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Representation of magnitude in rhesus monkeys (*Macaca mulatta*)

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Representation of magnitude in rhesus monkeys (*Macaca mulatta*)

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B.A. Macalester College, 2011

Advisor: Robert R. Hampton, Ph.D.

An abstract of
A thesis submitted to the Faculty of the James T. Laney School of Graduate Studies of Emory University in partial fulfillment of the requirements for the degree of Master of Arts in Psychology
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Abstract

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By Rachel F. L. Diamond

Humans mentally represent numbers along a number line, and the direction of this representation is culturally influenced (Dehaene et al., 1993). Evidence for spatial organization of magnitude has been demonstrated in humans using the Spatial Numerical Association of Response Codes, or SNARC, task. Evidence from list learning tasks with monkeys has suggested a spatial organization of ordinal information by providing evidence for distance effects, and similar cognitive mechanisms might control both ordinal information and magnitude information. While the distance effect has been demonstrated in monkeys, the SNARC paradigm has not been directly evaluated. To the extent that spatial organization of magnitude information is an ancestral primate trait, monkeys, despite lacking cultural tools such as number lines, should show similar evidence of spatial organization. Because the direction of putative spatial representations cannot be known *a priori*, in Experiment 1 we trained monkeys on touchscreen computers to associate “small” magnitude items with a rightward response and “large” magnitude items with a leftward response to establish a right-left orientation of representational space. In Experiment 2, we evaluated whether monkeys use a spatial organization of magnitude information when processing numerosity by presenting them with a SNARC task. Monkeys learned to associate magnitude with left-right spatial locations, and demonstrated a SNARC effect congruent with the direction of the spatial training in Experiment 1. However, the SNARC effect attenuated after extended testing. Thus, results indicate that monkeys represent information spatially, but additional testing is required to determine the robustness of spatial representation of magnitude.

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Table of Contents

Figures and Tables

Introduction

A spatial representation is a particularly efficient mechanism for mentally organizing information, and it may underlie numerical and mathematical cognition (Brannon & Terrace, 2002; Dehaene, Bossini, & Giraux, 1993; Göbel, Shaki, & Fischer, 2011). Research with nonhuman animals has hinted that ordered information, such as memory for lists and transitive inference, may be represented spatially (Gazes, Chee, & Hampton, 2012; MacLean, Merritt, & Brannon, 2008; Templer & Hampton, 2012; Terrace & McGonigle, 1994; Treichler & Van Tilburg, 1996). However, the evidence for said spatial representation is based on tasks not designed to specifically test how the information is organized cognitively. A direct test of the spatial representation of magnitude or order in nonhuman primates is therefore required.

Humans represent numerical information along a mental number line (Dehaene et al., 1993). For example, people who read and write from left–to-right respond more quickly to small magnitude items with a leftward response and large items with a rightward response. This is called the Spatial-Numerical Association of Response Codes, or SNARC, effect (Dehaene et al., 1993). The classic SNARC task, which has now become a primary test for spatial representation of number, requires participants to respond to the numerals 0-9 with their right hand if the number is odd and with their left hand if the number is even. Within a session participants switch which response key corresponds to odd and even so that they respond on both sides of space for each numeral. Participants are faster to respond on the left side than the right side when presented with small numbers and faster on the right side than the left side when presented with large numbers. Humans implicitly process the magnitude of numerals even when the task does not require it, and the SNARC task suggests they do so using a spatial representation. This paradigm has become a standard by which spatial representation of magnitude and number are measured (Dehaene et al., 1993; Fischer, 2003; Holmes & Lourenco, 2011, 2012, 2013; Shaki & Fischer, 2008; Shaki, Fischer, & Petrusic, 2009; Wood, Willmes, Nuerk, & Fischer, 2008).

Researchers have also concluded that the SNARC effect is found across domains. The SNARC task has been modified to test spatial representations of dimensions of magnitude beyond the presentation of Arabic numerals (Fias, Brysbaert, Geypens, & D'Ydewalle, 1996; Holmes & Lourenco, 2011, 2013; Nuerk, Wood, & Willmes, 2005; Patro & Haman, 2011; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006). Results similar to those found for Arabic numerals have been found for participants that respond to numerals read aloud (Nuerk et al., 2005), pitch (Rusconi et al., 2006), non Arabic-numeral numerosities (Nuerk et al., 2005; Patro & Haman, 2011), and emotional magnitude (Holmes & Lourenco, 2011). Holmes and Lourenco (2013) found that even physical magnitudes, such as weight, can affect SNARC. They found that the numeral based SNARC effect was attenuated by adding a heavy weight to the left arm, an incongruent condition to the left-to-right organization of the mental number line, while adding a heavier weight to the right arm increased the effect. Experiencing a heavy weight on the side of space that participants, under normal conditions, associate with “small” affects that representation and causes participants to respond equally quickly to both sides of space. Because consistent results with adult humans for the SNARC task have been found across many magnitude domains, not just with numerals, this representation system may come online early, and therefore, similar results may also be found in children and nonhuman primates who may have a magnitude representation system but who do not have experience with Arabic numerals.

Human infants appear to possess an early non-verbal, non-symbolic general representation of magnitude (Lourenco & Longo, 2010). Infants look longer at stimuli that have previously been associated with a magnitude, i.e. “small” or “large,” that are presented later in an incongruent condition suggesting that they had a representation of magnitude. Most importantly, this looking time effect is consistent across magnitude dimensions, which suggests that preverbal infants have a general magnitude representation. Additionally, rhesus monkeys can use an approximate number system to add numerosities, and their performance follows patterns similar to those found in humans using an approximate number system (Brannon & Terrace, 2002; Cantlon & Brannon, 2007a). These studies suggest that there may be a general magnitude system shared by humans and nonhuman primates that is present early in human development.

Although Lourenco and Longo (2010) provided evidence for a general magnitude system in preverbal infants, they did not address how or if that system is organized in space. In order to test for the spatial representation of magnitude in young children, Patro and Haman (2011) modified the SNARC task for use in pre-counting preschoolers by using stimuli with variable numbers of shapes rather than Arabic numerals. When asked to “point to more” or “point to less,” pre-counting children were faster to respond to “more” when it was on the right side of space and “less” when it was on the left side of space, consistent with the SNARC effect shown by adults (Patro & Haman, 2011).

While there is evidence supporting an early spatial representation of magnitude in humans, the effect becomes more pronounced with age (Wood et al., 2008) which could be a result of cultural experience influencing the representation. Therefore, a number of studies also have investigated what role language and culture play in one's spatial representation of magnitude and whether the left to right organization illustrated by SNARC is primarily an artifact of training and instruction (Dehaene et al., 1993; Göbel et al., 2011; Hung, Hung, Tzeng, & Wu, 2008; Ito & Hatta, 2004; Shaki & Fischer, 2008; Shaki et al., 2009; Zebian, 2005). Reading and counting direction play a role in modifying the direction of the spatial representations of magnitude. Shaki et al. (2009) compared Canadians, who read and count from left to right, to Palestinians, who read and count from right to left. They found a strong SNARC effect for both Canadians and Palestinians, but in opposite directions; Canadians showed the typical left-to-right SNARC effect, while Palestinians showed a right-to-left SNARC effect. Similarly, tests of bilingual Russian and Hebrew speakers reveal a language specific priming effect on the direction of the SNARC effect (Shaki & Fischer, 2008). Participants who read a passage in Russian (from left to right) before the task, show a strong left-to-right SNARC effect, but participants show an attenuated effect after reading a passage in Hebrew (from right to left). Additional evidence suggesting that the representation of magnitude is flexible is found by priming participants to think about numbers as on a clock face rather than on a ruler (Bächtold, Baumüller, & Brugger, 1998). Participants that show a left-to right representation when thinking about a ruler show a right-to-left representation when thinking of numbers on a clock face, with small numbers on the right and large numbers on the left. These studies indicate that the direction of the SNARC effect is greatly influenced by prior experience and may even be flexible within individuals. These studies suggest that without cultural training it is difficult to predict the direction of the spatial organization underlying the magnitude representation.

The SNARC paradigm is based on humans' automatic processing of numerical magnitude when presented with numerals or non-numeric numerosities. Fortunately, numerical value is a salient feature of stimuli for rhesus monkeys (Cantlon & Brannon, 2007b). Cantlon and Brannon (2007b) found that monkeys attended to number even when they did not have to. Additionally, monkeys attending to numbers show similar patterns of responding as those found in humans, such as Weber's Law (Beran, 2007; Jordan & Brannon, 2006). Using these magnitude comparison abilities, we designed a SNARC task for monkeys to test whether nonhuman primates, with no prior exposure to numerical cultural training, have an innate spatial organization mechanism.

Monkeys do not experience cultural training and therefore represent a unique study population in which to test the mechanisms underlying previous results that indicate a ubiquitous spatial organization of magnitude. If monkeys spatially represent magnitudes, they should have shorter response latencies on either the left or right sides of space when presented with a small numerosity and should show shorter response latencies on the opposite side of space when presented with large numerosities, similar to result patterns found in human SNARC tasks.

Experiment 1: Magnitude Training

To directly test whether monkeys spatially organize magnitude, we used a modified SNARC paradigm. However, monkeys do not experience the left-right training associated with learning to read and count along a number line. Therefore, in order to normalize the direction of the SNARC effect, we trained monkeys to associate small numbers with the right side of space and large numbers with the left side of space. To facilitate generalization of the magnitude-space mapping, monkeys were trained three magnitude dimensions: size, numerosity, and line length.

Subjects

Subjects were 6 male rhesus macaques (*Macaca mulatta*) aged approximately five years at the start of testing. Monkeys were pair housed and kept on a 12:12 light:dark cycle. Monkeys had ad libitum access to water and received full rations each day at the end of testing. Subjects had prior experience with cognitive testing using touchscreen computers, but did not have experience classifying magnitudes.

Apparatus

Monkeys were tested in their home cages 6 days a week for 7 hours a day. Portable touchscreen computer systems were attached to the front of each monkey’s home cage. This test system consisted of a 15-in. color LCD touch-screen (3M, St. Paul, MN) running at a resolution of 1024x768 pixels, generic stereo speakers, and two automatic food dispensers (Med Associates Inc., St Albans, VT) that dispensed food rewards into wells located below the screen. Food rewards were nutritionally balanced banana or fruity flavored pellets (Bio-Serv, Frenchtown, NJ). All choices required the monkeys to touch the screen twice (FR2) to avoid registering spurious touches as responses.

Procedures

Size Discrimination

During this initial training phase, monkeys were rewarded for associating large and small magnitudes with response keys on the left and right sides of space (Fig. 1). To begin a trial, monkeys touched a green square in the bottom center of the screen. After the monkey touched the start square, either a “large” (175x175 pixels) or “small” (50x50 pixels) magnitude stimulus would appear in one of four quadrants around the top center of the screen. First monkeys were only presented with a circle of the small or large magnitude. After reaching criterion on the circle alone, monkeys were presented with one of nine different shapes, including clipart images, of the same small or large area as the circle. When the monkey touched the sample stimulus, two identical choice stimuli (200x100 pixels) would appear on the bottom right and bottom left corners of the screen (Fig. 1). The monkey was rewarded for touching the bottom left key when presented with a “large” magnitude stimulus and the bottom right key when presented with a “small” magnitude stimulus (Fig. 1). Trials were counterbalanced such that subjects had the opportunity to respond correctly to the left and right sides equally often, saw the sample in each of the four quadrants equal numbers of times, and saw each sample stimulus an equal number of times. Correct responses were rewarded with auditory reinforcement, on 80% of the trials with a food pellet, and followed by a 3 s ITI. Incorrect responses were followed by negative auditory feedback and a 5 s timeout during which time the screen was black. If the monkey responded incorrectly, correction procedures were initiated such that the exact same trial would be presented a second time with the same reinforcement contingencies. If a second incorrect response was made, the trial was

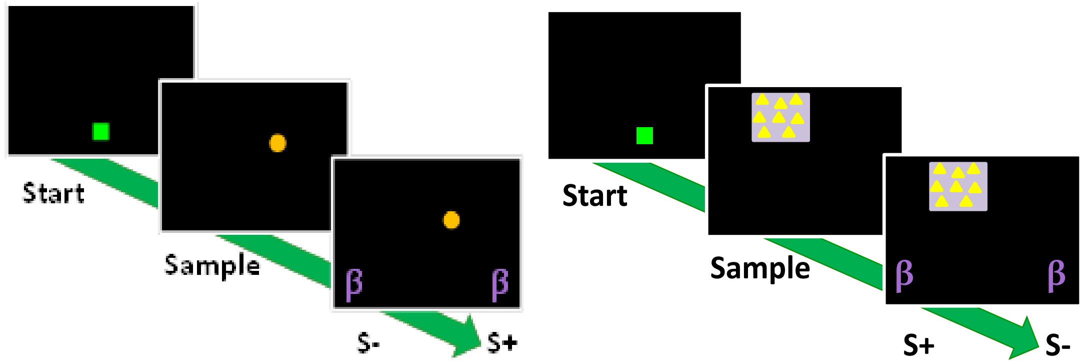

Figure 1. Example discriminations of size and numerosity (left and right, respectively). Monkeys were rewarded for touching the left response key (S+) when the sample was large (right) and the right response key (S-) when the sample was small (left).

presented once again, but with only the correct answer present. This procedure was intended to discourage side biases. Monkeys were trained on this discrimination until they were correct on 90% of the trials in a 288 trial session.

Numerosity Discrimination

After they reached criterion on the size discriminations, monkeys were trained to make numerical discriminations using an identical procedure. Instead of different sized circles, magnitude stimuli consisted of a consistently sized square (175x175 pixels), filled with two, i.e. *small*, or eight, i.e. *large*, shapes (Fig. 1). Within a trial, these shapes could be triangles, squares, hexagons, or octagons, and they were blue, red, green, and yellow. The area of each individual shape was the same for all numerosities and shapes (surface area of 400 pixels). As in the size discrimination, monkeys were rewarded for touching the choice on the right for the small stimulus and the choice on the left for the large stimulus. Errors initiated the same correction procedure, and criterion was set at 90% correct within one 256 trial session before moving on to line discriminations. Trials were counterbalanced such that they responded to the left and right equally often, saw the sample in each of the four quadrants equal numbers of times, saw each shape an equal number of times, and saw each numerosity an equal number of times.

Length Discrimination

After meeting criterion on the numerosity discrimination, monkeys were trained to make length discriminations, following the same procedure as the previous discriminations. Monkeys discriminated long white lines (150 pixels) from short lines (50 pixels). Lines were presented horizontally or vertically, again in one of the four presentation locations around the top center of the screen. Correction procedures were in place, and again the monkeys had to reach 90% criterion in a 256-trial session.

All Discriminations Intermixed

Following individual discrimination training, monkeys received sessions with all discrimination types intermixed. There were 64 trials of each discrimination type per session, for a total of 192 trials per session. Again, correction procedures were in place and monkeys had to reach 90% correct overall and at least 85% correct for each discrimination type separately within an intermixed session.

Data Analyses

Each monkey’s sessions to criterion for each discrimination type were totaled. A repeated-measures ANOVA was run comparing the amount of training required for each discrimination type.

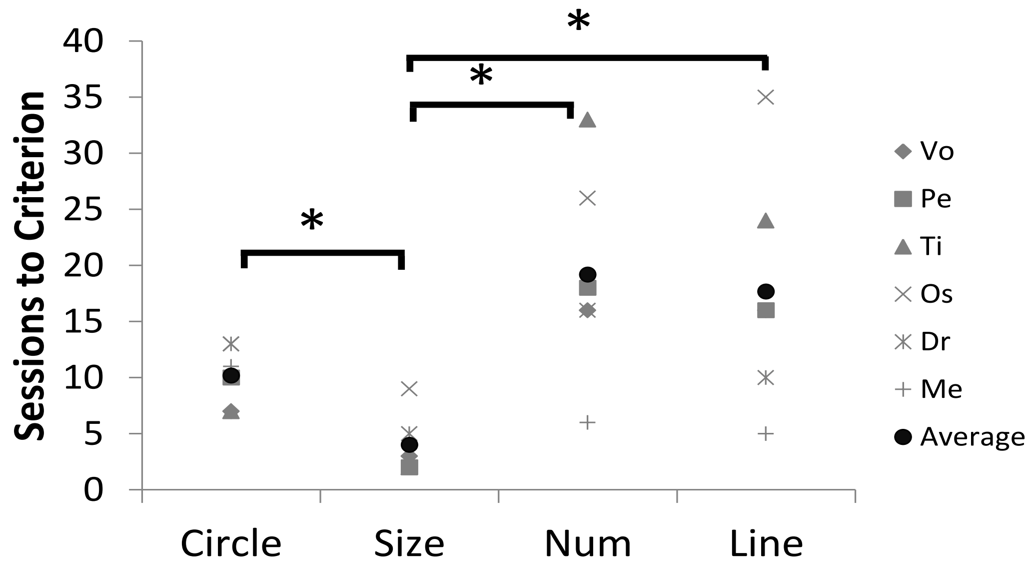

Figure 2. Sessions to criteria across discrimination types. Monkeys were faster to reach criterion when moving from circle size discrimination to general size discrimination, but this did not generalize for number or line length discriminations.

Results and Discussion

All 6 monkeys met the criterion of 90% correct for all discrimination types. In the initial circle size discrimination, they required an average of 10.17 $\pm$ 2.70 sessions to reach criterion (Fig. 2). Their sessions to criterion for each dimension were as follows: general size training (M=4, SD=2.68), numerosity training (M=19.167, SD=9.3), and line training (M=17.67, SD=10.63). When all three discrimination types were combined, monkeys reached criterion in an average of 13.5 $\pm$ 15.33 sessions. Monkeys reached criterion for the different discrimination tasks at different rates (Geisser-Greenhouse corrected $F(1.42, 7.12) = 8.09$, $p = 0.019$). Monkeys generalized from the circle size discrimination to the general shapes discrimination ($t(5) = 7.4$, $p = .001$), and the shape discrimination was significantly different from both the number and line discriminations ($t(5) = 4.03$, $p = .01$, and $t(5) = 3.6$, $p = .02$). The sessions to criterion for the other dimensions were not statistically different from each other (Fig. 2). The training across dimensions gave monkeys extensive experience associating magnitude with space.

If the magnitude and space mapping training successfully modeled the directional cultural training that humans experience with reading and counting, monkeys should show a SNARC effect in a direction consistent with their training. Because monkeys were trained to associate small items with the left side of space and large items with the right side of space, if monkeys spatially represent magnitudes and this training affected that representation, monkeys might be faster with a rightward response to small items and a leftward response to large items.

Experiment 2: SNARC Test

In Experiment 2, we developed a SNARC task to test whether monkeys showed a spatial organization of magnitude. In the human parity judgment (odd/even) SNARC task, participants are asked to categorize a number; they are not required to process the magnitude of that number. And yet, participants do process the magnitude of the number, and we see reaction times differ according to numerical magnitude and space mapping. To model the implicit processing of numerosity underlying the human SNARC task, we asked monkeys to categorize items according to a feature other than numerosity while still presenting items of different numerosities. If monkeys respond more quickly to small items with a rightward response and to large items with a leftward response, this will suggest a horizontal spatial organization for magnitude information and implicit processing of numerosity by the monkeys.

Subjects and Apparatus

Subjects and apparatus were the same as in Experiment 1.

Procedure

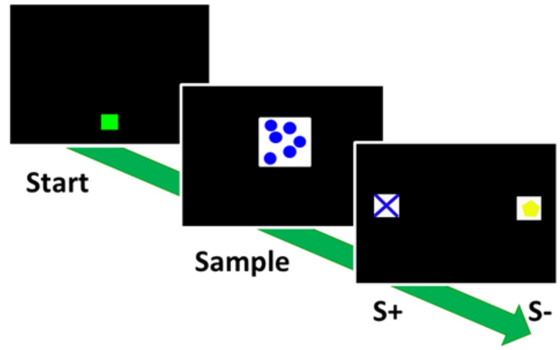

Figure 3. SNARC-like color matching trial. Monkeys were rewarded for touching the blue choice X stimulus when the sample dots were blue and the yellow hexagon when the sample was yellow. The number of dots varied between 1 and 10 with each numerosity being presented equally.

Trials began with a green start square presented in the bottom center of the touchscreen. A white square (300x300 pixels) then appeared in the center of the screen, containing between one and 10 blue or yellow colored dots. Each numerosity was presented equally often, and all dots had the same surface area (1590.43 pixels^2). All dots on a given trial were the same color, and blue and yellow dot trials appeared equally often, counterbalanced such that the same color was never the sample color more than 4 times in a row (Fig. 3). After touching the white square, it disappeared and two choice symbols appeared to the right and left sides. To obtain a reward, monkeys had to select the choice stimulus that matched the color of the dots presented in the sample. The correct response was on the left and right sides equally often. No correction procedures were used. Monkeys were reinforced in the same manner described in Experiment 1. Monkeys were trained until they reached 85% accuracy in a single 160 trial session.

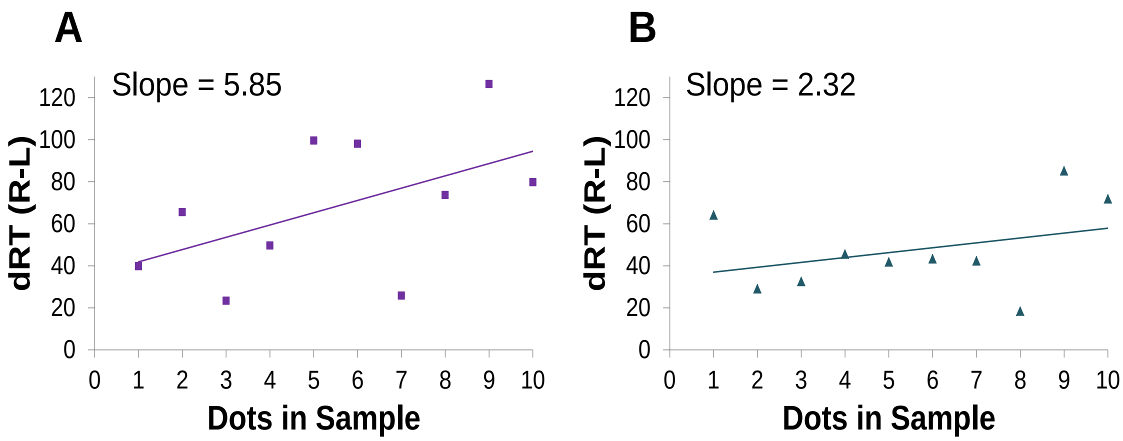

Figure 4. Average response time differences first 4,000 trials (*A*) and last 4,000 trials (*B*). RT Right-RT Left for each numerosity was averaged across each monkey. The slopes for the first 4,000 trials (*A*) were significantly different from 0, while the slopes for the last 4,000 trials (*B*) were not. They did not differ significantly from each other.

Data Analyses

Response times were collected for each choice. Median response latencies for all correct responses when the choice stimulus was on the left and right sides of the screen were calculated separately for sample numerosities 1-10. Difference in response times between rightward and leftward responses (R-L) were then determined for each numerosity. For each monkey, the slope of these difference scores was calculated. These slopes were then used to determine whether there was a group difference in the speed with which the monkey responded to small numbers on the left and large numbers on the right. In addition to an overall slope, data were binned by the first 4,000 responses after criterion and the last 4,000 response after criterion to compare their response time patterns at the beginning and at the end of testing.

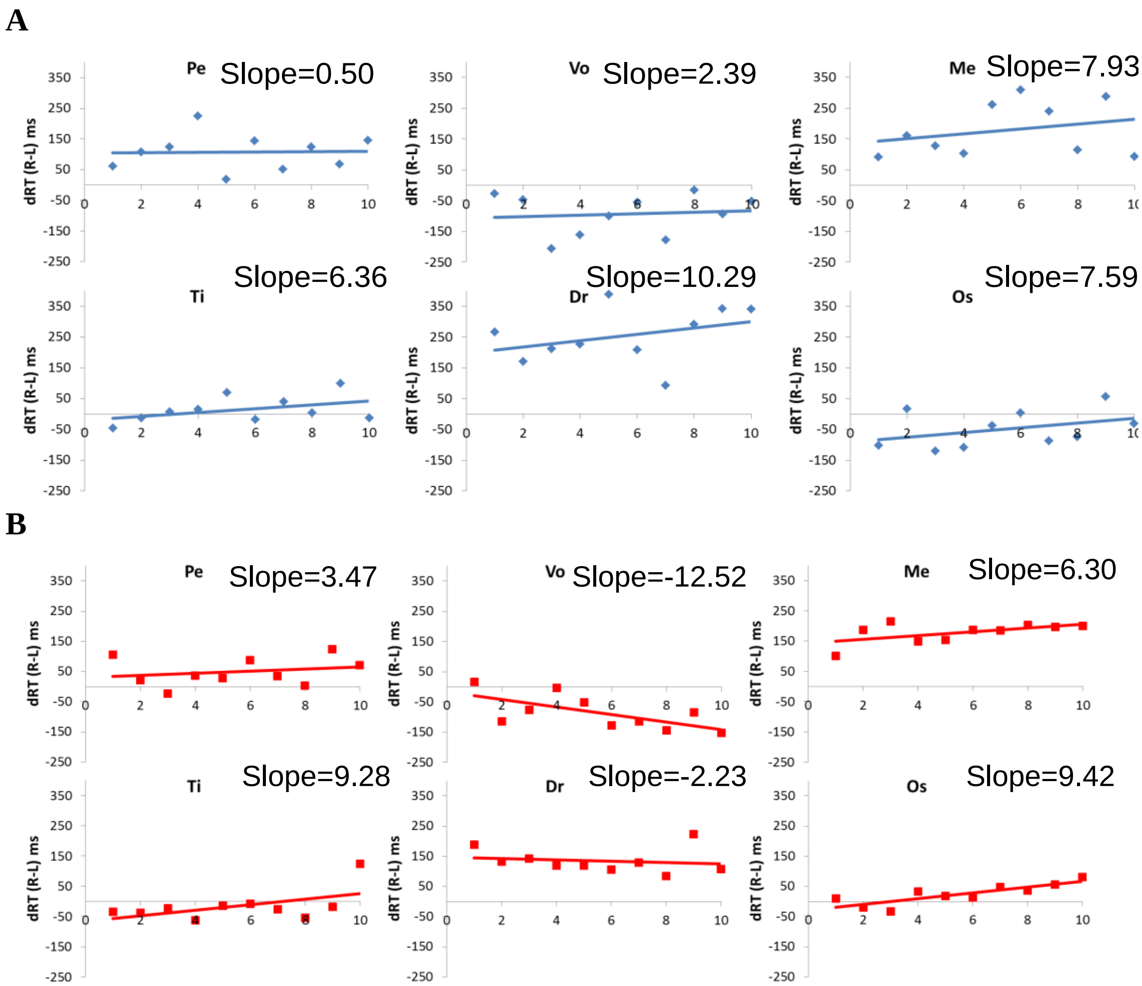

Figure 5. Individual monkey slopes for the first and last 4,000 trials after criterion. Slopes for the response time difference (R-L) at each numerosity for each monkey are shown for the first 4,000 trials in blue (A) and the last 4,000 trials in red (B).

Results and Discussion

Monkeys showed a SNARC effect in the first 4,000 trials after criterion. Slopes differed significantly from 0 (Fig. 4A; $t(5) = 3.89$, $p = 0.01$,), and this was in the direction congruent with the training in Experiment 1. Monkeys met the criterion of 85% correct in an average of 14.17 $\pm$5.88 sessions. After reaching criterion, monkeys ran at least 11,800 trials. Slopes based on response latencies from the whole dataset did not differ significantly from 0 ($t(5)=1.43$, $p=0.21$). However, the data seemed to be trending in a positive direction, and the monkeys had run many more trials than the 204 trials run in the original SNARC task (Dehaene et al., 1993). We binned the data so that we were able to compare early trials to late trials to see whether the effect changed over time. We found that this effect attenuated with extensive training; the slopes of the response latency difference scores did not show a statistically-significant SNARC slope in the final 4,000 trials (one sample t-test: t(5) = 0.67, *p* = 0.53). In the first 4,000 trials, 5 out of 6 monkeys produced slopes in the positive direction, with one monkey producing a slope very close to 0 (Fig. 5A). In the last 4,000 trials the average slope remained positive (Fig. 4B), but the magnitude of the positive slopes did not increase while two monkeys even started to show negative slopes (Fig. 5B, for raw data breakdowns see Appendix). The slopes for the first and last 4,000 trial blocks were not statistically different from each other (t(5)=1.067, *p*=.33, Fig. 4, *B*). It is possible, that continued testing would lead to a significant difference between these groups.

There are several possible explanations for the attenuation of this effect with prolonged testing. One possibility is that some monkeys stopped attending to numerosity. They may have learned to ignore the information not relevant for task completion. Monkeys do not have extensive number and math training that might make them more likely to continue to implicitly process the magnitude presented as humans do. Humans have extensive experience outside of the experimental setting processing numerosity, while monkeys do not. It is

Average Proportion		
Num.	**Left**	**Right**
1	0.48	0.52
2	0.48	0.52
3	0.55	0.45
4	0.53	0.47
5	0.46	0.54
6	0.48	0.52
7	0.50	0.50
8	0.48	0.53
9	0.38	0.62
10	0.45	0.55

Table 1. Average proportion choices to each side. The average proportion of 6 monkeys choices to each response side for the first session of SNARC trials.

possible that the attenuation is a natural feature of a task that doesn't explicitly require numerical processing, and humans do not show said attenuation because of their extensive outside experience. Additionally, humans never run this many trials, so it is unclear whether this attenuation would be found in a similar task run with humans.

Yet, a change in direction doesn't necessarily mean a lack of spatial representation. It is also possible that some monkeys innately organized magnitude information from left to right, so as they moved further from the training in Experiment 1, they started organizing information in their original direction. At a group level, averaging positive and negative slopes results in a less positive slope overall. Therefore, even if several monkeys maintained their right-left spatial organization of magnitude, if their slopes do not increase enough to combat the switch in direction made by two monkeys, we would see this attenuation at the group level.

Another possible explanation for these results is that the positive effect is just a carryover from the training such that the monkeys were already prepared and moving in the direction of the training before they noted the responses and made their final decision. This would make them faster to respond to the left with large numerosities and right with small numerosities because it would be a continuation of the anticipated movement while they would be slower if they had to stop their current movement and switch sides. If monkeys were preemptively moving in a particular direction due to training on the previous task, early in their SNARC task training, they would probably make more choices to the right side when they had seen small numerosities and to the left side after seeing large numerosities. However, in Session 1, monkeys chose at chance levels to both response sides (Table 1). This indicates that monkeys were not immediately transferring the behavior of choosing the left or right side of space learned in Experiment 1 to Experiment 2, and our SNARC results might not be due to interference from the training task.

General Discussion

When the SNARC task has been run with humans, the observed slopes that are significantly different from 0 are interpreted as illustrating people's spatial representation of number and magnitude (Dehaene et al., 1993). These slopes are consistent with the direction of their cultural training (Göbel et al., 2011). Monkeys seem to show a SNARC effect that can be influenced by prior spatial training. These comparative results indicate that the spatial representation mechanism may be ancient, while the specific direction may be shaped by culture.

Monkeys do not naturally experience training in math or reading that could give them a direction specific orientation, but may innately spatially organize magnitudes. Humans do experience extensive training, and therefore many tests of spatial representation are based on a horizontal organizing principle. We therefore sought to give monkeys a consistent organizing direction that we could later test using the SNARC paradigm. In Experiment 1, monkeys were trained to associate large magnitudes with the left side of space and small magnitudes with the right side of space. When presented with a SNARC task in Experiment 2, monkeys showed SNARC slopes in the direction of the training. This is the first evidence with monkeys, based on a two choice categorization task with implicit processing of numerosity that supports the idea that nonhuman primates spatially represent magnitude information. These findings corroborate previous evidence that suggests that monkeys process numerosity similarly to humans (Beran, 2007; Cantlon & Brannon, 2007a, 2007b) while also providing new evidence that that information is spatially organized in a manner analogous to humans.

It is possible that our monkeys represented magnitudes from right to left before the training implemented in Experiment 1, and therefore the results from Experiment 2 did not indicate that the monkeys learned to associate space and magnitude in a novel way. To determine whether this is the case, a next experiment would be to train two groups of monkeys to represent magnitude in opposite directions and then test them on SNARC to see whether the training influenced the effect. Additional questions remain regarding whether this representation is similar to the representation underlying the distance effects found in list learning tasks, and whether similar results would be found for ordinal information.

Spatial representation of magnitude is seen in humans across domains, from pitch (Rusconi et al., 2006) to emotional expression (Holmes & Lourenco, 2011). It seems to be a mechanism that has been coopted for many cognitive tasks, and these early results, in combination from work with young children (Lourenco & Longo, 2010; Patro & Haman, 2011), indicate that this is an ancient mechanism that developed early in our evolutionary history to facilitate cognitive processing.

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Appendix

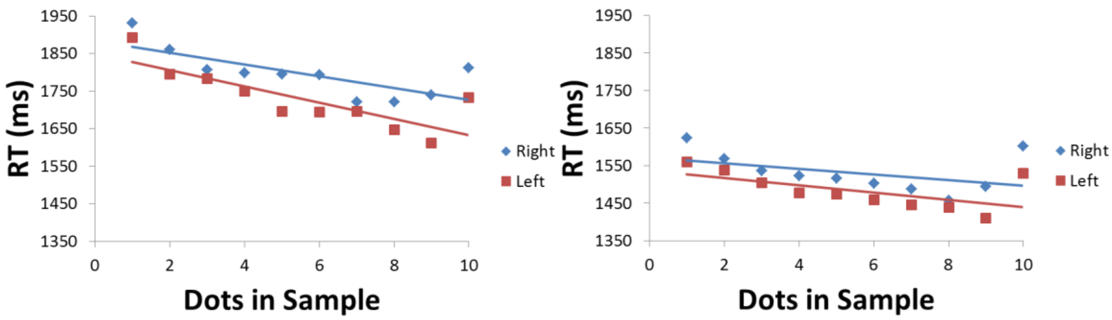

Figure 6. Average raw response times first 4,000 trials (*A*) and last 4,000 trials (*B*). RT Right and RT Left for each numerosity were averaged across each monkey. Monkeys were faster to respond to large numerosities than small numerosities.

When the raw data are analyzed, they show patterns not unlike those found in human studies. Humans respond more quickly on the right side of space than on the left side of space, and show main effects of magnitude (Dehaene et al., 1993). A RMANOVA shows that there is a main effect of numerosity for both the first ($F(9, 45) = 3.918$, $p = 0.001$) and last 4,000 trials after criterion ($F(9, 45) = 7.03$, $p < 0.001$). As numerosity increases, speed increases. The increasing speed associated with larger numerosities could be due to the fact that as numerosity increases, so does the amount of color on the screen. Since the task requires monkeys to match the color, it should be more salient when there is more color presented. There were no main effects of side ($F(1, 5) = 1.53$, $p = 0.27$ and $F(1, 5) = 1.45$, $p = 0.28$ respectively), and no interactions ($F(9, 45) = 1.56$, $p = 0.15$ and $F(9, 45) = 1.28$, $p = 0.28$ respectively). Fias et al. (1996) established the slope analyses as the preferred method for interpreting SNARC results, so the lack of interaction does not change our initial interpretation of the data.