Numerical Values Leave a Semantic Imprint on Associated Signs in Monkeys

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Abstract

■ Animals and humans share an evolutionary ancient quantity representation which is characterized by analog magnitude features: Discriminating magnitudes becomes more difficult with increasing set sizes (*size effect*) and with decreasing distance between two numerosities (*distance effect*). Humans show these effects even with number symbols. We wondered whether monkeys would show the same psychophysical effects with numerical signs and addressed this issue by training three monkeys to associate visual shapes with numerosities. We then confronted the monkeys with trials in which they had to match these visual signs with each other. The monkeys' performance in this shape versus shape protocol was positively correlated with the numerical distance and the magnitudes associated with the signs. Additionally, the monkeys responded significantly slower for signs with higher assigned numerical values. These findings suggest that the numerical values imprint their analog magnitudes characteristics onto the associated visual sign in monkeys, an effect that we also found reflected in the discharges of prefrontal neurons. This provides evidence for a precursor of the human number symbol knowledge. ■

INTRODUCTION

Humans and animals are able to estimate quantities based on an analog magnitude system (Nieder, 2005). This analog magnitude system is characterized by noisy representations of numerosities and can be traced in number comparison tasks by two psychophysical effects: We make more errors and need more time to discriminate quantities when the numerical distance between two values decreases (e.g., 3 vs. 7 is much easier than 6 vs. 7). Error rates and response latencies increase even more when the absolute set size increases (e.g., it is easy to discriminate 2 and 4, but very hard to distinguish between 28 and 30, even if the distance is the same, namely, 2). These effects have been termed numerical distance and numerical size effect and are captured by Weber's law, which states that the threshold of discrimination between two stimuli scales with their magnitude (Weber, 1850). Analog magnitude characteristics have been observed in number discrimination tasks in human adults (Beran, Taglialatela, Flemming, James, & Washburn, 2006; Cantlon & Brannon, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Barth, Kanwisher, & Spelke, 2003), children (Beran, Johnson-Pynn, & Ready, 2008; Cantlon, Brannon, Carter, & Pelphrey, 2006; Jordan & Brannon, 2006a), apes (Beran, 2001, 2004), and monkeys (Beran et al., 2008; Merten & Nieder, 2008; Beran, 2007; Cantlon & Brannon, 2006; Jordan & Brannon, 2006b; Nieder & Miller, 2004a; Brannon & Terrace, 2000). The similarities between the performance of humans and animals point to a common and evolutionarily old quantity representation system. Indeed, functional magnetic imaging in humans (Piazza, Pinel, Le Bihan, & Dehaene, 2007; Cantlon et al., 2006; Piazza et al., 2004) and single-cell recordings in monkeys (Nieder & Merten, 2007; Roitman, Brannon, & Platt, 2007; Nieder, Diester, & Tudusciuc, 2006; Nieder & Miller, 2004b; Nieder, Freedman, & Miller, 2002) constitute evidence for homolog structures that encode numerosities as analog magnitudes.

Nonverbal numerical cognition is limited to approximate quantity representations. In contrast, humans familiar with number symbols are able to address numerosities with a high precision. Interestingly, the number size and distance effect can still be observed with number symbols in human adults who are pressed for time, despite the digital character of the signs they are using (Koechlin, Naccache, Block, & Dehaene, 1999; Dehaene, Dupoux, & Mehler, 1990; Buckley & Gillman, 1974; Moyer & Landauer, 1967). Functional imaging studies have shown these effects on the level of brain activation (Piazza et al., 2004). These observations suggest that symbolic and nonsymbolic notations converge onto a common representation format in humans as proposed by Dehaene's (1992) triple code model. In this model, analog magnitudes function as an amodal abstract semantic representation that forms the basis of numerical processing. Human adults are thought to retrieve the appropriate number symbols for a given quantity code and, conversely, have to translate number symbols into analog magnitudes in order to interpret them semantically. The acquisition of number symbols is thought to result from categorizing the number

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line continuum into segments of different lengths, each associated with a specific visual sign (Dehaene, 1992).

The association of shapes and quantities, a necessary first step toward the utilization of number symbols in linguistic humans, can even be mastered by animals (Xia, Emmerton, Siemann, & Delius, 2001; Washburn, 1994; Washburn & Rumbaugh, 1991; Boysen & Berntson, 1989; Matsuzawa, 1985). Washburn (1994) convincingly showed that the numerical value assigned to Arabic numerals interferes in a Stroop-like way with set sizes in a relative-numerosity task. Further, we have shown that single neurons in prefrontal cortex (PFC) of monkeys are capable of encoding analog magnitudes as well as their associated visual shapes (Diester & Nieder, 2007). Here, we complement these findings by analyzing in detail to what extent monkeys treat shapes associated with analog magnitudes as numerical signs. We investigated this aspect by applying three different versions of a delayed match-to-numerosity task: (1) a dot versus dot protocol in which monkeys had to compare the numerosity of two sets of dots and which we used as performance baseline; (2) a shape versus dot protocol in which monkeys learnt to associate visual signs with numerical values; and (3) a shape versus shape protocol in which monkeys that had learnt an association between visual shapes and numerical values were required to match these signs. We hypothesize that the representation of analog magnitudes is transferred to the associated visual signs (*semantic linking hypothesis*). Alternatively, if the monkeys performed pure shape matching, only the visual characteristics of the shapes might be used to solve the task (*shape matching hypothesis*). Both hypotheses make testable predictions. The semantic linking hypothesis predicts that the numerical size and distance effect should be observable even if the monkeys have to compare two visual shapes. Furthermore, just as observed with dot numerosities (Nieder & Miller, 2004a), the monkeys should need more time to evaluate signs associated with higher numerical values. In contrast, the shape matching hypothesis predicts that in a shape versus shape protocol, there is no need for making associations in order to solve the task; consequently, error rates and reaction times should remain constant across different numerical values and distances.

METHODS

Subjects and Apparatus

Subjects were three adult male rhesus macaques (*Macaca mulatta*) weighing 6.3, 6.7, and 8.7 kg. They were housed in groups of two to six monkeys. All monkeys were also used for electrophysiological recordings (Diester & Nieder, 2007, 2008; Nieder et al., 2006). Care and treatment of the monkeys were in accordance with the guidelines for animal experimentation approved by the Regierungspräsidium Tübingen, Germany. The animals were trained to sit in a monkey chair positioned at a viewing distance of 57 cm in front of a computer screen inside a dark booth. A head post affixed to the skull using standard surgical procedures under general anesthesia was used for fixing the head position during the trial, thus enabling us to monitor eye movements with an infrared eye tracking system (ISCAN, Burlington, MA). A personal computer running the CORTEX software (NIH) controlled experimental events and behavioral data collection.

Delayed Match-to-Numerosity Task

A trial started when the monkey grasped a lever and fixated a central fixation target. A sample display conveying the numerical information 1 to 4 was shown for 800 msec. Following a memory delay (1000 msec), during which a green background circle without items was shown, a test display was presented for up to 1200 msec. It was either a match (it contained the same numerical value as the sample display) or a nonmatch. The nonmatch stimuli ranged from 1 to 4. Match and nonmatch displays appeared pseudorandomized and with equal probability [p = .5 (50%)]. If the test display was a match, monkeys released the lever before it disappeared to receive a juice reward. If the test display was a nonmatch, the monkeys held the lever until the second test display, which was always a match, appeared. This also required a lever release to receive a reward. Trials were randomized and balanced across all relevant features (i.e., match vs. nonmatch trials, standard vs. control trials, and dot vs. dot, shape vs. dot, and shape vs. shape trials). The chance level for this task protocol was 50% correct responses. The two basic error types included fixation breaks (eye movements away from the fixation point) and false responses (i.e., bar releases to nonmatch stimuli, or continue to hold the bar in match stimuli). Fixation breaks were not counted when calculating performance level; only incorrect numerical judgments were taken into account. Both errors terminated the trial immediately. Monkeys performed between 500 and 1000 correct trials per session (day). They had to keep their gaze within 1.75° of visual angle of the fixation point during sample presentation and the memory delay.

Standard and Control Stimuli

The dot stimuli contained black items (diameter range from 0.5° to 0.9° of visual angle) that were displayed on a gray circular background (diameter: 6° of visual angle). To prevent the monkeys from simply memorizing the visual patterns of the displays, each quantity was tested with 100 different images per session (by randomly varying the size and location of the items). Moreover, the sample and test displays in each trial were never identical. The monkeys were trained with standard stimuli, which comprised dots of different sizes and in different positions. On average, the surface area, the circumference, and the density of the items increased with increasing numerosity for the standard stimuli. Therefore, controls were included with displays in which the total circumference was equated across different quantities and, at the same time, the total area decreased. In addition, we controlled for dot density effects by keeping the density constant across all numerosities. The dot density was determined by calculating the average distance between dots. Finally, the dots were linearly arranged in the configuration controls. There were four numerosities, and all four were used in each session. For the shape stimuli, the black Arabic numerals 1, 2, 3, and 4 were presented on a gray circular background (diameter: 6° of visual angle). Each numeral was tested with 100 different images per session. In these images, font size (range 26 to 42 points) and location varied randomly from trial to trial. Animals were first trained with the standard font type Arial. Later, the control fonts Times New Roman, Lithograph Light, and Souvenir were introduced. Each day, one of these controls was used in 50% of trials. All displays were newly generated for each session by pseudorandomly shuffling all relevant item features (i.e., position, size, identity).

Training Procedure of the Association Task

We used color as an additional cue to make the association task easier for the monkeys in the beginning. The animals first learned to match a black "1" with one dot, a green "2" with two dots, a red "3" with three red dots, and a blue "4" with four blue dots. Color was slowly reduced from session to session until all shapes and dots were black. We chose this teaching scheme because color is a very obvious cue for monkeys and facilitates learning.

Data Analysis

Data analysis was carried out with custom-written Matlab software. Data were averaged across all sessions of a particular testing protocol. Average performance accuracy (P_{avrg}) for each sample numerosity was calculated as follows:

$$P_{\mathrm{avrg}} = 100 \cdot \frac{n_{\mathrm{Mcorr}} + n_{\mathrm{NMcorr}}}{n_{\mathrm{all}}} \tag{1}$$

where n_{Mcorr} is the number of correct responses in match trials (response after the first test stimulus), n_{NMcorr} is the number of correctly recognized nonmatch trials (response after the second test stimulus), and n_{all} is the number of all presented test stimuli for the particular sample.

We derived behavioral functions that described the relation between the numerical values and the monkeys' ability to respond correctly to them. Because the delayed match-to-sample paradigm allows either a correct or an incorrect response per trial, a performance probability of 50% correct responses indicates chance level, and a probability of 100% represents perfect discrimination. For each numerical value shown during the sample period, the percentage of all trials in which the monkeys judged that sample and test stimulus were equal was plotted against the first test stimulus on the x-axis. To derive the tuning width of these behavioral performance curves, Gaussian functions were fit to the performance curves of each monkey separately (χ^2-minimization). The Gaussian was chosen because it represents a standard symmetric distribution.

$$F(x) = y_0 + a e^{-\frac{(x-x_c)^2}{2\sigma^2}} \tag{2}$$

To acquire the best fit to the data, σ (standard deviation of the Gaussian distribution) and y-axis offset (y_0) were adjustable during the fitting procedure. The peak function's a (amplitude) was set to the maximum of the performance curve, and the center of the fitted distributions (x_c) was fixed at the function's sample value.

To investigate the numerical magnitude effect and to address the question of the scaling scheme, standard deviations of the Gaussian fits (σ) describing the widths of the behavioral filter curves were plotted versus numerosity on a linear and on a logarithmically compressed scale. A logarithmic relationship between the sensation (S) and the physical magnitude of the stimulus (I) [$S = k \times \log(I)$] was first proposed by Fechner (1860). Linear functions were fitted to the standard deviations of the performance curves. Here, positive slopes of the fits to the data on a linear scale indicate a correlation between standard deviations and numerical values. On a logarithmic scale, the standard deviations of the Gaussian fits (σ) should be a constant if numerical values, such as various sensory phenomena, are best represented on this scale.

For the analysis of response latencies, only trials with correct responses to match trials were used. Response latencies of nonmatch trials were not included because the match stimulus in the second test was predictable and only used to ensure that subjects were paying attention. We fitted sigmoidal curves to the response latencies of each monkey separately for illustrative purposes.

RESULTS

Protocol, Stimuli, and Performance

We trained three monkeys in three different versions of a delayed match-to-sample task (Figure 1). Training started with the matching of two sets of dots (*dot vs. dot* protocol; Figure 1A). After solving this task on a level of at least 80% correct trials per session in a row of

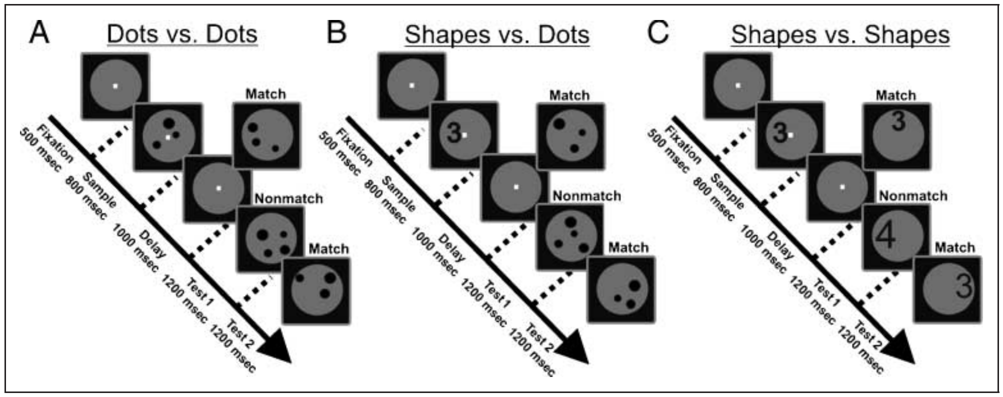

Figure 1. Behavioral protocol. Monkeys had to fixate and were cued for a given numerical value by a sample display. The animals had to memorize the numerical value in a 1-sec delay period and match it to a subsequent test stimulus by releasing a lever. Either the first or the second test stimulus was correct. Numerical values ranged from 1 to 4. Size and position of dots and shapes varied from trial to trial. (A) Dot versus dot protocol. Sample and test stimuli consisted of sets of dots. (B) Shape versus dot protocol. The sample stimulus was a shape (Arabic numeral) that had to be matched to an array of dots during the test phase. (C) Shape versus shape protocol. Sample and test stimuli consisted of shapes (Arabic numerals).

several consecutive days, the *shape versus dot* protocol was introduced that required an association of shapes with numerical values (Figure 1B). Importantly, this association had to be mastered reliably by the monkeys (80% correct in each session) before we moved on to the third version of the task, the *shape versus shape* protocol. In this protocol, the monkeys had to compare the numerical value of two visual shapes (Figure 1C).

A hundred dot and shape stimuli were generated newly every day to prevent the monkeys from memorizing the low-level visual features of the images. For the dot stimuli, we randomized size and position of the dots from trial to trial and introduced controls for all potentially confounding nonnumerical features (Figure 2A). A detailed description of the control stimuli and variations can be found in the Methods section. To reach the same level of generalization for the shape stimuli, we randomized size and position of the shapes in the standard trials and additionally used four different font types (Figure 2B).

Figure 3 shows the behavioral performance for the three different protocols and standard and control conditions. Each data point is based on at least 226 trials. In all cases, the performance was significantly above chance level (binomial test, $p < .001$) with an average performance between 100% and 80%. The monkeys' responses in the standard and control trials were similar. All behavioral curves showed typical tuning: If sample and test stimuli were identical, monkeys correctly responded in the majority of the cases (more than 85%). Most of the errors were based on incorrect responses in cases of a nonmatch test display. This occurred most often when the nonmatch trial deviated from the sample stimulus by the minimum numerical value (± 1).

Numerical Distance Effect

To test if and how shapes were associated with analog magnitudes, we compared the monkeys' performance curves with the two hypothetical outcomes. The semantic linking hypothesis predicts tuning curves with shallow shoulders, indicating decreasing error rates with increasing numerical distance (numerical distance effect). In contrast, the tuning curves should have steep flanks according to the shape matching hypothesis; that is, a

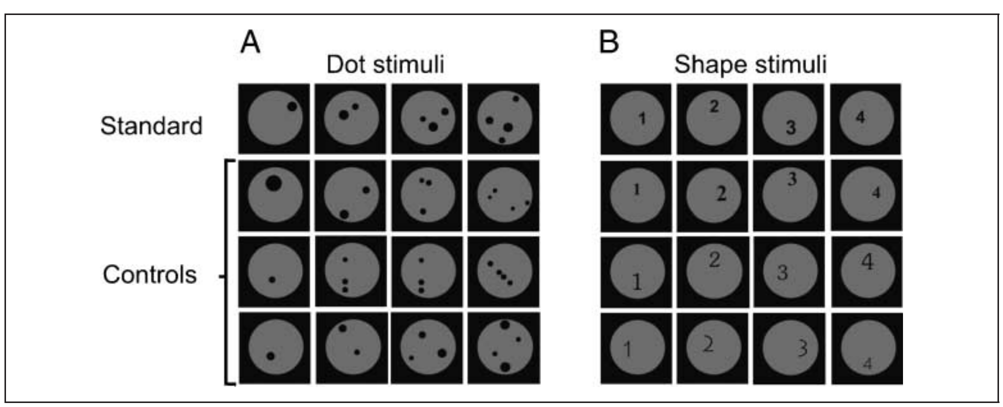

Figure 2. Standard and control stimuli. (A) In the standard dot stimuli, position and size of the dots were randomized from trial to trial (upper row). Additionally, three different control conditions were introduced with constant circumference, configuration, or density for all four numerosities (rows 2 to 4). (B) In the standard shape stimuli, position and size of the shapes were randomized from trial to trial. The font type was Arial (upper row). In the control conditions, the sample shape's font was either Times New Roman, Lithograph Light, or Souvenir (rows 2 to 4).

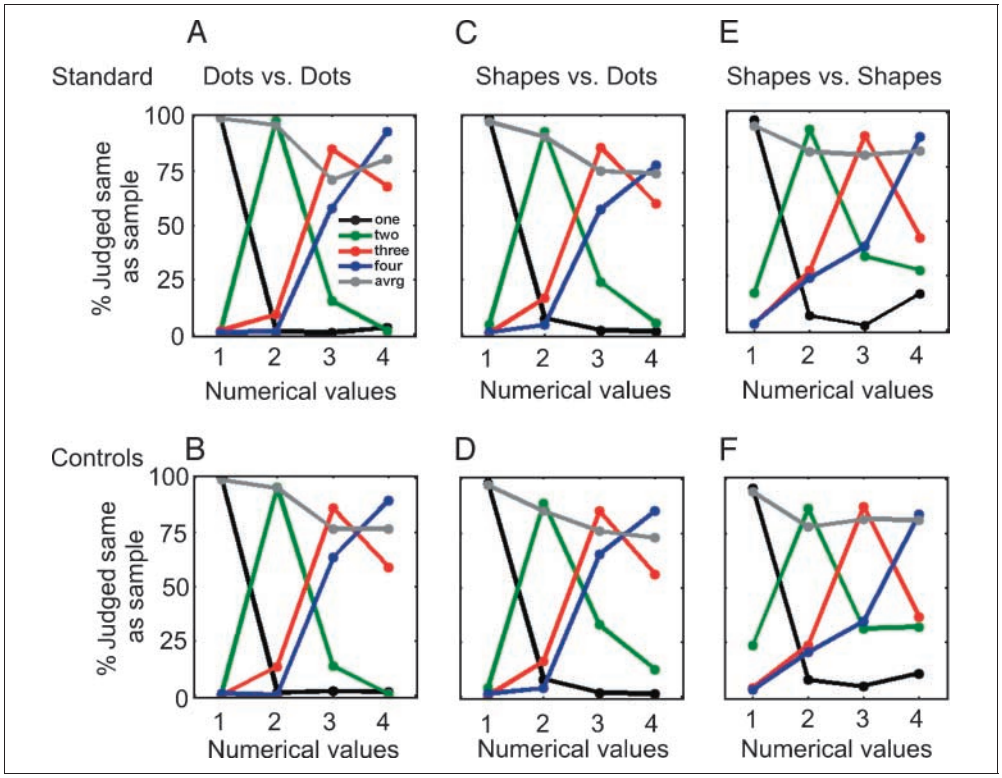

Figure 3. Performance in standard and control trials. The behavioral performance curves indicate whether the monkeys judged the first test stimulus (after the delay) as containing the same numerical value as the sample display (% judged same as sample). Colors represent performance curves for a given sample numerosity (black = numerical value 1; green = numerical value 2; red = numerical value 3; and blue = numerical value 4 has been presented as sample stimulus). A high peak of the curves at the respective sample numerosity (e.g., at the *x*-value 2 for the green curve) indicates good performance, whereas all other points (e.g., at *x*-values 1, 3, and 4 for the green curve) indicate a better performance the lower they are. (A, B) Performance in the dot versus dot protocol in standard (A) and control trials (B), (C, D) in the shape versus dot protocol, and (E, F) in the shape versus shape protocol.

high peak at the correct numerical value and constant error rates for all deviating numerical values.

We found that the monkeys made more errors when the numerical distance between the tested numerosities was small (±1). They confused numerical values less often that were further apart (distance effect; see Figure 3). In order to analyze the behavioral performance of each monkey, we split the data into three datasets. Figure 4 shows the performance for each monkey in a separate panel. Each data point is based on at least 101 trials and represents the monkey's performance for a specific numerical distance between test and sample stimulus. Again, the behavioral tuning curves of all three protocols showed the numerical distance effect: The error rate dropped with increasing numerical distance between the numerosities. The behavioral curves resembled each other across the task protocols even though each monkey showed specific performance characteristics. Monkey B deviated from the monotonically decreasing error rates with increasing numerical distance for the numerical distance of +3 in the shape protocol (Figure 4A). Monkey R showed shallower performance curves for the shape versus shape protocol than for the other two protocols (Figure 4B), whereas for Monkey H the performance curves had the steepest flanks in the shape versus shape protocol (Figure 4C). However, all monkeys made significantly more errors when the numerical distance between the tested numerosities was

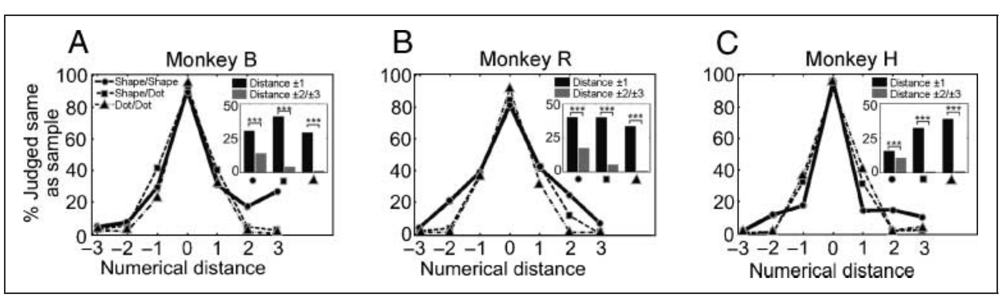

Figure 4. Performance curves show numerical distance effect. (A) Data for Monkey B. Mean behavioral performance curves for the dot versus dot (triangle with dashed–dotted line), the shape versus dot (squares with dashed line), and the shape versus shape (circles with solid line) protocols. Insets depict the error rates for numerical distance ±1 versus the larger distances of ±2 and ±3. (B, C) Data for Monkey R and Monkey H, respectively.

small (±1) as compared to larger numerical distances of ±2 or 3 ($p < .001$, χ^2 test; see insets in Figure 4).

Numerical Size Effect

The semantic linking hypothesis predicts that tuning curves will get broader with increasing numerical values (numerical size effect) for all three protocols alike. Constant widths across numerical values in the shape versus shape protocol would favor the alternative shape matching hypothesis.

We found evidence for the presence of the numerical size effects in all three protocols. For the dot versus dot protocol, the behavioral filter functions became broader with increasing numerosity (see Figure 3) as shown previously (Merten & Nieder, 2008; Nieder & Merten, 2007; Nieder & Miller, 2003). For larger quantities, the two numerosities had to be numerically more distant for performance to reach the level obtained with smaller quantities and closer numerical distance. Less than 10% errors occurred when the monkeys compared three dots with two dots (numerical distance −1). In contrast, the error rate only dropped below the 10% level for sample stimuli consisting of four dots when the test stimulus consisted of two or less dots (minimum numerical distance −2; Figure 3A and B). This effect was also present for the shape versus dot protocol (see Figure 3C and D). Interestingly, a similar effect could be observed in the shape versus shape protocol. The error rate was 25% when the monkeys had to compare sign 3 with sign 2 (numerical distance −1) and only dropped below the 25% level for the sample stimulus 4 when the test stimulus consisted of sign 2 or 1 (minimum numerical distance −2; Figure 3E and F). To quantify this behavior, we fitted a normal distribution (Gaussian) to the measured data. The Gaussian was chosen because it represents the standard symmetric distribution, and thus, allows a comparison of the behavioral functions (Nieder & Miller, 2003). We plotted the data along two scales: a linear scale and a logarithmic scale. As predicted by the numerical size effect, the half-width (σ of the Gaussian fit) of the performance curves increased proportionally for the dot versus dot, and shape versus dot protocol (slope for linear scale for all monkeys >0.2) with numerosity when the data were plotted on a linear scale (Figure 5). The widths of the distributions became constant across numerical values when the data were plotted on a logarithmically compressed scale (slope for log scale for all monkeys <0.03). Most interestingly, these effects were also present for the shape versus shape protocol in two monkeys (Monkey B: slope for linear scale 0.2, slope for log scale 0; Monkey R: slope for linear scale 0.3, slope for log scale 0.07; see Figure 5A and B). Only Monkey H showed constant widths across numerical values for both scales in the shape versus shape protocol (slope for linear scale 0.02, slope for log scale −0.06; see Figure 5C).

Response Latencies

Response latencies have been used previously for the evaluation of the performance of numerical tasks in humans (Moyer & Landauer, 1967). Time was used to evaluate the difficulty of a numerical comparison. Here we tested whether monkeys—similarly to the observations in humans—needed more time to evaluate signs associated with higher numerical values as predicted by the semantic linking hypothesis. Alternatively, the shape matching hypothesis would predict constant reaction times for all shapes.

Figure 6 depicts the response latencies in match trials for each of the three monkeys. The reaction times became

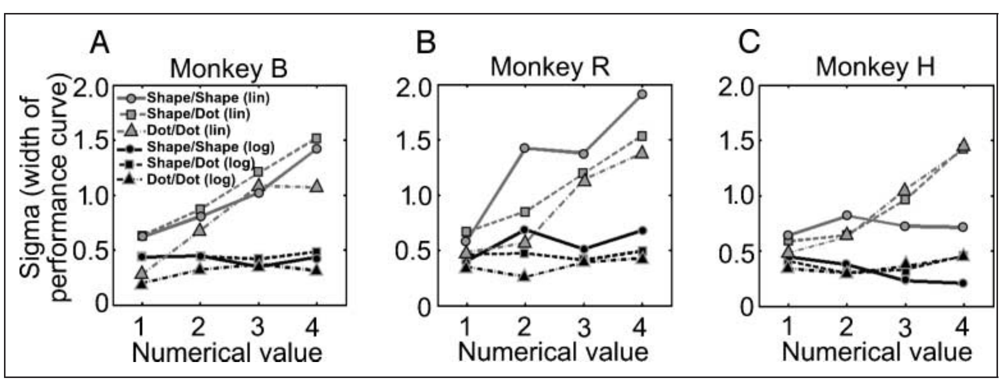

Figure 5. Width of behavioral filter functions reveals the number size effect. (A) Data for Monkey B. The standard deviation (sigma) of the Gaussian fits is plotted against the center of the Gauss function (which is identical to the numerical value of the match stimulus). The values of sigma are derived from the linear (gray line) and logarithmic (black line) compression scheme. Triangles with dashed–dotted line: dot versus dot protocol; squares with dashed line: shape versus dot; and circles with solid line: shape versus shape protocol. (B, C) Data for Monkey R and Monkey H, respectively.

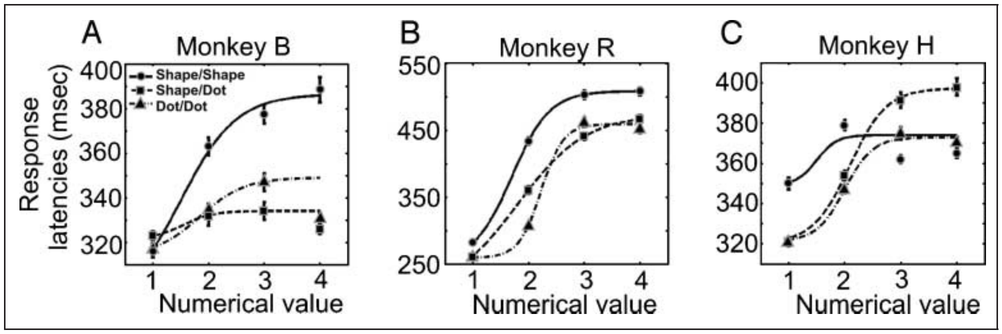

Figure 6. Response latencies. (A) Data for Monkey B. Median reaction times ± *SEM* with sigmoidal fits in the dot versus dot (triangle with dashed–dotted line), shape versus dot (squares with dashed line), and shape versus shape (circles with solid line) protocol. (B, C) Data for Monkey R and H, respectively. Sigmoidal fits are for illustrative purposes only.

significantly longer with increasing set size (ANOVA, $p < .001$). Again, each monkey performed according to its own pace. Monkey B responded faster in the shape versus dot and dot versus dot protocol as compared to the shape versus shape protocol (Figure 6A). Monkey R responded similarly fast in all protocols and showed increasing latencies with increasing numerical values (Figure 6B). Monkey H showed increasing latencies for the dot versus dot and shape versus dot protocol, but the pattern was less clear for the shape versus shape protocol; however, he was fastest for the numerical value 1 when compared with the other numerical values (Figure 6C).

DISCUSSION

Here, we tested monkeys that had learnt to associate signs with numerical values in a shape versus shape protocol. This task could have been solved by a simple shape matching algorithm. However, the performance of the monkeys relied mainly on the numerical values associated with the shapes indicating that these signs were indeed judged according to their assigned analog magnitudes. This semantic imprinting of analog magnitudes onto visual shapes argues for an understanding of the relation of signs and numerical values in monkeys. On a behavioral level, these results complement our previous findings with single-unit recordings (Diester & Nieder, 2007), providing evidence for a putative early precursor (Dehaene, 2005) of the human number symbol knowledge.

Numerical Distance and Size Effect

Despite individual differences between monkeys, we found a common response profile with typical size and distance effects. The monkeys' performance curves resembled each other strongly across protocols (Figure 3). Particularly remarkable was the presence of the distance effect in the shape versus shape protocol because this task could potentially be solved by a simple shape matching algorithm without the need to access associated numerical magnitudes. However, the performance in the shape versus shape protocol did not follow the predictions made by the shape matching hypothesis but rather showed an analog magnitude signature. Remarkably, monkeys did not confuse those shapes which resemble each other more often (like 2 and 3 sharing round components, or 1 and 4 sharing straight lines), ruling out the possibility that the effects are just reflecting covariant like stimulus similarities. Further evidence for the semantic linking hypothesis came from the correlation between the half-width of the performance curves and the numerical values on a linear scale in the dot versus dot and shape versus dot protocol for all three monkeys and in the shape versus shape protocol for two out of three monkeys (Figure 5). This argues for the presence of a symbolic number size effect in monkeys. On a logarithmic scale, no such correlation was present. Because the logarithmically compressed scale is a typical feature of the analog magnitude system (Nieder & Miller, 2003; Fechner, 1860), these findings suggest a transfer of the logarithmic scaling from the magnitude system onto the associated signs. This argues further for the formation of a semantic link between the learnt signs and analog magnitudes. Finally, we found a systematic increase of response latencies with numerical values in all three protocols (Figure 6). We speculate that this effect is a reflection of the numerical size effect for analog magnitude judgments. Even in match trials (that were exclusively analyzed in Figure 6), the animals had to discriminate the match numerical value from putative nonmatch values (that appeared with equal probability in the nonmatch trials). At a given numerical distance, this discrimination is harder, and thus, takes more time with increasing numerical values. The increase in response latencies in the shape–shape protocol may thus constitute a reflection of the numerical size effect characteristic for analog magnitude representations. A similar effect has previously been observed in humans (Moyer & Landauer, 1967) and has been implicated in the mental transformation of number symbols into analog magnitudes. Our results argue for a similar transformation in monkeys.

Individual Differences between Monkeys

On average, we found evidence for the numerical symbolic size and distance effect in the behavioral data of our monkeys. However, our monkeys differed with respect to details in performance and reaction times. Monkey B had a bias to respond to the Shape 4 when Shape 1 was the sample stimulus. This resulted in a higher error rate for the numerical distance +3 as compared to the distance +2 (Figure 4A). Furthermore, Monkey B showed a reduction of response time for four dots compared to three dots (Figure 6A), which is probably due to the end-effect (Mandler & Shebo, 1982). Monkey B and Monkey R both responded slower in the shape versus shape protocol as compared to the other two protocols (Figure 4A and B). This might have been due to the extensive training with the first two protocols, whereas the shape versus shape protocol was introduced at once without further training. Monkey R's performance curves for the shape versus shape protocol were less steep than in the other two protocols (Figure 4B), whereas Monkey H showed the steepest flanks in his performance curve in the shape versus shape protocol (Figure 4C). Hence, Monkey R provided strong evidence for the distance effect in the shape versus shape protocol, whereas this effect in Monkey H was less pronounced. Finally, the half-width of Monkey B's and R's performance curves increased with numerical value in the shape versus shape protocol arguing for a size effect, whereas they stayed constant in Monkey H (Figure 5). Taken together, the performance of Monkey B and Monkey R provided stronger evidence for a semantic imprint of analog magnitudes onto the visual shapes than the performance of Monkey H. Monkey H might have even tried to solve the task without semantic associations. We suspect that the differences in behavioral performance reflect different learning strategies adopted by individual monkeys.

Differences to Earlier Studies

Previous studies have shown that animals can be trained to assign numerical values to visual shapes (Xia et al., 2001; Boysen, Bernston, Hannan, & Cacioppo, 1996; Washburn, 1994; Washburn & Rumbaugh, 1991; Boysen & Berntson, 1989). It has also been demonstrated that animals can learn ordered sequences of shapes (Inoue & Matsuzawa, 2007; Kawai & Matsuzawa, 2000; Boysen, Berntson, Shreyer, & Quigley, 1993; D'Amato & Colombo, 1990). Three of these studies are of particular importance for the data presented here.

Xia et al. (2001) investigated the ability of birds to link letters with numerosities. They trained pigeons to associate letters with specific set sizes. In case of an error, the birds mainly chose a visual sign that neighbored the correct shape in numerical value, thus displaying the numerical distance effect. In the current study with monkeys, we expanded the task range by a condition in which visual shapes had to be discriminated from each other in a shape versus shape design. This allowed to test whether the psychophysical laws apply in situations that do not require an association with numerical values.

In a study with capuchin monkeys (D'Amato & Colombo, 1990), the symbolic distance effect was investigated with ordered sequences of stimulus pairs. The authors addressed the ordinal aspect of the symbolic distance effect. They trained capuchin monkeys with stimulus pairs drawn out of a sequence of five stimuli. The monkeys were required to choose the stimulus that preceded the other in the overall sequence. In contrast, we investigated cardinal aspects and tested whether the inherent order of numerical quantities was transferred to the associated signs. Importantly, the stimulus order had never been taught to the monkeys and the monkeys were not required to order stimuli but simply to discriminate them. Hence, the monkeys did not learn separate rules for the signs. Consequently, all psychophysical effects observed in our studies are based on a semantic transfer of analog magnitude characteristics to signs.

Washburn and Rumbaugh (1991) trained monkeys to associate Arabic numerals with specific amounts of food pellets. In a follow-up experiment, these monkeys were trained to select the larger of two arrays of items on a computer screen (Washburn, 1994). When the authors substituted the items by the previously learnt Arabic numerals, they observed Stroop-like effects in trials in which set size and Arabic numerals gave contradictory cues; that is, the monkeys made more errors and needed more time if the larger array consisted of numerals conveying the smaller numerical value (e.g., seven 1s vs. six 2s). This effect grew stronger with increasing numerical distance between values of the Arabic numerals, providing evidence for a numerical distance effect. We extended these findings to another context. In contrast to the smaller–larger discrimination in the relative-numerosity task used by Washburn, we trained our monkeys to discriminate the absolute magnitudes in a delayed match-to-sample design. This approach provided full-performance filter functions. With these filter functions, we could address the numerical size and distance effect in more detail and even investigate the potential coding scale. As an important refinement compared to the studies by Washburn and coworkers, our animals learned to associate numerals with quantities without getting differentially rewarded for numeral values. This avoids one of the criticisms of earlier tests, namely, that monkeys could use hedonic value in making numerical judgments.

Evidence for a Precursor of Symbolic Understanding

Here, we report the presence of the number size and distance effect in monkeys. We observed these effects in tasks with arrays of dots as well as with numerical signs. These effects can be found in humans dealing with number symbols and nonsymbolic numerical formats (Koechlin et al., 1999; Dehaene et al., 1990; Buckley & Gillman, 1974;

Moyer & Landauer, 1967). In humans, they have been explained by a convergence of analog magnitudes and number symbols onto a common format of representation (Dehaene, 1992). Our results argue for a similar convergence of analog magnitudes and numerical signs in monkeys. This hypothesis is further supported by similarities between imaging studies in humans and single-cell recordings in monkeys. Imaging studies have shown that numerosities are encoded in human PFC and intraparietal sulcus in a notation-independent way, suggesting an abstract coding of approximate numerosity common to dots, digits, and number words (Piazza et al., 2007). In previous single-cell recordings, we found neurons in monkey PFC that encoded numerosities and the assigned visual shapes alike (Diester & Nieder, 2007). Such association neurons were absent in the intraparietal sulcus in the monkey. The strong involvement of PFC indicated that the shape–numerosity association was not automatically executed in the monkey brain but constituted a cognitively highly demanding task. Similar activation patterns were observed in functional magnetic resonance imaging studies with human children. In comparison to adults, preschoolers lacking proficiency with number symbols show more PFC activity when dealing with symbolic cardinalities (Kaufmann et al., 2006; Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Rivera, Reiss, Eckert, & Menon, 2005). Only with age and proficiency did the activation seem to shift to parietal areas. The putatively homolog structures involved in the initial mapping of visual shapes onto numerosities in humans and monkeys, namely, PFC, suggest an evolutionary early precursor of the symbolic number representation in monkeys.

An animal endowed with the number symbol precursor can represent relations that are based on similarities or fixed temporal or spatial correlations between object and sign. The human understanding of symbols, however, is based on associations of relations between numbers and relations between empirical objects. This has been called ''dependent linking'' and cannot be established without language (Wiese, 2003). Hence, the language facility only, enables humans to make the step from the context-dependent representations to a generalized concept of number (Peirce, 1931). Based on these considerations, our data suggest that monkeys were able to understand the numerical meaning of the visual signs in the specific context in which we trained them; however, it remains an open question to what extent they can grasp the symbolic reference system behind the signs.

Here, we showed that numerical values imprint their analog magnitudes characteristics onto the associated signs in monkeys in situations in which no association between shapes and numerical values was needed. The imprinting argues for a semantic understanding of the relation between visual signs and numerical values which goes beyond a simple association. The performance of our monkeys resembles the human way to handle number symbols which is characterized by an automatical translation of symbols into analog magnitudes. The most parsimonious explanation for the similarities across species is an analog mechanism in monkeys judging numerical signs and humans dealing with number symbols. Hence, our findings provide evidence for an evolutionary early nonverbal precursor of the human symbol knowledge in monkeys. Future experiments should test the monkeys' capability to transfer the numerical signs into new contexts, for instance, a switch from absolute numerosity discriminations to a relative-numerosity task in a transfer trial style. This would approach the central feature of symbols—their universal applicability—and would allow for defining the exact limits of the monkeys' understanding of signs.

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