena. We show here that using a computational model of known neural coding characteristic may lead us predictions of behavior beyond the scope of representational metaphors.

**References**


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