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Jonathan Paul Gulledge
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HEMISPHERIC DIFFERENCES IN NUMERICAL COGNITION:
A COMPARATIVE INVESTIGATION OF HOW PRIMATES PROCESS NUMEROSITY

by

JONATHAN PAUL GULLEDGE

Under the Direction of David A. Washburn

ABSTRACT

Four experiments, using both humans and monkeys as participants, were conducted to investigate the similarities and differences in human and nonhuman primate numerical cognition. In Experiment 1 it was determined that both humans and monkeys display a SNARC effect, with similar symbolic distance effects for both species. In addition, both species were found to respond faster to congruent stimulus pairs. In Experiment 2 both species were found accurately to recognize quantitative stimuli when presented for durations of 150 msec in a divided visual field paradigm. Performance for humans and monkeys for numerals and dot-patterns was almost identical in terms of accuracy and response times. In Experiment 3 participants were required to make relative numerousness judgments in a divided visual field paradigm. Both species responded faster and more accurately to stimuli presented to the right visual field. Species differences appeared, with monkeys performing equally well on both trial types whereas the humans performed better on numeral trials than on dot trials. In Experiment 4 repetitive transcranial magnetic stimulation (rTMS) was combined with the divided

visual field paradigm. Accuracy was significantly disrupted for both species when compared to a no stimulation condition. A facilitation effect was also evident with both species exhibiting significant decreases in response time for all trials. Right-handed participants took longer to respond to stimuli presented to the left visual field. These findings add to the body of knowledge regarding both the similarities and differences of how quantitative stimuli are processed by humans and monkeys.

INDEX WORDS: Numerical Cognition, Numerosity, Transcranial Magnetic Stimulation, rTMS, Numeric Processing, SNARC effect

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by

Jonathan Paul Gulledge

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

in the College of Arts and Sciences

Georgia State University

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2006

HEMISPHERIC DIFFERENCES IN NUMERICAL COGNITION: A COMPARATIVE INVESTIGATION OF HOW PRIMATES PROCESS NUMEROSITY

by

Jonathan Paul Gulledge

Major Professor: David A. Washburn
Committee: Duane M. Rumbaugh
Eric J. Vanman
Claudio C. Cantalupo

Electronic Version Approved:

Office of Graduate Studies
College of Arts and Sciences
Georgia State University
May 2006

Dedication

This dissertation is dedicated to my family, without whom I would not have been able to complete such a daunting task. To Sonya, my wonderful wife, whose gentle spirit makes each day of my life better than the previous one. To Meg, whose charm, beauty, and intellect never ceases to amaze me or make me smile. To Abbie, whose strength, both of body and mind, is a constant source of joy and strength for me. To my mom, who was a constant source of encouragement. To my grandfather who taught me that the right thing to do is never the easy thing to do. To my dad, whose ability to persevere in the face of adversity and loss inspires me onward. To my Savior, for He is a constant source of strength, wisdom, grace, and love.

Acknowledgments

The author wishes to gratefully acknowledge all of those who made completion of this project possible. Without the help and wisdom of those most wonderful and wise this dissertation would never have been completed.

Thank you Claudio for your hard work, and technical expertise. Thank you Eric for your willingness to serve and your thoughtful advice. Thank you Duane for your laughter, support, and encouragement for these many years. Lastly, thank you David for your wisdom, your friendship, and for showing me what it means to be both a Christian and a man of science.

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Hemispheric Differences in Numerical Cognition:

A Comparative Investigation of How Primates Process Numerosity

Whereas an interest in the numerical abilities of animals has existed for centuries, recent research has firmly established the numerical competence of various species of nonhuman primates. Much of the early research involving the numerical competencies of animals was criticized as being a reincarnation of "Clever Hans" (Romanes, 1882, 1883). However, a review of currently available research clearly establishes nonhuman primates as apt pupils for demonstrating various levels of numerical competence (Beran, 2004; Boysen & Berntson, 1986; Brannon & Terrace, 1999; Matsuzawa, 1985; Menzel, 1960; Olthof, Iden & Roberts, 1997; Washburn & Rumbaugh, 1991; for more extensive reviews see Beran, Gulledge & Washburn, 2006; Boysen and Capaldi, 1993; and Davis and Perusse, 1991). The majority of research involving the numerical abilities of nonhuman primates falls into one of four general categories: judgments of numerousness, ordinality, summation, or counting.

Varieties of numerical cognition

Judgments of numerousness typically refer to participants' selections of one group of objects over another on the basis of numerosity. Numerousness judgments can take the form of either absolute or relative judgments. Judgments of absolute numerousness require participants to respond to a fixed number of items from among other choices that differ in quantity. For example, Hicks (1956) suggested that his subjects had a "concept of threeness" when he trained rhesus monkeys to choose cards containing 3 geometric patterns when the alternative cards contained either 1, 2, 4, or 5 geometric-patterns.

Hayes and Nissen (1971) reported that Vicki, a common chimpanzee (Pan troglodytes), was able successfully to complete a match-to-sample version of a relative numerousness task. Vicki was first presented with a sample card containing a small array of dots. Later, she was presented with two cards from which to choose, one of which matched the sample in number of dots. Both the size and placement of dots were randomized across all cards. Vicki was able accurately to match the sample for quantities of three dots when the choices given to her were between sets of three and four. However, when she had to match from a sample of four dots and her choice was between four and five dots, she was unsuccessful. Vicki was also unable to match a sample presented in the auditory mode. She was unable to reproduce the same number of taps on a table that a human produced, even when presented with only two or three taps.

Matsuzawa (1985) showed that another common chimpanzee, Ai, could learn to choose the correct Arabic numeral key from an array when required to determine the quantity (1 to 6) of objects shown through a display window. Also, when presented with an Arabic numeral, Ai was able to select the array with the correct quantity of objects from among several arrays.

In contrast to such studies of absolute numerousness judgments, relative numerousness discriminations simply require the subject to choose between two or more stimuli on the basis of which stimulus has the greater or lesser quantity of items. Menzel (1960) reported that chimpanzees appear to have a natural tendency to evaluate food portions and to select the larger of the two. Boysen and Berntson (1995) reported similar findings for chimpanzees during acquired food sharing (where animals share their food with others), with the animal allowed to make the choice reliably choosing the larger

food portion for itself. Two chimpanzees, Sheba and Sarah, were trained to select between two arrays of candy (1 to 6 pieces). One subject was to be the "selector" whereas the other was the "receiver." The selector was to choose one of the two arrays for delivery to the receiver, whereupon the selector would be given the remaining array. Therefore, the optimal strategy for the selector would involve choosing the lesser quantity array, resulting in the selector thereby receiving the greater quantity array. However, neither chimpanzee was able to select the lesser array consistently; that is, their choices resulted in receiving the smaller amount of reinforcers. However, when Arabic numerals were substituted for the choice arrays, one of the animals, Sheba, evidenced more optimal performance by immediately selecting the smaller quantity numeral and thus receiving the larger reward. (See also Biro & Matsuzawa, 1999 for a similar result).

Thomas, Fowlkes, and Vickery (1980) trained squirrel monkeys to choose from two cards that contained different numbers of black circles (2 to 9). Reinforcement was contingent upon the subject choosing the card that contained the smaller quantity of circles. Training proceeded in the order 2 versus 9 (2:9), 2:8….2:3, 3:9, 3:8 and so on up to 8:9, or until failure to meet criterion of 75% correct in 500 trials. Both monkeys met criterion through comparisons of 7:8, with one subject able to choose a card of 8 circles consistently over a card of 9 circles.

Rhesus monkeys (Macaca mulatta) have also been shown to exhibit a propensity for judgment of amounts (Washburn, 1994). In a test of Stroop-like effects, the monkeys quickly learned reliably to choose a stimulus array containing more stimuli (letters or numerals) over an array containing fewer stimuli (e.g., the monkeys selected five Bs instead of four Cs). They performed better than chance with randomly selected and

configured arrays, even if the smaller array contained numerals of greater value (for example, the monkeys selected five "2's" over four "6's).

Related to the capacity to make judgments of relative numerousness, nonhuman primates have also exhibited the ability to make ordinal judgments as well. Ordinality refers to an ability to place objects in a series on the basis of some quantitative property (e.g., tallest to shortest, or least to greatest). Boysen, Berntson, Shreyer, and Quigley (1993) taught three chimpanzees to order Arabic numerals (1 to 4) in proper ordinal sequence. The apes were trained with adjacent pairs of numerals (e.g. 1:2, 2:3, 3:4) to choose the greater quantity of the pair. When presented with a novel pairing (2:4), one chimpanzee, Sheba, responded accurately by selecting the numeral 4. Later, after additional training, the other apes were also able to choose the correct numeral in the novel pair condition. The experimenters concluded that with appropriate training chimpanzees could learn the proper serial order of symbolic stimuli.

In a series of experiments with two rhesus monkeys, Washburn and Rumbaugh (1991) presented the monkeys with two Arabic numerals on a computer monitor and required the monkeys to choose between the numerals by manipulating a joystick so as to bring the cursor into contact with one of the numerals. Whichever numeral the monkey chose resulted in delivery of the corresponding quantity of fruit-flavored chow pellets (e.g., selection of the numeral 5 resulted in the delivery of 5 pellets). Both monkeys tended to choose the greater quantity numeral within pairs that involved combinations of the numerals 1 to 9. One animal chose the greater number significantly above chance levels even on probe trials of unfamiliar pairings of numerals. In a later test, both animals were presented with five numbers simultaneously and were allowed to choose

each of the numbers in their preferred sequence. At each of the choices among arrays of 5, 4, 3, and 2 numerals, both monkeys chose the greater quantity numeral at levels significantly better than would be expected by chance alone. In other words, the monkeys tended to "count downward" in proper reverse ordinal sequence from the greatest to least quantity numerals in the array. These results, which have now been replicated with dozens of additional rhesus macaques (Washburn, personal communication), suggesting that the monkeys may have learned a comparison strategy. They could have attached a value to each numeral as a result of the original training, and learned that they profited most by comparing each of the numerals and choosing the one with the largest value. In support of this interpretation, consider again the findings of Washburn (1994) in which the monkeys selected the larger of two arrays of stimuli (letters or numerals). The animals were able to do this, even when the larger array was made up of the smaller of the Arabic numerals (e.g., five 3s versus two 7s, where the correct response was the five-item array). On such incongruous trials, response times were significantly slowed (compared to trials in which the identity of the letters was not incongruous with the number of items in the arrays), indicating that the Arabic numerals were meaningful symbols for the monkeys that represented quantities. Gulledge (1999) also reported data that indicated that the numerals represented quantities for the monkeys in that the monkeys were able to judge pairs of stimuli of different stimulus types (e.g., dots versus numerals) to be of equal quantity.

In an influential replication of the earlier findings, Brannon and Terrace (1998) trained two rhesus monkeys to order arrays of visual stimuli under conditions that controlled for cues like surface area and brightness. Monkeys were presented with

exemplars representing the numerosities 1 to 4 and were rewarded for responding in ascending numerical order. To control for non-numeric cues, exemplars varied with respect to size, shape, and color. Later, the monkeys were presented with exemplars for the novel numerosities 5 to 9 to which they also responded accurately in ascending order. Like Washburn and Rumbaugh, Brannon and Terrace concluded that their results indicated that rhesus monkeys can represent the numerosities 1 to 9 on an ordinal scale.

A third type of numerical ability that has often been attributed to nonhuman primates is the capacity for summation. Summation is a process that allows organisms to make an accurate choice when asked to determine the greater numeric quantity between two or more pairs of stimuli. In a series of experiments, two common chimpanzees, Sherman and Austin, compared pairs of stimuli and choose the pair of stimuli representing the greater total quantity (Rumbaugh, Savage-Rumbaugh, & Hegel, 1987). Sherman and Austin selected accurately from two pairs of wells, each containing from 0 to 4 chocolate chips, the pair of wells containing the larger sum of chocolate chips. They did this without the benefit of a correction procedure (they received the chocolate chips from whichever pair of wells they chose). Summation, in this instance, was defined as reliably "choosing one of a pair of quantities whose overall sum is greater than the sum of another pair of quantities for all possible pairs within a stated numerical range" (Rumbaugh et al., 1987, p. 107). The authors pointed out that surface area was not controlled, therefore the subjects' responses may have based on that variable rather than due to a quantitative discrimination (a shortcoming that was later addressed by Pérusse & Rumbaugh, 1990). However, even if surface area were the relevant variable, the combining of discontiguous areas necessarily represented a summation response. The

authors explicated these results as arising from the process of subitization. Subitization is thought to be a process related to pattern matching. When a small number of items are presented in an array, they may be identified in the same manner that one may recognize a pattern. However, in this case the name of the pattern is actually a number. To the extent that arrays and patterns are small (1 to 4 items), recognition is very rapid, accurate, and no formal enumeration is required. The authors speculated that Sherman and Austin chose the larger sum of chocolates in the following manner: First, the apes subitized the quantity of chocolates in each well for each pair of wells; next they summed the subitized amounts for each pair of wells; and finally, they compared the sums and made their choice based on the pair of wells that provided the greater reward.

In a follow-up study Rumbaugh, Savage-Rumbaugh, and Pate (1988) sought to determine whether the chimpanzees might have been either selecting the well with the greatest single number of chocolates or avoiding the well with the single least number of chocolates. To test this possibility, chimpanzees Sherman and Austin were presented with pairs of wells in which one pair of wells contained a common quantity. For example, one pair of wells contained four chocolates each whereas the other two wells contained quantities that differed from one another, with one being greater and the other less than the common quantity (e.g. 4:4 versus 2:5). Quantities of chocolates 1 to 5 were used. The results indicated that the chimpanzees were highly accurate both on trials where the common quantity was less than and greater than the other two quantities. These findings indicate that the chimpanzees were not focusing on a single well and choosing the pair that contained the greatest single amount or avoiding the well with the smallest single amount.

Pérusse and Rumbaugh (1990) examined the influence of wells containing zero or one chocolate chip on summation. They also investigated the consequences of eliminating the requirement to sum discontiguous areas by interspersing trials where only two wells were compared rather than four. Performance by the chimpanzees improved when only two wells were present. These results indicated that when the apes were forced to choose between pairs of wells they negotiated the distance between each pair of food wells and then summed the two pairs of wells. Conversely, when only two wells were present the animals simply made a relative numerousness judgment in order to obtain the larger reward.

Olthof and collaborators (1997) used a similar paradigm to extend earlier findings that squirrel monkeys possess some level of numerical competence (Thomas & Chase, 1980; Thomas, Fowlkes, & Vickery, 1980). In one experiment, squirrel monkeys were allowed to choose between wells containing various amounts of food. As in the study by Rumbaugh, Savage-Rumbaugh, & Hegel (1987), the animals reliably chose the well containing the larger total amount. In a subsequent experiment the monkeys were required to choose between pairs of stimuli containing 2 numerals versus 2 numerals, 1 numeral versus 2 numerals, and 3 numerals versus 3 numerals. Arabic numerals 0, 1, 3, 5, 7, and 9 were used. The animals again reliably chose the pair with the greater sum. More recently, Beran (2001) investigated chimpanzees' abilities for summation and numerousness judgment. The apes were required to compare quantities of M&M's dropped sequentially into a pair of opaque cups. The chimpanzees were never able to view the quantities in their totality, and the candies were only visible, one at a time, before placement into one of two cups. Despite these difficult conditions, the

chimpanzees were able to identify the cup containing the greater quantity. Later research (Beran, 2004) revealed that the chimpanzees could also make accurate judgments when asked to compare a third visible array of candies to the quantities sequentially dispensed, but not visible, in the two cups. Beran declared these findings to be evidence for an analogue-magnitude mechanism for representation of quantity similar to the one described by Dehaene and Cohen (1994).

The most controversial aspect of any discussion of the numerical abilities of nonhuman primates is the issue of whether animals are capable of counting. On the surface, counting would seem to be a much simpler cognitive process than summation; however, verification of the mental activity of counting is much more problematic. Typically, counting is seen as a process that relies upon a concept of number which includes an understanding of both ordinality and cardinality. Whereas the ability of several primate species to order quantities accurately is apparent, evidence for the ability to cardinate (one to one assignment of tags to a given array such that the last item tagged is the total number of items) quantities has proven to be much more elusive. Boysen and Berntson (1989) tested a chimpanzee, Sheba, on her ability to summate in two counting tasks. Sheba first learned to select the Arabic numeral corresponding to the total number of food items she found after visiting 2 or 3 foraging sites. The foraging sites contained a total of 1 to 4 food items. Later the food items were replaced with Arabic numerals (0, 1, 2, or 3). Sheba's performance remained at levels near those for the earlier functional counting task. Sheba's performance in this final task would seem to preclude the possibility that her responses were perceptually based, as Arabic numerals do not lend themselves to subitization. Given that Sheba has also shown evidence of ordinality

(Boysen et al., 1993) and that she has been shown to use acts akin to enumeration when attempting to determine numerosity of arrays of objects (Boysen, Berntson, Shreyer, & Hannan, 1995), the experimenters concluded that she is counting in much the same way as a human child.

Rumbaugh, Hopkins, Washburn, and Savage-Rumbaugh (1989) reported that another female common chimpanzee, Lana, was able to count. Lana manipulated a joystick to remove the correct number of boxes from a computer screen corresponding to randomly selected Arabic numerals 1, 2, or 3. In the final version of this task, no visual feedback was provided. Lana was forced to rely only on her memory to determine when she had removed the correct number of boxes and when she should terminate a trial. The authors concluded that this process must have entailed some form of ordinality and cardinality because the value of the target numbers (1 to 3) changed unpredictably throughout testing. Furthermore, Lana's skill for removing each box via manipulation of the joystick constituted an enumerative act on her part. Therefore, Rumbaugh et al., (1989) inferred from these data that Lana was engaged in counting as she showed evidence of ordinality, cardinality, and enumeration. Subsequent research by Beran, Rumbaugh, and Savage-Rumbaugh (1998) furthered these findings. On a similar computerized task, a male common chimpanzee, Austin, was able to select accurately from arrays of random dots the quantity equal to a given target number (1 to 4).

Cerebral localization of numerical cognition

These investigations and others have established that nonhuman primates are capable of impressive feats of numerical cognition, albeit for ranges and at levels of precision far below those characteristic of performance by humans. In fact, it would

appear that many species of nonhuman primate (as well as other animals) respond to numerosity as naturally as they respond to other stimulus attributes such as shape, color, and size (Beran, 2001; Brannon & Terrace, 1998; Call, 2000; Dehaene, 1997; Hauser, 2000). The development of functional imaging techniques in recent years has made it possible to identify the neuro-anatomical correlates of cognitive functions in healthy humans, and, to a lesser extent, nonhumans. With regard to numerical cognition (i.e., how numbers are mentally represented and processed), various theoretical proposals have been made for the cognitive components of number processing, but little is known as to the precise neural basis of these components.

Henschen's (1927) finding that lesions in various brain areas resulted in difficulties for humans in the representation of numbers and their calculation led to the abandonment of a hypothesis of a unique "calculation center" within the brain. Numerous studies of patients with lesions to the left posterior regions of the brain have revealed dramatic calculation deficits (Dahmen, Hartje, & Bussing, 1982; Delazer & Benke, 1997; and Ferro & Betelho, 1980; Jackson & Warrington, 1986). However, researchers have also found representation and calculation deficits in the presence of right posterior lesions (Dahmen et al., 1982; Gitelman, et al., 1999; Hécaen, Penfield, & Bertrand, 1956). Similarly, Dimond and Beaumont (1972) found a right hemisphere advantage for calculation when using a divided-visual-field presentation. In addition, other researchers have found similar representation and calculation deficits for frontal lobe lesions as well (Dahmen et al., 1982; Luria, 1966). Each of the aforementioned studies serves to highlight the functional distribution of numeric representation and processing throughout the brain; however the inconsistency of these results is somewhat

nettlesome for those researchers hoping to find conclusive evidence for a hemispheric advantage for numeric processing.

Thus far there have been few neuroimaging studies that have focused on numerical cognition and its neuroanatomical correlates. One of the earliest such studies was conducted in 1957 (Sokolov & Bu). Ironically, Sokolov and Bu found no difference in global oxygen consumption and cerebral blood flow between numerical calculation and a resting condition. Risberg, Risberg, and Ingvar (1975) measured regional blood flow changes via an intra-carotid xenon injection technique, revealing an increase in frontal lobe activity during performance of a backward digit-span task. A subsequent investigation (Roland & Friberg, 1985) revealed a posterior right hemisphere bias for processing during a repeated subtraction task.

Due to these inconsistencies, contemporary researchers have sought to overcome many of the technological and methodological flaws that may have compromised earlier results by using positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). However, in most cases researchers were concerned more with the particular functional aspects of the deficits rather than investigating the localization of the brain trauma. Once again, however, the search for a dominant hemisphere or localization of function resulted in contradictory findings with some researchers finding a left-hemisphere bias (Cippotti & de Lucy-Costello, 1993; Cohen & Dehaene, 1995a; McNeil & Warrington, 1996), others finding a right-hemisphere bias (Weddel & Davidoff, 1991), and still others reporting a bilateral frontal lobe bias (Fassotti, Eling, & Brener, 1992).

One of the first investigations using fMRI revealed significant activation of the middle frontal gyrus during subtraction, but curiously not during a counting task

(Burbaud, et al., 1995). Further analysis revealed a strong left-hemisphere bias for right-handed participants during the counting task with no such bias for left-handed participants. One criticism of this study however, is that for technical and theoretical reasons only activity from the frontal lobes was recorded. A similar study (Reid et al., 2002) also compared cerebral activity during repeated subtraction and counting exercises, though over the entire cerebral cortex. Their results showed extensive bilateral activation in the prefrontal cortex as well as bilateral posterior parietal activation. Work by Dehaene, Spelke, and Pinel (1999) revealed that when compared to approximate calculation, verification of addition problems produced more activation in the inferior frontal lobe, the cingulate gyrus, the precaneus in the left-hemisphere, the parieto-occipital sulcus and the middle temporal gyrus in the right hemisphere. The task also resulted in bilateral activation of the angular gyrus. Later work by Pinel and colleagues (1999) revealed a left-hemisphere bias when participants were asked to perform a number comparison task in which they had to declare whether a given number was greater or less than 5.

Researchers utilizing PET found that a repeated subtraction task, relative to rest, caused elevated activation in the parietal cortex, the prefrontal cortex, and the cerebellum bilaterally, as well as the left pre-motor and cingulate cortices, and the Supplementary Motor Area (SMA; Ghatan, Ingval, & Eriksson, 1998). In a task that involved a more basic form of numerical processing, number comparison, participants were presented visually with pairs of single digits and were required either to compare or to multiply them mentally. In both conditions the responses were given covertly. The results showed bilateral activation of the lateral occipital cortices, the pre-central gyri, and the

SMA in both the comparison and multiplication conditions, whereas the left and right inferior parietal lobes were activated only in the multiplication condition (Dehaene & Cohen, 1994).

These results suggest that the left and right parietal lobes as well as the left frontal lobe play a substantial role in arithmetic processing. However, there are numerous theoretical issues that must be taken into consideration when trying to draw conclusions from these results. First, many of the tasks involved did not focus on clearly defined numerical processes such as approximate calculations. Second, many of the tasks involved placed a heavy load on working memory. Third, almost all of the studies required the participants to respond orally or in some overt manner that may have inadvertently caused activation of motor or vocal cortex thereby leading to less than convincing results. Given these criticisms it is difficult to interpret whether cortical activation was due to numeric processing or representation, or possibly due to the more general processes involved such as working memory, attention, or language. In an attempt to clarify the physiological correlates of numerical cognition Dehaene and Cohen (1994) have proposed a neuro-anatomical model of number processing. This model implies that areas within the intra-parietal sulci bilaterally are the "cerebral localization of a category specific internal representation of numbers" (Chochon, Cohen, & van de Moortele, 1999, page 625) that is involved in calculation as well as in quantification operations, and in comparison of numerical magnitudes (Dehaene & Changeux, 1993). In his Triple-Code Model, Dehaene postulated that different types of numerical operations are processed by different areas of the brain (Dehaene, 1992, Dehaene & Cohen, 1994). The hypotheses about these operations are summarized below.

TABLE 1. SUMMARY OF TRIPLE-CODE MODEL NEURAL CORRELATES

(Dehaene & Cohen, 1994).

Representation	Numerical Tasks	Localization
Verbal	Processing number names Counting Simple addition facts Simple multiplication facts	Left inferior frontal
Visual	Processing Arabic digits Parity judgments Mental multi-digit operations	L-R Occipito-temporal
Analog	Processing analog quantities Numerical comparisons Approximate calculations	L-R inferior parietal

At the functional level the Triple-Code model assumes three different types of representation directly interfaced by situation specific comprehensions and production mechanisms and connected by translation paths. Each representation would specifically be used for a given type of numerical task. A visual representation (i.e., strings of Arabic digits manipulated on a spatially extended representational medium) something akin to a mental "number line" would be used to process Arabic numerals in multi-digit operations and in parity judgments. A verbal representation (i.e., syntactically organized sequences of number words) would be involved when hearing or reading number words, when counting, and when solving simple addition and multiplication problems. These arithmetical facts would be stored and retrieved as declarative knowledge through verbal associations. Finally, an analog representation (i.e., mental continuum oriented left to right, from small to large quantities, and compressed near the larger quantities, representing numerical quantities as distributions of activation) would give rise to approximate calculations and would give rise to judgments of number comparison

(Pesenti, Thioux, Seron, & De Volder, 2000). In support of the Triple-code model, Dehaene and Cohen (1997) have recently described a double dissociation that is compatible with this theoretical hypothesis. Two patients with normal number reading and writing, but with severe calculation deficits, were compared. One patient was impaired in operations taxing quantity manipulation such as subtraction due to an inferior parietal lobe lesion, but showed preservation of rote multiplication abilities. Conversely, the other patient exhibited deficits in operations taxing rote verbal memory due to a left subcortical lesion.

From a neuroanatomical standpoint the model is simplistic and theoretically driven. Visual representations and analog representation are hypothesized to be processed in the occipto-temporal areas (close to the ventral visual pathway) in both hemispheres and in the inferior parietal lobes. The verbal representations are theorized to be processed only in the left-hemisphere in the classic language areas. Additionally, there are possible connections between the various representations as well as an interconnection between the left and right visual and analog representations via the corpus callosum.

These propositions of implementation of the Triple-code model mainly stem from a review of published single-case acalculia studies (Cohen & Dehaene, 1995b; Dehaene & Cohen, 1997; Cohen, Dehaene, & Verstichel, 1994). However, results that do not necessarily support the Triple-code hypothesis do also exist. Dehaene, Dupoux, & Mehler (1997) and Pesenti et. al., (2000) have provided data showing that arithmetical calculation may not rely on language functions, and, in fact, good calculation despite severe language problems has been described (Hermelin & O'Connor, 1990; Warrington

& Cipolotti, 1996). There are several models based on experimental data that claim that arithmetical facts are not retrieved via verbal association, but by the activation of preverbal magnitudes (Gallistel & Gelman, 1992), stored arithmetic elements (Rickard, Healy, and Bourne, 1994), or semantic network nodes (Ashcraft, 1990, 1992, 1993; Siegler & Jenkins, 1989).

Several arguments have been offered to explain the discrepancies between the expectations of the Triple-code model and these results. First, the parietal activation often seen during multiplication has been tentatively described as reflecting the need for semantic elaboration in some problems for which the answer was not directly retrieved from memory. Indeed, performance greatly varies across problems and individuals, and a direct memory retrieval accounts for only 80% of the reported strategies. Participants also have reported that they use strategies such as applications of rules, decomposition of difficult problems, or other more complex backup strategies (Bisanz, Morrison, & Dunn, 1996; LeFevre, Saldsky, & Bisanz, 1996) that may require some processing of the magnitude information in the parietal cortex. Second, from a methodological point of view, using a resting state as the control task for PET studies does not make it possible to distinguish the areas involved in number processing from those related to more general nonnumerical processes. Indeed, participants may have simply been rehearsing the arithmetic problems seen previously during the rest period thereby masking or altering any possible effects.

It would appear then that the more complex the numerical operations we study, the more clouded the neuro-anatomical picture seems to be. Is the scene just as ambiguous for more simple quantitative judgments? Moyer and Landauer (1967) were

the first to measure response times (RTs) for number comparison. They presented participants with pairs of digits and asked them to press a response key on the correspondent side of the largest digit (or on the side of the smallest). They reported a distance effect; participants responded more slowly and made more errors when the two numbers were numerically close (e.g., 7 vs. 9) than when they were further apart (e.g., 3 vs. 9). This effect has been extensively replicated with both human and nonhuman participants. The curve relating reaction time to numerical distance is a continuously decreasing line as numeric distance increases (e.g., Dehaene, 1989). This distance effect remains even when 2-digit numbers are compared. For instance, when comparing numbers to a standard of 65, 61 is classified more slowly than 59, which is itself slower than 51 (Dehaene, Dupoux, & Mehler, 1990; Hinrichs, Yurko, & Hu, 1981). The distance effect does not disappear with training (Poltrock, 1989) and is observed early in childhood (Duncan & McFarland, 1980; Sekuler & Mierkiewicz, 1977). Nonhuman primates also show this same distance effect when choosing the greater quantity from among two Arabic numerals (Gulledge, 1999: Washburn & Rumbaugh, 1991). Thus the distance effect appears to be a universal characteristic of (human and nonhuman) elementary numerical cognition (Dehaene & Changeux, 1993).

Nothing in the visual appearance of digits betrays that 7 and 9 are conceptually more similar than 3 and 9. Thus, the distance effect implies the existence of an abstract numerical representation of numbers that rationalizes numerical relations not obvious in the digit symbols. The typical interpretation of the distance effect theorizes that the input numerals are mentally transformed into an analogous representation similar to a mental number-line (Dehaene & Changeux, 1993; Moyer & Landau, 1967; Restle, 1970).

Interestingly, Dehaene et al. (1993) showed that individuals were faster to respond to small numbers with the left hand and to large numbers with the right hand in a task requiring participants to respond based on numerosity, again lending credence to the existence of a mental number-line that represents quantities in a spatial fashion, with smaller numbers to the left of larger numbers. The internal representation of two numbers close in quantity would be more similar or would overlap more than those of numbers that are numerically more distant, thereby explaining the distance effect.

For the sake of parsimony some models of number processing have assumed that the same magnitude representation is accessed regardless of the input format of the numerals (Dehaene, 1992; Glucksberg & McCloskey, 1992). According to these models, the semantic representations of the Arabic numeral 6, the written word *SIX,* and the spoken word "Six", are identical because the meaning of these symbols is expressed by the same mental magnitude. Accordingly, the processing steps in the number comparison task can be decomposed into three major operations, 1) a notation-specific stimulus identification, 2) activation of the magnitude representation and retrieval of larger-smaller relations, and 3) preparation and execution of the motor gesture assigned to the "larger" or "smaller" response (Dehaene, 1996).

Surprisingly, relatively little research has been conducted regarding the neuro-anatomical correlates of numerical comparison and judgment. Dehaene (1996) conducted one of the few investigations of the process and structures involved in making such judgments. Dehaene collected event related potentials (ERPs) from participants while they were judging numerals to be either greater than or less than 5. Results revealed the existence of a bilateral system for identifying Arabic digits and the

convergence of activation toward a right posterior system for magnitude comparison whereas there was a left-hemisphere bias for verbal presentation of numerals. However, note that in this task there was also a demand placed on working memory resources by the participants having to keep "5" in mind.

In other experiments many different types of words (not just numeral-words) have elicited a left-lateralized bias (Dehaene & Akhavein, 1995; Neville, Kutas, & Chesney, 1986). PET studies have identified a left ventro-medial extra-striate area activated by the presentation of real words and pronounceable pseudo-words, but not by consonant strings or false-font stimuli (Petersen, 1990). A lesion in this area produces pure alexia with letter-by-letter reading, suggesting a deficit of the visual word form (Shallice, 1988). Thus PET and ERP data seem to converge in isolating a left posterior ventral system related to word identification. The system would first become specifically activated by words as opposed to digits around 110-160 milliseconds post-onset. Additional evidence indicates that words and consonants are not discriminated until about 150 to 200 milliseconds post-onset (Dehaene & Akhavein, 1995; Posner & McCandliss, 1993).

Why then would some researchers have found evidence for bilateral activation with Arabic digits? In the left-hemisphere it seems likely that the same brain area is responsible for the identification of words and digits. There is evidence that alexic patients with left-hemisphere lesions often have difficulty naming multi-digit Arabic numerals (Dehaene & Cohen, 1991). However, a number of cases on record indicate that the identification of Arabic digits may be preserved even when word identification is impaired (Tranel, Damasio, & Damsaio, 1998; Cohen & Dehaene, 1995a; Dehaene & Cohen, 1991). Some abilities for digit identification have remained after massive left-

hemispheric lesions (Barbizet, & Bundefield, 1967; Dehaene & Cohen, 1991), and even left-hemispherectomy (Vargha-Khaden, & Polkey, 1992). Dehaene (1996) found evidence for a right-hemisphere activation during digit identification and judgment. Accordingly, Dehaene postulated that the right-hemisphere activation found with Arabic digits may reflect the functioning of a right-hemisphere digit-identification system.

Are the left- and right-hemispheric identification processes redundant? Data from neurospychology suggests that the two areas may play slightly different roles in numeric cognition. The left-hemisphere may play a special role in phonological representation whereas the right-hemisphere may be involved with accessing numerical meaning without necessarily permitting patients to read aloud. For example, patients NAU (Dehaene & Cohen, 1991) and GUI (Cohen, et al, 1994) both suffered from large posterior left-hemisphere lesions and the obligatory reading deficits. When asked to name Arabic numerals, both had to count before naming the numeral, yet both were easily able to make accurate greater-than/less-than judgments about pairs of numerals. Patient GUI could not read aloud Arabic numerals, but was still able to name and understand familiar numerals such as 1789 (French Revolution) and 1918 (World War I), indicating preserved access to number meaning (Dehaene & Cohen, 1991). More recent work by Cohen and Dehaene (1995a) demonstrated that a small lesion to the left posterior ventral region was sufficient to impair digit naming, but digit comprehension remained virtually intact. These cases would seem to fit well with a theory of two systems for digit identification, one biased toward phonological retrieval and the other toward semantic access.

Recall that Dehaene (1996) required participants to make greater-than/less-than judgments when comparing the visual Arabic numerals 1, 4, 6, and 9 and verbal numerals ONE, FOUR, SIX, and NINE to a standard of 5. Participants were slower and made more errors when comparing two close quantities than when comparing two more distant quantities. With regard to activation, a significant difference between near and distant trials emerged for sites located close to the parieto-occipito junction, with a significant right-hemispheric lateralization. Most importantly, a similar pattern was found whether the numbers were presented in Arabic-numeral or verbal notation. This finding suggested that the distance effect originates from a level of representation that is not dependent upon the physical and notational characteristics of the stimulus (Dehaene, 1992; Glucksberg & McCloskey, 1992).

Previous research has shown the left parieto-occipito-temporal junction to be a critical site for acalculia in brain lesioned patients (Benton, 1987; Henschen, 1926; Warrington, 1982). It is surprising that Dehaene (1996) obtained a similar localization of function albeit with a right lateralization. As Dehaene pointed out however, these findings are consistent with several other investigations in which a significant right-hemispheric contribution to magnitude comparison was also found. First, numerous investigations with patients who have massive left-hemisphere damage have shown that knowledge of number magnitudes and of quantity relations is often preserved (Lanarés, Waeny, & Assal, 1987; Dehaene & Cohen, 1991). Neuro-imaging studies have revealed both right and left inferior parietal lobe activation during calculation (Roland & Friberg, 1985). Third, a recent model of the development of numerical abilities of animals and human infants has underscored the natural relationship of number perception to object

localization and size perception abilities (Dehaene & Changeux, 1993). Because the latter two depend on the integrity of the right parietal areas, it is perhaps plausible that number representation should follow a similar pattern.

Pesenti and colleagues (2000) used PET to study brain activation during magnitude comparison of numerals has revealed activation in the left inferior parietal lobule, the left intra-parietal sulcus, and the left superior lobule with some minor activation in the right superior lobule. Indeed, these results confirm a greater participation of the left-hemisphere in comparison judgments, whereas the Triple-code model predicts a right-hemisphere predominance (Cohen & Dehaene, 1995b; Dehaene & Cohen, 1994, 1997). At the anatomical level, the results of Pesenti and colleagues indicate that the critical area for numeric magnitude processing is in the left parietal lobe. These data fit well with that of a lesion study carried out by Takayama, Sugishita, and Akiguchi (1994) with similar results. However, this location of function appears to be more posterior, superior, and lateralized than the area theorized by the Triple-code model (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Pinel et al., 1999; Sathian et al., 1999).

When it comes to the hemisphere of activation for the internal representation of numbers for purposes of number comparison, the results are similarly inconsistent. Rushworth, Ellison, and Walsh (2001) suggested the many divergent results obtained in studies of hemispheric differences in number comparison may be due to the investigators using different reference numbers, different absolute numbers sizes, and different control conditions. Stanescu-Cosson et al. (2000) reported left intra-parietal sulcus activation for numbers close to the reference number (5) and right intra-parietal sulcus activation for numbers far from the reference number. Only two fMRI studies have used numbers

larger than 10 in a number-comparison task (Dehaene, Le Clec'H, & Cohen, 2000; Rickard, Romero & Basso, 2000). Rickard and colleagues used number detection as a control task. They reported reliable bilateral angular gyrus activation during number comparisons in some of their participants. Dehaene and colleagues used a body-part-comparison task as a control and found right intra-parietal sulcus activation for the number-comparison task.

Overall, the evidence suggests that the internal representation of numbers draws heavily on both working memory and attentional resources. Numerous investigations have been reviewed herein and there seems to be no firm conclusion as to what particular brain areas are involved, or even what hemisphere (see Table 2.).

Numerous techniques have been employed by researchers that have yielded data showing activation in either or both hemispheres from the frontal lobe to the cerebellum and all areas between. For the most part, findings have been inconsistent as to which cortical areas are active during numeric calculation and/or numeric judgment. Many of the previous investigations, and lesion studies in particular, are "hampered" by the plasticity of the brain. Following a brain injury, brain functions may reorganize in an attempt to compensate for lost abilities, and therefore the observations might yield inaccurate or tainted results. Furthermore, cognitive capabilities might be globally impaired after a brain insult so that the patient might not be suited for extensive, detailed, testing of a given ability. Additionally, patients will frequently have more than a single brain injury; therefore, the brain injury might be larger than the brain area under study, making the discovery of a correlation between regional brain function and disturbed

Table 2

Summary of investigations of localization of function of numerical cognition

Left-Hemisphere Activation

Benton (1987)
Burbaud (1998)
Cippotti & de Lucy-Costello (1993)
Cohen & Dehaene (1995a)
Dehaene & Akhavein (1995)
Dehaene & Cohen (1997)
Delazer & Benke (1997)
Ferro & Botelho (1980)
Jackson & Warrington (1986)
McNeil & Warrington (1996)
Neville et al. (1986)
Pesenti et al. (2000)
Pinel et al. (1999)
Warrington (1982)

Right-Hemisphere Activation

Dehaene (1996)
Dehaene et al. (2000)
Dimond & Beaumont (1972)
Graham et al. (1982)
Hecaen et al. (1961)
Takayam et al. (1994)
Weddel & Davidoff (1991)

Bilateral Activation

Dahmen et al. (1982)
Dehaene (1996)
Dehaene & Changeux (1993)
Dehaene & Cohen (1994)
Fassotti et al. (1992)
Reid et al. (2002)
Rickard et al. (2000)
Roland & Friberg (1985)
Sokolov et al. (1957)
Stansco-Cosson et al. (2000)

behavior difficult to ascertain. Finally, lesion studies with humans depend on the opportunistic and chance occurrence of a given brain injury, and thus cannot be planned in advance or designed with care, are generally limited to a single or few cases, and therefore cannot be empirically tested for confirmation. Functional neuroimaging techniques such as PET have, at times, shown convincingly the association between certain behaviors and specific patterns of joint activation of cortical and subcortical structures. Functional magnetic resonance imaging (fMRI) can add greater anatomical resolution and the temporal profile of the pattern of activation of such cortical networks for specific behaviors. However, in the best of circumstances, these neuro-imaging techniques only provide supportive, correlational evidence of the neural network associated with a given behavior rather than direct, causal evidence. Activation of a given neural network by a behavior can establish an association between neural activity and behavioral manifestations, but does not provide insight into the functional role that a given neural structure or its connections play in the behavioral manifestation. In addition, different strategies in behavior are difficult to control for and might induce misleading results in such associative approaches of correlation between behavior and brain activity.

The major question of interest for the present research is do humans and nonhuman primates represent numerosity differently? First, I sought to replicate with humans, and to extend to monkeys, the earlier findings of Dehaene (1993) that humans respond faster to smaller numbers presented on the left and faster to larger numbers on the right. Second, I used a divided visual field paradigm to determine whether humans and monkeys represent numerals (symbolic stimuli) in a manner different from how they

represent random-dot patterns (analogue stimuli). Finally, I utilized repetitive transcranial magnetic stimulation (rTMS) with both human participants and monkeys to extend and explicate earlier findings with regard to possible lateralization of numeric comparison abilities.

Experiment 1: A Comparative Study of the Mental Number Line

This experiment was designed to replicate the finding that humans respond faster to smaller quantity numeric stimuli that are presented on the left side of visual fixation and faster to larger quantity numeric stimuli that are presented on the right side of visual fixation (Dehaene (1993). Recall that this phenomena is often interpreted as confirming that humans represent numerosity in a number-line fashion with smaller quantities appearing on the left and greater quantities appearing to the right. In addition, data were collected from rhesus monkeys in a similar task format and were analyzed to determine what, if any, similarities their response topography may have to that of humans. In addition to numeric characters, arrays of dots were also presented in order to determine whether humans and nonhumans show the same response topography to both symbolic (i.e., Arabic numerals) and analog (random dot-pattern) stimuli.

Method

Participants. Participants were 12 students (average age 26.4 years, range 19 to 36 years, 6 males) from Georgia State University. In exchange for their efforts they each received one hour of research participation credit.

Data from 5 male rhesus monkeys (*Macaca mulatta*, ages 10 to 19 years, 2 were left-handed as determined by their preferred hand for joystick manipulation) performing identical tasks were also collected. None of the animals were food deprived or reduced in

weight for purposes of this experiment. Each animal was singly housed and had continuous access to water. Each animal had an extensive history of successful completion of with computer-based numerical cognition tasks that required responses to be made via a joystick (Gulledge, 1999; Washburn & Rumbaugh, 1991; Washburn 1994).

Apparatus. All participants were tested using the Language Research Center's Computerized Test System (LRC-CTS; Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989). The LRC-CTS consists of a joystick connected to a Compaq Pentium II computer. All stimuli were presented on a 17-inch color monitor. The computer provided audio feedback, generated through an external speaker/amplifier for the participants, collected response time and accuracy data, and controlled delivery of 97-mg fruit-flavored pellets (Research Diets) to the monkeys.

Tasks and Procedure for human participants. Participants were asked to be seated with their backs positioned against the backrest of a standard office chair. The distance from their eyes to the center of the computer monitor was then measured. Chair position was then adjusted such that the distance between each participant's visual midline and the center of the monitor was 43 cm. At that time the position of the chair was marked so that the experimenter could determine whether any chair movement occurred during the experiment. No participant was observed to alter the position of the chair during testing. Participants were read instructions as to how to perform the tasks. Participants were first instructed (see appendix A) as to how to complete the trial-initiation sequence by manipulating the cursor ("+"), via the joystick, into a 2-cm diameter circle whereupon a pair of task stimuli was presented. Task stimuli consisted of either a pair of 3 cm by 3 cm Arabic numerals (1-9) or a pair of random quantity (1-9) dot-patterns composed of white

dots each 1 cm in diameter. Each member of the Arabic numeral stimulus pair subtended a visual angle of approximately 4.3 degrees when displaced 2 degrees from focus and when viewed from a distance of 43 cm. The visual angle subtended by the random-dot patterns varied from a low of 1 degree for one dot to a high of 7 degrees for nine dots when viewed from a distance of 43 cm. Participants were then instructed to bring the cursor into contact with the greater quantity stimulus. Successful completion of a trial resulted in a rising tone sounding for 1 second. An incorrect response resulted in presentation of a buzzing tone for 1 second. Five seconds after a trial was completed, a new trial appeared on the computer screen. Participants averaged completion of 208 trials. Afterward, participants were given time to ask questions regarding the task procedure. Once all questions had been answered testing began.

Task and Procedure for nonhuman primates. The five rhesus monkeys were tested in their home cages which were attached to test stations containing the joystick, computer monitor, pellet dispenser, and external speaker-amplifier. The monkeys were allowed to roam freely throughout their home cages during testing. However, in order to ensure that the viewing angle was comparable to that of the human subjects the monkeys were required to view the monitor through a Lexan viewing port. The viewing port was constructed of 1.5 mm thick black opaque Lexan and was 60 cm long and 30 cm tall with a 12 cm by 18 cm open section through which the monkey could view the task stimuli. Test station monitors were then positioned so that each monkey could only view the entire monitor at a distance of 43 cm or less.

As with the human participants, the monkeys were required to complete a trial initiation sequence by manipulating the cursor "+," via the joystick, into a 3 cm diameter

circle whereupon the task stimuli were presented. For successful completion of a trial the monkeys were rewarded with a 97 mg fruit-flavored chow pellet and a rising tone. For unsuccessful trial completion the monkeys received only audio feedback in the form of a low tone. The monkeys previous test history afforded them extensive knowledge of the current task (Gulledge, 1999; Washburn, 1994; Washburn & Rumbaugh, 1991).

Results

Accuracy was very high for both human and nonhuman participants. Mean accuracy for humans was 99.9% for all trials. Whereas the monkeys made more errors, monkeys' accuracy still averaged 92% across trial types. Given these high accuracy levels, additional analyses were not conducted on this measure.

Congruent trials were defined as those in which the lesser quantity stimulus was presented on the left and the greater quantity stimulus was presented on the right (e.g., as would be expected in a number line). A 2 stimulus type (numerals vs. dots) x 2 trial type (congruent vs. incongruent) x 2 species (humans vs. monkeys) analysis of variance (ANOVA) was conducted to assess the response time data. Analysis revealed main effects for stimulus type, $F(1, 15) = 12.63$, $p < .05$, species, $F(1, 15) = 7.45$, $p < .05$, and trial type $F(1, 15) = 11.32$, $p < .05$. A significant interaction between stimulus type and trial type was also found, $F(1, 15) = 10.87$, $p < .05$ (see Figure 1). Planned comparisons revealed significant differences, $t(16) = 2.74$, $p < .05$, in mean response times for random dot-patterns for the congruent (1.12 seconds) and incongruent (1.48 seconds) trial types. No other comparisons were significant.

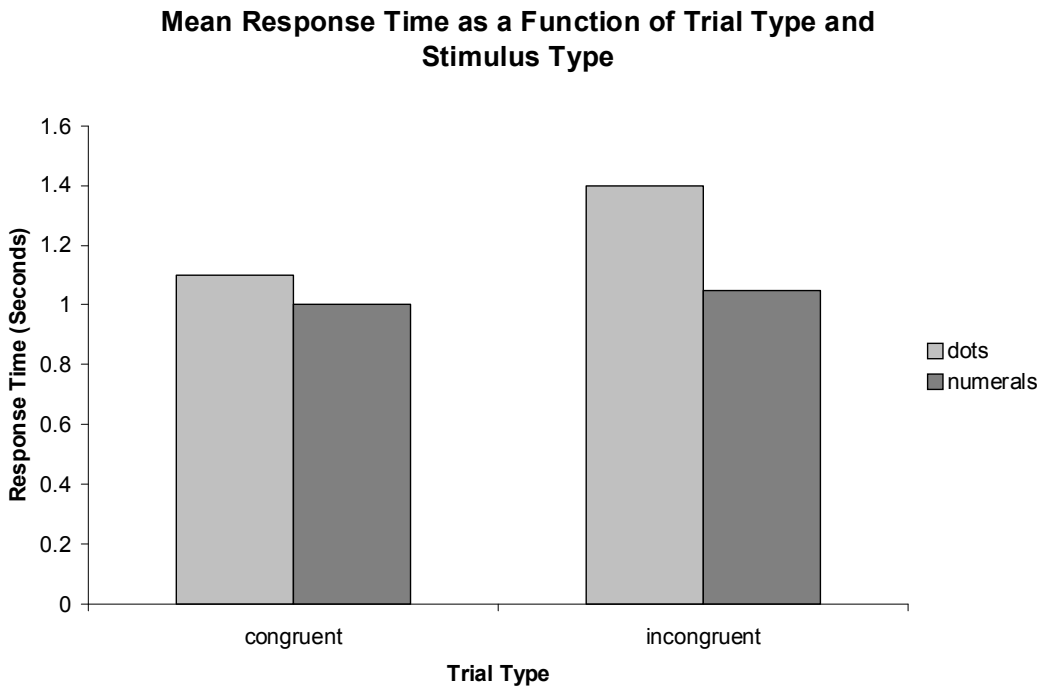

Figure 1.

Symbolic distance effects were present, with species having longer response times as symbolic distance decreased (see Figure 2, and Appendixes A, B, C, and D).

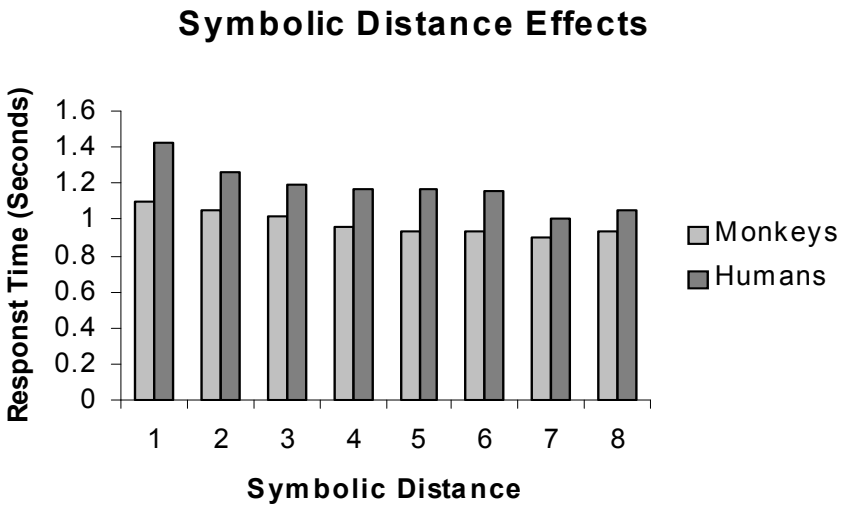

Figure 2.

Discussion

Dehaene (1993) reported that humans respond faster to greater quantity numeric stimulus when they are presented on the right side of visual fixation. He interpreted these results as further evidence that humans represent numerosity in a number-line fashion otherwise known as a Spatial-Numerical Association of Response Codes (SNARC) Effect. The current research replicates these findings for humans as well as provides new evidence that nonhuman primates display this same SNARC effect. In addition, symbolic distance effects were present for both species with increasing response times as the distances between the stimuli became smaller and smaller. In other words, as the "distance" between the number line positions of the stimuli (both numeral and dot pattern) becomes smaller, it takes the participants longer to make a judgment as to which stimulus is larger in quantity. This also provides further evidence for a number-line like representation strategy for both numerals and random-dot pattern stimuli. Taken together, these findings suggest strongly that number magnitude is represented as a number line with an orientation from left to right.

Both humans and monkeys showed slower response times for judgments of the random-dot pattern stimuli. As noted earlier, accuracy levels were high for both species regardless of stimulus type albeit with significantly slower response times for the random-dot pattern stimuli. The author assumes that the differences in response time for the participants was due to execution of some type of visual scanning process necessary to make judgments of dot pattern stimuli. Humans showed significantly longer response times for incongruent dot pattern trials when compared to congruent dot pattern trials. This result would appear to indicate that humans also process analog stimuli in a number

line like fashion as well, albeit at significantly different response times than for numeric stimuli. Symbolic distance effects were present for the analog stimuli as well with, once again, increased response times as the differences between the two comparison stimuli decreased. Do humans represent dot patterns in an analog manner as the Triple-code hypothesis suggests? Significant differences in RT were evident for dot patterns versus numerals thereby indicating that numeric and analog stimuli may indeed be processed differently—perhaps even, as the triple-code model suggests, in different regions of the brain.

Importantly, the monkeys showed a response bias similar to that found for humans, here and by Dehaene (1993). Just as was found with the human participants, the monkeys responded faster on congruent trials than on the trials with stimuli presented in an incongruent fashion. Given these data, it would appear that the monkeys represent numerosity in a way that is very similar to humans, possibly in a number-line like fashion as well. Due to the fact that numerals are merely symbols used for representing quantities, response biases exhibited by the monkeys may also indicate the presence of a neurological system for symbolic representation much like that of humans.

Additionally, just as the human participants did, the monkeys showed a similar response bias for dot-pattern stimuli. The monkeys exhibited longer response times for incongruent presentations than for congruent ones. Accuracy remained high however, regardless of presentation type. For this particular investigation however, the monkeys' performance for all numerals, dot patterns, and across both congruent and incongruent presentations mirrored that of their human counterparts.

Experiment 2: Functional Cerebral Asymmetries of Numerical Recognition

As noted earlier, there is ambiguity in the literature regarding the laterality of various numerical cognition functions. Indeed, the studies conducted seeking a localization of function for numerical judgments have produced divergent findings. Researchers at present, including proponents of the Triple-code model (Cohen & Dehaene, 1995b; Dehaene & Akhavein, 1995), disagree as to which hemisphere is more specialized for the processing required for numerical judgments. Humans characteristically show a left-hemisphere advantage for production and comprehension of language, and accordingly show a left-hemisphere advantage for the recognition of linguistic symbols (e.g., words). Do humans process numerals as they would other symbols or are numerals processed in a manner more consistent with the spatial specializations characteristic of the right cerebral hemisphere? One can ask a similar question of the functional cerebral asymmetries that characterize numerical cognition by nonhuman animals, because numerous researchers have shown that several nonhuman primate species possess numerical abilities similar in quality to that of humans. Is it possible that nonhuman primates may show similar hemispheric literalities to those of humans for symbolic numerical representation even without the presences of language skills?

All divided visual field (DVF) studies of cerebral organization depend upon the contralateral organization of the primary visual system. Information concerning stimuli falling to the left of the visual fixation point (i.e., in the left visual field, or LVF) is initially projected to the right cerebral hemisphere, whereas information concerning stimuli to the right of the visual fixation point (i.e., right visual field, or RVF) is initially

processed in the left cerebral hemisphere. Information is then distributed between regions of both cerebral hemispheres via the corpus collosum, so that the hemisphere ipsilateral to the visual field of presentation receives stimulation indirectly. This gives one hemisphere (the hemisphere contralateral to the visual field in which the stimulus was flashed) privileged access to the visual stimulus with respect to time and quality. Of course, the presentation of a stimulus outside central vision usually results in movement of the eyes (a saccade) to bring the stimulus into central or foveal vision, which in turn results in bilateral transmission of the image to the primary visual cortex of both hemispheres. For this reason it is necessary to use brief exposures that present the stimuli used in DVF experiments for less than the time needed for such saccades to occur. Saccadic eye movements have been extensively studied and numerous extensive reviews are available (for example, see Alpern, 1971; Carpenter, 1978; Miles, 1936). The use of exposure durations up to a maximum exposure of 150 msec precludes the possibility of eye movements to bring the stimuli into foveal vision (Dimond & Beaumont, 1972) thereby allowing for control of stimulus presentation to one visual field at a time.

Method

Participants. Nineteen undergraduate students participated in exchange for one hour of research credit. Human participants were all right-handed, as determined by self-report, with an average age of 23.4 years (range 18 to 33 years).

Data from 5 male rhesus monkeys (ages 10 to19 years, 3 right handed and 2 left handed as determined by the preferred hand for joystick manipulation) performing identical tasks were also collected. These were the same animals that were tested in Experiment 1. Again, the monkeys' previous test history made them very familiar with

the demands of the current task. Prior research (Gulledge, 1999; Washburn & Rumbaugh, 1991; Washburn 1994) afforded the monkeys familiarity with the task stimuli and extensive skill in making the relative numerousness judgments (RNJ) necessary for trial completion.

Apparatus. The apparatus for humans and monkeys was identical to that used in Experiment 1.

Task and Procedure. A recognition task with 150-msec presentations of lateralized stimuli was used to determine whether there are functional cerebral asymmetries in the processing of numeric information. To ensure the midscreen fixations necessary to guarantee that stimuli were transmitted initially only to the contralateral hemisphere within the DVF paradigm, participants were required to complete a trial initiation sequence before the task began. The cursor and a 3-cm diameter trial-initiation circle appeared on the monitor (see Figure 3a). To begin a trial the participant maneuvered the cursor into the center of the circle (see Figure 3b).

When the cursor was centered in the circle, either a single Arabic numeral or a random-dot pattern was immediately presented for 150 msec (see Figure 3c) and then followed by a 4 x 5-cell black-and white-checkerboard pattern mask for 100 msec (see Figure 3d). These stimuli were flashed either to the left or the right of fixation and were separated from the fixation stimulus by 8.6 degrees of visual angle when viewed from 43 cm. The numerals subtended a visual angle of 5 degrees, the dot arrays subtended a visual angle between 1 and 7 degrees depending upon the quantity of dots presented, and the mask subtended a visual angle of 7 degrees. Immediately after the mask disappeared, a pair of stimuli of the same type (i.e., numerals if the target stimulus was a numeral, dot

arrays if the target stimulus was an array of dots) appeared on the monitor screen. One stimulus appeared above the cursor, the other below (see Figure 3e). One of the two stimuli was identical to the target stimulus, whereas the other was a randomly selected foil stimulus. The participants were required to move the cursor, via the joystick, into contact with the stimulus that matched the originally presented target stimulus. A rising tone sounded for a correct response and a buzzing tone sounded for incorrect responses. .

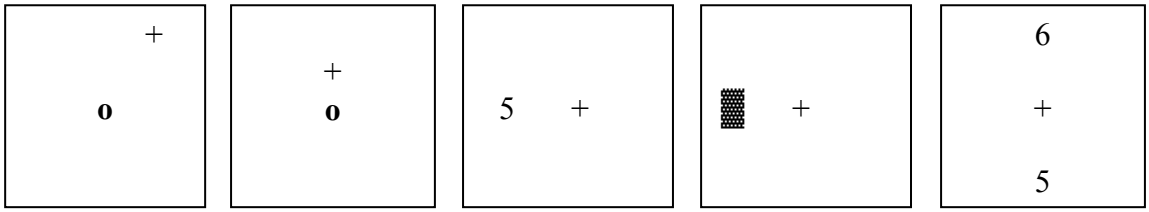

Figure 3a. Figure 3b. Figure 3c. Figure 3d. Figure 3e.

Figure 3. A schematic of a divided visual field matching-to-sample trial from Experiment 2

Human participants were required to sit in a straight-back chair with their backs against the lumbar support. While they were sitting in the chair participants were asked to move their chair either closer to or further away from the monitor until their eyes were positioned 43 cm from the center of the screen, as measured by the experimenter. Once proper chair position was established the experimenter placed tape behind the four legs of the chair to ensure that the participant did not change viewing positions during the experiment. Participants were then read instructions on how to perform the tasks. Afterward, the participants were given time to ask questions regarding the instructions. Once all questions had been answered testing began.

Unlike the human participants, the monkeys received a pellet reward in addition to the audio feedback for successful completion of a trial. Again, for unsuccessful trial completion no pellet was given and a 50-Hz tone sounded for 3 seconds. In order to

ensure that the monkeys were seated at the proper angle and distance for administration of DVF trials, the monkeys were required to view the monitor through a Lexan viewing port. The viewing port was constructed of 1.5 mm thick black opaque Lexan and was 60 cm long and 30 cm tall with a 12 cm by 18 cm open section through which the monkey could view the task stimuli. Cage position and monitor position within the test station were then adjusted so that the viewing distance for the monkeys was 43 cm. The monkeys underwent training on the tasks, in their home cages, until such time as their performance over the last 100 trials was significantly better than chance. Each monkey reached the criterion level of performance in fewer than 1,800 trials. Each of the monkeys was then required to complete 2,000 test trials.

Results

Accuracy data for the recognition task were analyzed via a 2 (species) x 2 (stimulus type) x 2 (visual field) ANOVA. This analysis revealed a main effect for stimulus type, $F(1, 22) = 8.81$, $p < .05$, with humans and monkeys being more accurate for numerals (92% correct) than for random dot-patterns (85% correct). A significant interaction between stimulus type and visual field of presentation was obtained, $F(1, 22) = 6.57$, $p < .05$ (see Figure 4). Planned comparisons revealed that dots were recognized significantly more accurately when presented in the left visual field than the right visual field, $t(23) = 3.25$, $p < .05$. In contrast, numerals were recognized significantly more accurately when presented in the right visual field, $t(23) = -2.34$, $p < .05$.

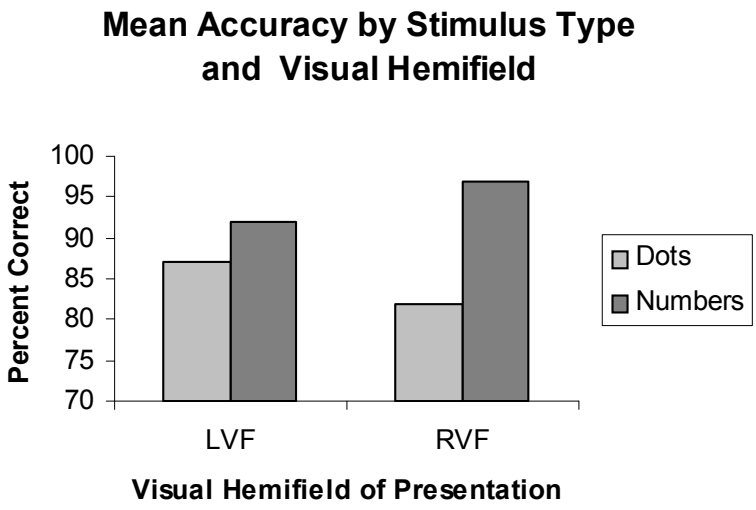

Figure 4.

Response time data for the recognition task were analyzed via a 2 (species type) x 2 (stimulus type) x 2 (visual field) ANOVA. This analysis revealed a main effect for species with the monkeys (mean response time 0.98 seconds) performing the task significantly faster than humans (mean response time 1.27 seconds), $F(1, 22) = 3.87$, $p < .05$. A main effect for stimulus type was also evident, $F(1,22) = 3.45$, $p < .05$, with average response times for the random dot-patterns taking significantly longer (1.36 seconds) than for the Arabic numerals (1.02 seconds). A main effect was also found for visual field $F(1, 22) = 4.33$, $p < .05$, with processing occurring more quickly when stimuli were presented to the RVF (mean response times of 1.16 seconds versus 1.25 seconds when presented to the LVF). The analysis also revealed a significant interaction between stimulus type and visual field $F(1, 22) = 5.32$, $p < .05$ (see Figure 5). Planned comparisons revealed significant differences in RT when comparing Arabic numerals in the left versus the right cerebral hemisphere $t(23) = 3.47$, $p < .05$. No species interactions were evident.

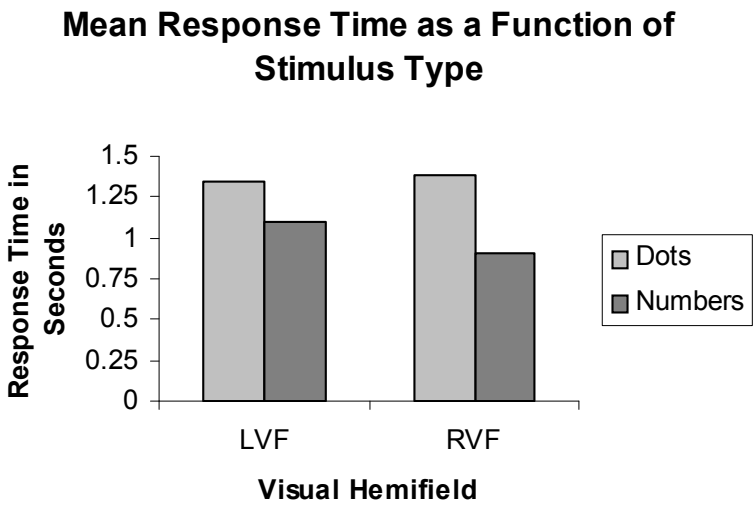

Figure 5.

Discussion

Both monkeys and humans accurately recognized quantitative stimuli when presented for durations of 150 milliseconds. The Triple-code model (Dehaene & Cohen, 1994) predicts that humans process Arabic digits as a visual representation predominately in the left cerebral hemisphere. Data from the current experiment serve to support this conclusion for humans. Numerals were recognized significantly faster and more accurately when presented in the right visual field as compared to the left visual field. It is assumed that humans process numerals better in the left hemisphere due to lateralization of language/symbolic function; however, no such lateralization has yet been reported for monkeys. Notwithstanding, the similarities between the performance of the monkeys and humans in the current experiment is striking. The monkeys recognized numerals with mean accuracy levels of 84% (LVF) and 90% (RVF), compared to 92% (LVF) and 96% (RVF) for the humans. The mean response times for these match-to-sample judgments were similarly patterned between the species, with monkeys requiring

1.02 seconds (LVF) and 0.94 seconds (RVF), compared to humans' response times of 1.37 seconds (LVF) and 1.17 seconds (RVF).

With regard to hemispheric differences in processing random dot-pattern stimuli, judgments were significantly more accurate when the stimuli were flashed to the left visual field (i.e., a right-hemisphere advantage for processing). Again, this pattern is comparable across species: The monkeys' accuracy and response times for the dot patterns presented to the left visual field were 84% correct with a mean RT of 1.17 seconds, and 79% correct with a mean RT of 1.10 seconds when presented to the right visual field. Accuracy and response times for the human participants' were 88% correct with an RT of 1.49 seconds for left visual field presentations and 83% correct with an RT of 1.31 seconds for right visual field presentations. The Triple-code model suggests that processing of such analog stimuli should be conducted via an analog representation and processed in both the left and right inferior parietal lobes, although the current data clearly suggest an advantage for the right-hemisphere.

Indeed, the only species difference observed in Experiment 2 was an overall difference in response times, with the monkeys performing the tasks significantly faster than the humans for both stimulus types. Interestingly, both humans and monkeys completed trials with random dot-pattern stimuli with equivalent speed when presented to either visual field, but with greater accuracy when presented to the left visual field (e.g., processed in the right-hemisphere). Is it possible that both monkeys and humans have a similar representation system for analog stimuli that is lateralized to the right-hemisphere? Importantly, the data clearly show that the only major species difference evident, at least with regard to quantitative stimulus recognition, is one for overall speed

of responding. This phenomenon is robust and has been replicated by many researchers (see Washburn & Rumbaugh, 1997 for a review).

Experiment 3: Functional Cerebral Asymmetries of Relative Numerousness Judgment

To date, little research has been published in which a DVF paradigm was used to examine hemispheric specializations in the processing of numeric stimuli (Dehaene et al., 1997; Dimond & Beaumont, 1974). No study has required relative numerousness judgments by humans or nonhuman animals of pairs of stimuli that are briefly and laterally presented. It would appear that this technique would allow for determination as to whether either hemisphere possesses an advantage (faster and more accurate representation and processing) over the other for making numerical judgments, as a function of the type of numerical stimulus (analog dot arrays, Arabic numerals). According to the triple-code-model (Dehaene, 1992, Dehaene & Cohen, 1994) Arabic digits are presumably processed in either the left or right occipital or temporal lobe via a visual mental representation. Conversely, analog stimuli are thought to be processed in the left and right inferior parietal lobes via an analog mental representation. However, numeric comparisons are theorized to take place in either the left or right inferior parietal lobe as well also via an analog mental representation. The model does not stipulate in which hemisphere this processing takes place or where analog comparisons might take place.

Method

Participants. Human participants were the same 19 volunteers from Experiment 2. They each participated in exchange for an additional one hour of research credit. All

were right-handed, as determined by self-report, with an average age of 23.4 years and a range of 18 to 33 years.

Data were also collected from the same 5 male rhesus monkeys (ages 10 to19 years, 3 right handed and 2 left handed) from Experiments 1 and 2.

Task and Procedure. Human participants were required to sit in a straight-back chair with their backs against the lumbar support. While they were sitting in the chair participants were asked to move their chair either closer to or further away from the monitor until their eyes were positioned 43 cm from the center of the screen, as measured by the experimenter with a tape measure. Once proper chair position was established the experimenter placed tape behind the four legs of the chair to insure that the participant did not change viewing positions during the experiment. Participants were then read instructions as to how to perform the tasks. Afterward, the participants were given time to ask questions regarding the instructions. Once all questions had been answered, testing began.

Participants were required to complete the same trial-initiation sequence as in Experiment 2 (see Figures 6a and 6b). Once the trial-initiation sequence was completed the stimulus pair appeared in either the right or left third of the screen. One stimulus appeared above the midline of the monitor, the other below (see Figure 6c). Each 4 cm by 4 cm stimulus subtended 5 degrees of visual angle at a viewing distance of 43 cm. The stimuli consisted of unequal pairs of either Arabic numerals or random-dot patterns representing the quantities 1 through 9. Arabic numeral stimuli were the same size, shape, and color as those used in Experiments 1 and 2. Each of the dots in the random-dot pattern stimuli was 1 cm in diameter and white in color. The stimulus pair remained

on the screen for 150 ms, and then the stimuli were masked for 100 msec by 4 x 5 cell black-and-white checkerboard patterns (see Figure 6d). Immediately following the offset of the mask, a two-choice response screen appeared. The response screen appeared with the cursor in the center of the screen with red blocks 7 cm above and 7 cm below the cursor (see Figure 6e). To declare the previously viewed upper stimulus greater in quantity participants were required to manipulate the cursor into contact with the upper block. To declare the lower stimulus greater in quantity participants has to manipulate the cursor into contact with the lower block. Correct responses were followed by a rising tone. Incorrect responses were followed by a 3-second buzz. Five seconds after completion of a trial the trial initiation stimulus reappeared in advance of beginning a new trial.

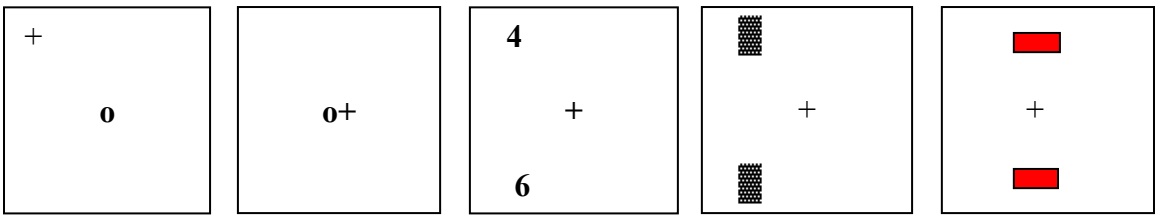

Figure 6a. Figure 6b. Figure 6c. Figure 6d. Figure 6e.

Figure 6a-e. Schematic of a divided visual field relative numerousness trial from Experiment 3.

The monkeys received a pellet reward in addition to the audio feedback for successful completion of a trial. Again, for unsuccessful trial completion no pellet was given and a 50-Hz tone sounded for 3 seconds. In order to ensure that the monkeys viewed the task stimuli at the proper angle and distance for administration of DVF trials, the Lexan viewing port from Experiment 2 was installed in the monkeys' home cages. Cage and monitor position were again adjusted to ensure the proper viewing distance of 43 cm. for all test sessions. Monkeys underwent training on the tasks, in their home cages, until such time as their performance over the last 100 trials was significantly better

than chance. Each monkey reached the criterion level of performance in fewer than 700 trials. Each of the monkeys was then required to complete 1,000 test trials.

Results

Accuracy data for the relative numerousness judgment task were analyzed via a 2 (species) x 2 (stimulus type) x 2 (visual field) ANOVA. A main effect for stimulus type was present, $F(1, 22) = 16.42$, $p < .05$, with participants responding more accurately to the Arabic numeral stimuli (91% correct) than for the random dot-patterns (77% correct). A significant interaction between stimulus type and species also occurred, $F(1, 22) = 15.83$, $p < .05$ (see Figure 7). Planned comparisons revealed no significant differences in accuracy for the monkeys regardless of stimulus type, $t(4) = 1.35$, $p > .05$. For human participants however, comparisons revealed significant differences, $t(18) = 3.25$, $p < .05$), in the accuracy of relative numerousness judgments (RNJs) with humans performing RNJs of Arabic numerals (98% correct) more accurately than for random dot-patterns (87% correct). No other significant main effects or interactions were observed.

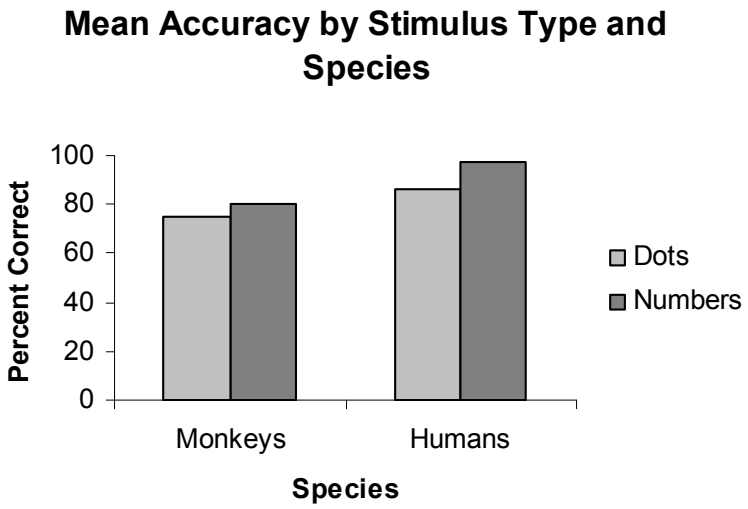

Figure 7.

Analysis of response time data revealed a main effect for visual field $F(1, 22) = 10.08$, $p < .05$, with faster response times occurring with presentations to the right visual field (3.16 seconds for RVF presentation versus 3.50 seconds for LVF presentations). A significant main effect for stimulus type was present $F(1, 22) = 4.41$, $p < .05$. Mean response times were shorter for Arabic numerals (3.16 seconds) than for random dot-patterns (3.58 seconds). The stimulus type variable also interacted significantly with species, $F(1, 22) = 12.05$, $p < .05$ (see Figure 8). Planned comparisons revealed no significant differences in the monkeys' mean response times to Arabic numeral and random-dot pattern stimuli, $t(4) = 0.98$, $p > .05$. Humans however, were significantly faster to judge the relative numerosity of Arabic numeral stimuli than dot-pattern pairs, $t(18) = 3.84$, $p < .05$.

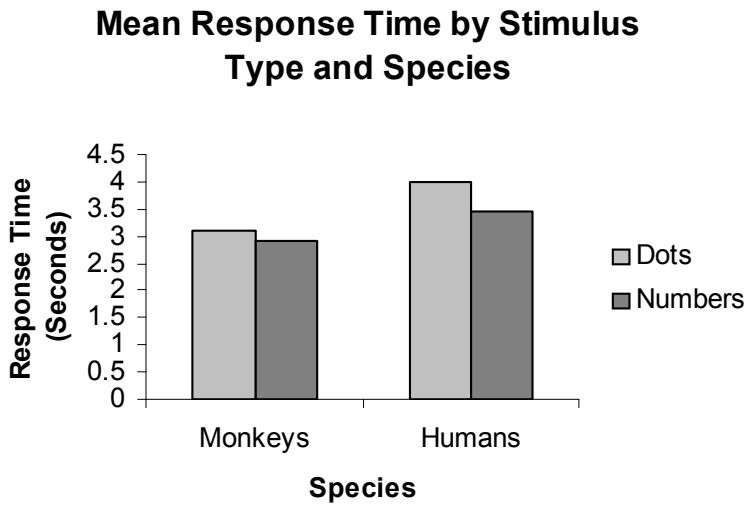

Figure 8.

Discussion

Requiring participants to make relative numerousness judgments rather than simple recognition responses resulted in findings divergent from those of Experiment 2.

Both species remained faster and more accurate for numerals than dot patterns. Both species continued to respond faster when stimuli were presented to the right visual field. But, the interaction between stimulus type and visual field found in Experiment 2 disappeared. Interestingly, stimulus type and species interactions were found for both accuracy and response time.

Analysis of monkeys' accuracy for RNJs of numeral pairs and dot patterns showed no significant differences, although monkeys' were slightly faster for comparisons presented to the right visual field. Given these data, it appears that monkeys may have a left-hemisphere advantage for processing Arabic numerals and other types of quantitative stimuli. Human participants also showed these same performance advantages. They too performed numeral comparisons significantly better than (faster and more accurately) dot pattern comparisons, particularly when presented to the right visual filed (e.g., processed in the left hemisphere. It would appear then that both humans and monkeys share some basic numerical cognitive processes for representing and processing quantities.

According to the Triple-code model (Dehaene & Cohen, 1994), humans make visual representations of numeric quantity when they process Arabic digits, as in Experiment 2 when they were required to make an accurate recognition of numeric and quantitative stimuli; however, according to this model humans utilize analog representations when they are required to make numeric and quantitative comparisons. In this instance, for humans to complete the task correctly, a two-stage process may be needed. Humans may first access visuospatial working memory resources in order to create an analog mental representation of the dot pattern shown on-screen in order to

make the comparison mentally, then convert it to an Arabic numeral (perhaps by counting the dots), and then reference a visual representation "number line" before making a judgment as to which quantity is greater. Such a processing strategy would account for at least a portion of the increase in response time by humans over that of monkeys. The monkeys, who complete both stimulus types with equivalent speed, may possibly have the same type of representational strategy (analog) for all types of numerical tasks, as was suggested by Beran (2004) and Gulledge (1999).

Experiment 4: Investigating Functional Cerebral Asymmetries With Repetitive Transcranial Magnetic Stimulation

Transcranial magnetic stimulation (TMS) represents a unique tool for investigating cortical brain function. Traditionally, lesion studies have been the typical method by which questions of asymmetry, lateralization, and localization have been answered. TMS represents a breakthrough in cortical investigation in that it allows for the creation of temporary and painless "virtual lesions" of cerebral cortex. To date there have been relatively few published studies utilizing repetitive transcranial magnetic stimulation (rTMS) to disrupt cognitive function (Epstein et al., 1996; Epstein & Zangaladze, 1996; Fitzpatrick & Rothman, 2000; Göbel, Walsh & Rushworth, 2001; Hallet, 2000; Pascual-Leone, Tarazona, & Keenan, 1999). Consequently, there are even fewer studies published utilizing animals as subjects, particularly nonhuman primates (O'Shea et al., 2004; Cantalupo, Gulledge, Washburn, & Hopkins, 2006). A more widespread implementation of rTMS with nonhuman species would be valuable for both practical and theoretical reasons. For example, rTMS clearly offers the possibility of avoiding most, if not all, of the typical limitations and shortcomings of more invasive

research techniques (e.g., lesion studies). Moreover, rTMS animal studies would create a baseline for a direct comparison with findings from the abundant rTMS studies conducted with humans. This comparative approach would, in turn, further our understanding of the relation of brain activity and behavior from a developmental viewpoint.

The lack of rTMS studies in nonhuman animals is likely due to many factors including high initial startup costs, novelty of apparatus and techniques, technical and procedural difficulties in implementing reliably the technology with different species. But, in recent years rTMS has become increasingly popular in human studies of the central motor pathways and the relationship between brain activity and behavior (Hallett, 2000; Pascual-Leone, Davey, & Rothwell, 2002). The application of rTMS to a given cerebral area results in the activation of the areas neurons and normal functioning of the area is painlessly, temporarily, and reversibly disrupted (Kircaldie , Pridmore, & Pascual-Leone, 1997; Pascual-Leone et al., 1999; Walsh & Cowey, 1998). If the stimulated area is vital for the cognitive task at hand then performance is impaired or slowed due to the disruption of neural activity by the magnetic field. If the stimulated area is not essential, the application of rTMS either has no effect or even results in facilitated performance (Cantalupo et al., 2006; Marzi et al., 2000; Oliveri, Rossini & Pasqualetti, 1999; Walsh et al., 1998). Such facilitation is likely due to two causes. First, rTMS-induced disruption of one cortical circuit may disinhibit competing cortical circuits (Oliveri et al., 1999; Walsh et al., 1998). Secondly, rTMS is associated with a sound and tactile sensation and these tend to speed performance due to an intersensory localization effect (Marzi et al., 2000). In other words, rTMS may improve performance by serving to help the recipient focus on the task at hand through various attention provoking sensory stimulations.

Numerous advantages are to be found when utilizing rTMS relative to traditional lesion studies for investigating brain-behavior relations. TMS can be used with normal participants thereby eliminating the potential confounds of the presence of additional unknown brain lesions in patients. TMS studies can be conducted acutely thereby avoiding possible reorganization of brain function often seen in lesion patients. TMS studies can be repeated with the same participant, providing an opportunity for careful, controlled, experimental designs. Multiple participants can be tested with the same experimental design thereby allowing for more powerful statistical evaluation of the results. Different brain areas can be targeted across participants thereby allowing for precise mapping of the behavior disruption to a given brain area. Finally, TMS allows for use of different behavioral tasks for the identification of the specific contribution of a given cortical area to a cognitive function (Pascual-Leone & Keenan, 1998).

Thus far, rTMS has primarily been utilized as an effective treatment of depression in humans (Avery, Claypoole & Robinson, 1999; Figiel, Epstein & McDonald, 1998; George, Wasserman & Kimbrell, 1997; Loo, Mitchell & Sachdev, 1999; Reid, Sajahan & Glabus, 1998; Triggs, McCoy & Greer, 1999). Relatively few investigations have been conducted utilizing rTMS to assess the various neuroanatomical correlates of cognitive function. However, Kosslyn, Pascual-Leone and Felician (1999) showed that visual imagery is impaired in humans when rTMS is localized to Broadman's area 17 of cerebral cortex. Boroojerdi, Phipps and Kopyler (2001) administered rTMS to the left and right prefrontal cortex (PFC) and over the left motor cortex during tests of memory and analogical reasoning. Significant increases in response time were found with rTMS over the left PFC, but only in an analogy recall condition. These findings indicate that

the left PFC is relevant to analogical reasoning and that rTMS applied to the PFC can slow down solution time in relation to application to posterior brain regions. Mottaghy et al. (2002) attempted to determine whether working memory and prefrontal function in general might be segregated according to the informational domain (e.g., spatial versus object-based information). Repetitive TMS was applied over the prefrontal cortex in normal males performing either a spatial or a face-recognition delayed-response task. Performance in the spatial task was disrupted by rTMS. Disruption of the dorsolateral prefrontal cortex affected performance on both tasks. Taken together, these findings provide evidence of domain-specific segregation of working memory functions in widely separated areas of prefrontal cortex.

At present, few investigations have been conducted using rTMS with humans or nonhumans to assess hemispheric organization with regard to numerical cognition. Göbel, Walsh, and Rushworth (2001) applied rTMS to the left or right angular gyrus while participants performed a number comparison task with numbers between 31 and 99. Repetitive TMS over the angular gyrus (parietal lobe) was found to disrupt performance on both the number comparison task as well as a visuospatial search task. Performance was particularly impaired for stimulation of the left angular gyrus (see Appendix E). This result would seem to indicate that the left angular gyrus mediates a spatial representation of number. Göbel concludes that this area of the parietal lobe may contribute to the representation of the mental number line. Numerous researchers have concluded that the angular gyrus and its cerebral neighbors (the intraparietal and superior temporal sulci) are closely involved in visuospatial attention (Corbetta et al., 2000;

Gitelman et al., 1999; Rushworth, Ellison, & Walsh, 2001). Therefore, the angular gyrus might be expected to play an important role in the spatial representation of quantity.

Recent evidence from neuroimaging studies has suggested that the left parietal lobe is an important cortical area for numeric representation by humans (Pesenti, et al., 2000; Stansesco-Cosson, et al., 2000). But to date, no investigations have been published pairing TMS and numerical cognition with nonhuman primates as participants that I am aware of. However, recently researchers using TMS with rats attempted to identify the direct neuronal effects of rTMS on learning and memory (Kling, Yarits, Yamamoto, & Matsumiya, 1998). Kling and colleagues studied rats that were allowed to drink distinctively flavored water that later received an IP injection of LoCl. In phase 1, between drinking and the onset of mild malaise, the experimental group of rats received rTMS to the head whereas controls received an equivalent amount of stimulation on the back. Later, when the flavored water was again presented, the experimental rats drank more thereby indicating that they had forgotten that the flavor was associated with illness. These results indicated that there was a mild retrograde memory disruption associated with TMS, but there was no evidence for any TMS-induced structural change within the brain causing the memory deficit. Conversely, Yamada, Tamaki and Wakano, (1995) found no effects of rTMS in three monkeys performing a delayed-response task that required spatial short-term memory.

Therefore, rTMS provides a noninvasive and relatively painless method for stimulation of the cerebral cortex. Repetitive transcranial magnetic stimulation can be used to disrupt the function of a given cortical target thereby creating a temporary "functional brain lesion." This process allows for the study of the contribution of a given

cortical region to a specific behavior. With rTMS we can therefore effectively "knock out" portions of either the left or right-hemisphere in order to determine the effect on numeric and quantitative processing.

Method

Participants. Human participants were two graduate student volunteers from Georgia State University, one left-handed male and one right-handed female (mean age = 28.5 years).

Nonhuman participants were two of the rhesus monkeys (103 & 104) from Experiments 1, 2, and 3. Both had substantial experience completing joystick tasks while under restraint during rTMS application (Canatalupo et al., 2006). One of these animals was left handed and the other was right handed, as assessed by the preferred hand for joystick manipulation.

Apparatus. Both human and nonhuman participants were tested using the same computerized testing system (LRC-CTS) used in Experiments 1, 2, and 3. However, additional hardware was necessary for administration of rTMS. Stimulation for rTMS was provided by a Neopulse Transcranial Magnetic stimulator (Neotonus, Marietta, GA) generating cosine pulses at durations up to 190 microseconds. The stimulator consisted of two main components, the generator unit and the stimulating coil. The generator unit provided manual controls for frequency of stimulation (1-50 Hz), intensity of stimulation (up to 1.5 Tesla, adjustable in 1% increments), and an external BNC connector through which the control unit could be piloted by an external device using a 5V TTL signal. The stimulating coil produced a magnetic field distribution comparable to that of a 5 cm x 10 cm figure-eight coil (Epstein et al., 1996).

The stimulator was controlled externally by an IBM-compatible personal computer (Compaq Deskpro, Intel Pentium II processor) with a digital I/O interface card (Keithley PIO-12) connected to an 8-channel I/O module board (Keithley SRA-01). One channel provided access to the 5 V signal directly from the PC for controlling the stimulator. For testing with the monkeys, two other channels controlled externally powered dispensers via solid-state relays that enable delivery of two kinds of rewards (97 mg fruit-flavored pellets and fruit juice) during testing with TMS.

TMS delivery for both human and nonhuman participants was controlled by a computer program module written using a Pascal-based, object oriented, visual programming tool (Borland Delphi, version 4, Cupertino, CA). The program module allowed full run-time control and manipulation of (a) time onset, (b) duration and (c) frequency of TMS delivery. The precision and reliability of the pulsed output generated by the program module was verified by means of a storage digital oscilloscope (Tektronic model 2221, Richardson, TX). The module controlled also time of delivery and quantity of pellets and fruit juice following TMS and task performance by the monkeys. The TMS program module could be used independently (e.g., for motor threshold assessment) or in full integration with computerized tasks.

Motor threshold assessment. Nonhuman participants were seated in a rhesus monkey restraint chair (Primate Products Inc., Woodside CA) with minimal restraint. Human participants were seated in a standard office chair during motor threshold assessment. Following common procedures in human studies (Reid, Chiappa, & Cross, 2002) the stimulating coil was placed laterally to the vertex and pressed tangentially to the scalp over the hemisphere contralateral to the preferred hand for joystick

manipulation. With the program module set for one second of TMS delivery at 5 Hz at 50% of maximum output the optimal position for eliciting overt twitches of the subject's hand and bicep was determined and marked on the subject's scalp. Subsequently, stimulus intensity was decreased in steps of one percent and stimulated ten times at every step on the marked position. In this manner, motor threshold was assessed as the lowest stimulus intensity that elicited discernable hand and bicep twitches in at least five of ten consecutive stimulations. For the monkeys, at the end of each stimulation, 1.5 oz of fruit juice was automatically delivered to the subject. Each set of ten stimulations was followed by a one minute break. For testing, all participants administered rTMS at levels 5% above motor threshold at 5Hz; this level is generally accepted as the optimum level for providing safe, temporary interference (Green) Pascual-Leone & Wasserman, 1997).

Task and Procedure. Both humans and monkeys completed the same task as in Experiment 3, but with the inclusion of rTMS of either the left or right cerebral hemispheres centered over the inferior parietal lobe. The spatial resolution of the coil did not allow for precise stimulation of an area of cortex smaller than 5 cm X 10 cm, thereby negating the capability to specifically target the angular gyrus, therefore the parietal lobe was targeted. Prior to testing, the magnetic coil was placed over the left and right parietal lobe of each subject. With the coil in place, the position of the coil was then marked with white chalk to ensure proper placement of the coil during each trial. After the participants completed the trial initiation procedure, the quantitative stimuli appeared for 150 ms. There was then a one-second interval between the offset of the stimulus pair and the appearance of the response screen. During this one-second interval, rTMS

application occurred or there was no stimulation. Immediately after the one-second interval, the response screen appeared thereby requiring the subjects to make a relative numerousness judgment.

For the RNJ task there were 12 trial types: Dots presented to the LVF with left-hemisphere magnetic stimulation, right-hemisphere magnetic stimulation, or no magnetic stimulation; dots presented to the RVF with left-hemisphere magnetic stimulation, right-hemisphere magnetic stimulation, or no stimulation; numerals presented to the LVF with left-hemisphere magnetic stimulation, right-hemisphere magnetic stimulation, or no magnetic stimulation; and numerals presented to the RVF with left-hemisphere magnetic stimulation, right-hemisphere magnetic stimulation, or no magnetic stimulation. Trial type and order were randomized throughout testing. Each monkey was required to perform approximately 20 trials of each type (at least 240 trials per animal). Human participants were required to perform approximately 10 trials of each type.

Results

Accuracy data were first analyzed via a 3 (TMS condition) x 2 (trial type) x 2 (visual field) x 2 (species) analysis of variance. The following TMS conditions were used: TMS to the same hemisphere as visual stimulation (e.g., rTMS of the right hemisphere on a trial with stimulus presentation in the left visual field), TMS to the hemisphere ipsilateral to visual stimulation (e.g., rTMS of the right hemisphere on a trial in which visual stimuli were flashed to the right of fixation), and no TMS (i.e., the coil positioned over the left or right hemisphere, but no magnetic stimulation delivered). A main effect for TMS presentation was found, $F(1, 2) = 21.15$, $p < .05$ (see Figure 9). Post-hoc analysis revealed that performance in the no stimulation condition was

significantly better than in either stimulation condition, which in turn did not differ from one another (Tukey's HSD = 8.87).

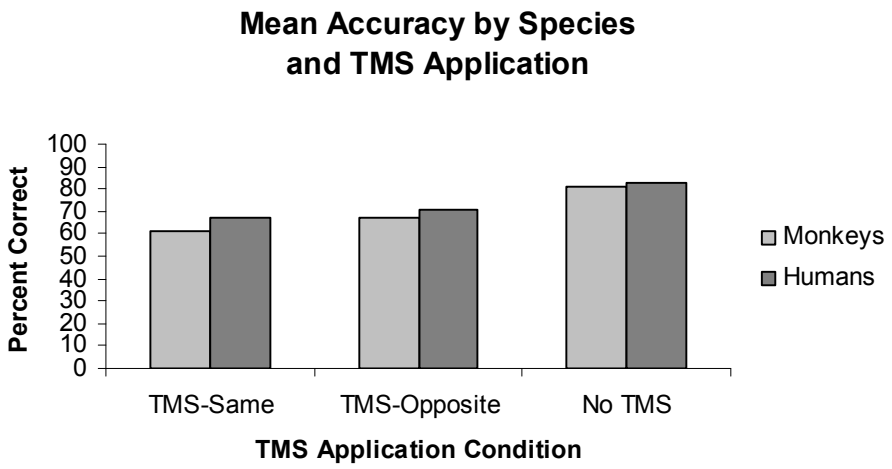

Figure 9.

A main effect for trial type was also found, $F(1, 2) = 35.17$, $p < .05$. Performance was significantly better on the numeral comparisons (81% correct) than on the random dot-pattern comparisons (67% correct). Interestingly, the analysis of visual field approached significance, $F(1, 2) = 15.87$, $p = .058$ (power = .562). Consistent with the response time findings from Experiment 3, mean accuracy for stimuli presented to the left visual field was 72% correct, whereas accuracy for the right visual filed was 76% correct. Analysis revealed no significant interactions. Because patterns of functional cerebral asymmetries may differ as a function of handedness (Hopkins & Washburn, 1994; Hopkins, Washburn, & Rumbaugh, 1989; Morris, Hopkins, & Rumbaugh, 1991) the accuracy data were subsequently analyzed using a 3 (TMS condition) x 2 (trial type) x 2 (visual field) x 2 (preferred hand) ANOVA. This analysis revealed no new main effects or interactions.

Accuracy data were next analyzed with a 2 (visual field of presentation) x 2 (hemisphere of rTMS stimulation) x 2 (trial type) x 2 (species) analysis of variance. The "no TMS" trials were not included in this analysis. A main effect for trial type was found, $F(1, 2) = 13.94$, $p < .05$. A main effect for hemisphere of rTMS stimulation was also found, $F(1, 2) = 5.22$, $p < .05$). Both species performed better with right hemisphere rTMS stimulations than when rTMS was delivered to the left hemisphere. A significant interaction was found between species and hemisphere of stimulation, $F(1, 2) = 6.29$, $p < .05$. The monkeys' performance was not significantly disrupted by stimulation to either hemisphere (69% correct for left hemisphere stimulations and 71% correct for right hemisphere stimulations), whereas the humans' performance was most significantly disrupted by stimulation to the left hemisphere (69% correct for left hemisphere stimulations and 79% correct for right hemisphere stimulations). There were no other significant main effects or interactions.

Response time data were first analyzed via a 3 (TMS condition) x 2 (trial type) x 2 (visual field of presentation) x 2 (species) ANOVA. Analysis of response times revealed a significant main effect for TMS condition, $F(1, 2) = 23.615$, $p < .05$. Response times on trials with application of rTMS were significantly slower than on trials with no rTMS application (mean RT of 708 msec on trials with rTMS application on same hemisphere as visual field of presentation, mean RT of 702 msec on trials in which rTMS and the visual stimuli were presented initially to opposite hemispheres, and 516 msec with no rTMS stimulation. A significant interaction between TMS and species was also evident, $F(1, 2) = 19.284$, $p < .05$ (see Figure 10). Post-hoc analysis revealed that there were no differences in monkeys' response times as a function of TMS

condition. However, humans' performance was significantly affected when presented with rTMS (Tukey's HSD = 179.64 msec). No other significant effects or interactions were found.

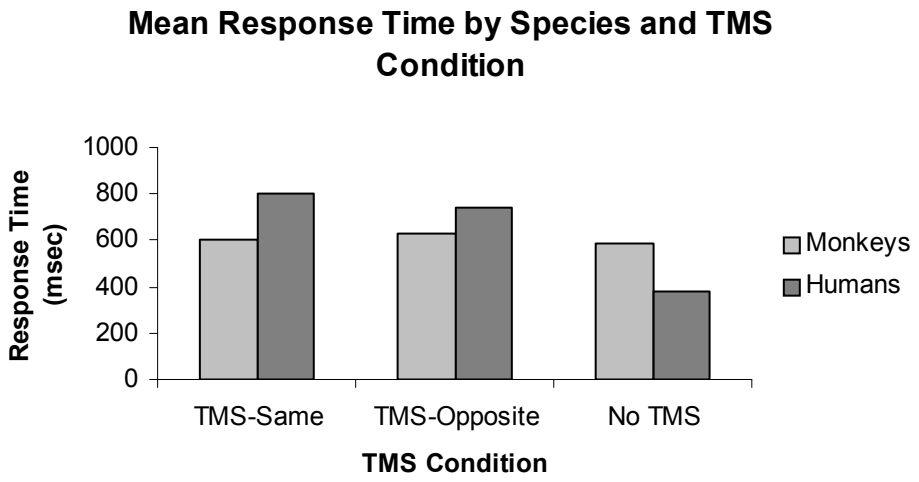

Figure 10.

Reaction time data were next analyzed with a 2 (visual field of presentation) x 2 (hemisphere of rTMS stimulation) x 2 (trial type) x 2 (species) analysis of variance. A main effect for trial type was found, $F(1, 2) = 10.11$, $p < .05$. A significant interaction was also found between species and hemisphere of stimulation, $F(1, 2) = 6.29$, $p < .05$. The monkeys' performance was not significantly disrupted by stimulation to either hemisphere 615 msec. for left hemisphere stimulations and 623 msec. for right hemisphere stimulations) , whereas the humans' performance was significantly more disrupted by stimulation to the left (762 msec.) rather than the right hemisphere (720 msec.). There were no other significant new main effects or interactions.

Because one monkey and one human were left handed, additional analyses of response times were conducted with a 3 (TMS condition) x 2 (trial type) x 2 (visual field

of presentation) x 2 (dominant hand). This analysis revealed a significant interaction between visual field of presentation and preferred hand, $F(1, 2) = 88.92$, $p < .05$ (see Figure 11). Post hoc analysis revealed, as in Experiment 3, that right-handed participants were slower to respond to stimuli presented to the left visual field (750 msec) than the right visual field (610 msec; Tukey's HSD = 115 msec). Response times for left-handed participants were statistically equivalent regardless of visual field of presentation (613 msec for LVF and 610 msec for the RVF).

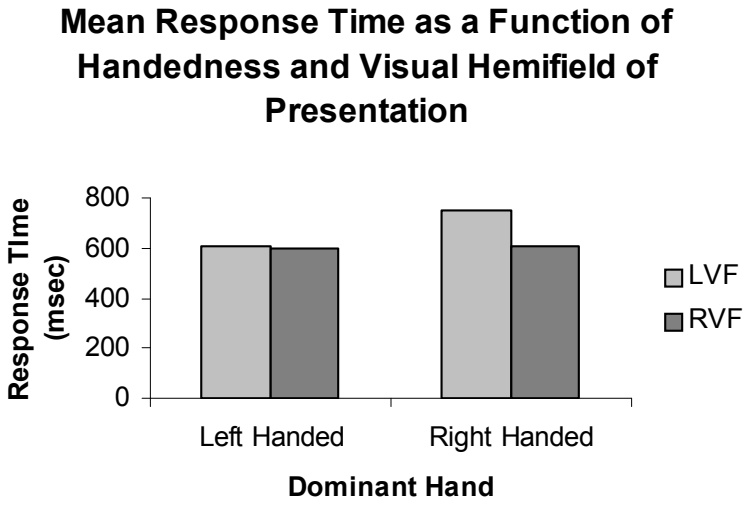

Figure 11.

Discussion

Application of rTMS disrupted numerical cognition. What was surprising in these data is that the effect of magnetic stimulation did not interact with stimulus type or hemisphere, despite the fact that significant main effects of stimulus type and visual field were again observed in the accuracy data for this study. Humans responded more slowly and less accurately on trials during which rTMS was administered, irrespective of the

hemisphere that was stimulated or the stimulus conditions of the RNJ task. The monkeys also responded significantly less accurately on trials in which rTMS was presented, regardless of the stimulus type or visual field of presentation of the RNJ task.

Human participants suffered the greatest disruptions in performance. Humans' average response times for both same- and opposite-hemisphere rTMS application conditions were about 50% greater than those for the no-stimulation condition, whereas monkeys' response times remained comparable across the three conditions. Why would this be? One could argue that perhaps the monkeys were much more acclimated to rTMS application than the humans as the cause for this difference in performance. The monkeys had extensive experience undergoing TMS application whereas the human participants had relatively little, if any, experience under such conditions prior to this study. Curiously, in the no-stimulation condition human response times were faster than those of monkeys, a rare occurrence indeed (e.g., Washburn & Rumbaugh, 1997). The expectation of TMS, though painless, is likely an arousing event. Perhaps the humans fell victim to the Yerkes-Dodson Law in that they may have been over-aroused by TMS application. This explanation might account for increases in RT for stimulation trials and improved performance on no-stimulation trials.

These findings also argue for interhemispheric competition in the cortical network of spatial attention of humans, but not necessarily for monkeys. Consequently, human performance was affected by TMS application to either cerebral hemisphere with left-hemisphere stimulation resulting in the greatest decreases in performance. Such asymmetrical processing by humans would serve to be a huge advantage from a neurological standpoint as it would likely serve to nearly double cognitive capacity. If

each cerebral hemisphere subsumes the lead role for different operations, but maintains communication with the other hemisphere, thereby providing for nearly twice as much processing capacity. The monkeys, on the other hand, were equally affected by TMS application to either cerebral hemisphere, suggesting that the monkeys may have a redundant cortical system for processing quantities with neither hemisphere possessing a significant advantage over the other.

Curiously, response times in Experiment 4 averaged 645 milliseconds whereas response times for Experiment 3 averaged 3,375 msec, an 80% decrease in response time. This reduction occurred despite the fact that the same task was administered in Experiment 3. There were however some procedural differences between the experiments, in addition to the use of rTMS in the fourth study. In the present experiment, the humans used a joystick rather than a keyboard to respond. Also, there was a 1-second delay for implementation of the TMS condition between offset of the stimulus pair and the response screen; however, the difference in mean RT between the studies is far greater than one second (2.73 seconds).

Other researchers have shown TMS to cause facilitative effects (Marzi et al. 1998; Oliveri et al., 1999; Walsh et al., 1998). One explanation for such an effect is the possibility that rTMS on a given trial leads the participant to devote more attentional resources to the task at hand, thereby leading to a decrease in response time (Marzi et al., 1998). A second explanation for this facilitation was provided by Walsh et al. (1998) and Oliveri et al. (1999) who stated that TMS disruption of one cortical area may disinhibit competing cortical circuits thereby leading to faster responding. This is precisely the

finding of Hilgetag, Theoret, and Pascual-Leone (2001) who reported a facilitation effect of rTMS over the ipsilateral parietal cortex of human participants.

For right-handed humans and monkeys, both dots and numerals were processed more rapidly when presented to the right visual field. Interestingly, right-handed participants showed similar response times to those of left-handed individuals for both stimulus types when presented to the right visual field. However, for stimuli presented to the left visual field, the right-handed humans and monkeys exhibited a significant increase in response time. This increase in response time may possibly be due to a delay in processing necessitated by the contralateral organization of the cortical system. Recall that information concerning stimuli falling to the left of the visual fixation point (i.e., in the left visual field) is initially projected to the right cerebral hemisphere, whereas information concerning stimuli to the right of the visual fixation point (i.e., right visual field) is initially processed in the left cerebral hemisphere. Information is then distributed between regions of both cerebral hemispheres via the corpus collosum, so that the hemisphere ipsilateral to the visual field of presentation receives stimulation indirectly. This gives one hemisphere (the hemisphere contralateral to the visual field in which the stimulus was flashed) privileged access to the visual stimulus with respect to time and quality. Right-handed participants are more likely to have left-hemisphere lateralized function for processing symbolic stimuli (e.g., Arabic digits) than are left-handed participants. Previous research has shown that 96% of right-handed participants are left-hemisphere dominant for language, whereas only about 70% of left-handed participants are left-hemisphere dominant for language (Rasmussen & Milner, 1977). Therefore, the right-handed participants may have exhibited longer response times for stimuli presented

to the left visual field in part because they must wait for the transfer of quantitative representation from the right to the left hemisphere before responding.

General Discussion

Numerous researchers have sought to determine whether human and nonhuman primates possess similar numerical skills, skills that are similar in quality if not kind. In almost every case, nonhuman primates have shown themselves to be apt pupils for various tests of numerical competence. The present investigation is no exception. In as much as the monkeys have rather limited cognitive skills when compared to those of humans, the monkeys have once again shown basic numeric abilities (e.g., RNJ's of pairs of numerals and dot patterns <10 in quantity) to be quite similar to that of their human counterparts. The real question however is whether these performance similarities are due to similar cortical structures or capabilities.

In this study, both species have displayed a propensity for more accurate responding to congruent than to incongruent stimuli. Monkeys' response times on such tasks are nearly identical to those of humans. The slopes of the symbolic distance curves for the monkeys and humans were also almost identical. Dehaene (1993) concluded that results like these (SNARC effects) occur because of a system of numeric representation that relies on a "mental number line" that is oriented left to right like a number-line with smaller quantities appearing on the left and greater quantities appearing to the right. From these data it would appear that both species represent numerosity in something akin to a number-line like fashion. Both humans and nonhumans responded more quickly when presented with congruent stimuli. Taken together, these findings argue strongly for

a cortical process of numeric representation and processing that is similar in both species, albeit one that is generally less accurate but faster for the monkeys

In an attempt to determine whether humans and monkeys differ with respect to hemispheric lateralization of numerosity, a divided visual field task was employed. The results indicated that the human and monkeys responded in very similar ways. Both were faster and more accurate in responding to numerals than to dots, and were faster and more accurate when stimuli were presented to the right visual field than the left visual field. Again, the results for the two species were generally similar; however for the first time in this investigation, species differences were apparent. In terms of accuracy and response time, monkeys' performance in the divided visual field paradigm was equivalent for both stimulus types. Humans however, performed significantly better on the numeral trials than on dot-pattern trials. This difference in performance likely occurs because humans are more familiar with numerals and more adept at symbolic (language) processing, whereas the monkeys are more familiar with the dot patterns. This would account for the species differences in performance on these tasks in Experiment 2. Recall that the performance of the humans and monkeys was almost identical although the monkeys showed consistently faster response times. Humans may be slower because they must necessarily take time for a transfer of representation codes from the right-hemisphere to the left. For example, patients NAU (Dehaene & Cohen, 1991) and GUI (Cohen, et al, 1994) both suffered from large posterior left-hemisphere lesions. When asked to name Arabic numerals, both had to count before naming the numeral, yet both were easily able to make accurate greater-than/less-than judgments about pairs of numerals. Patient GUI could not read aloud Arabic numerals, but was still able to name and understand familiar

numerals such as 1789 (French Revolution) and 1918 (World War I), indicating preserved access to number meaning (Dehaene & Cohen, 1991).The monkeys, on the other hand, are not bound by such a transfer as they may have a redundant representation system active in both hemispheres. This explains how the monkeys can display equivalent performance for stimuli presented to both visual fields whereas human performance is better for numerals when processed in the left hemisphere and better for dots when processed in the right hemisphere.

From a methodological standpoint, it might be advantageous to increase or decrease stimulation intensity in the TMS conditions to determine whether accurate performance can be further disrupted or whether response time facilitation can be further increased. In addition, the use of a smaller coil would allow for stimulation of more focused areas of cortex thereby allowing for more definitive conclusions to be drawn about localization within a hemisphere as well as lateralization between the hemispheres.

Future research should concentrate on furthering the already robust findings reported here and elsewhere. The inclusion of language-trained apes would provide an interesting link between the monkeys and the humans. Monkeys, not bound by linguistic coding, already show impressive quantitative abilities, similar to those of humans. The addition of language trained apes and apes with no language training to this research paradigm would promote a better understanding of the development of numerical competence as well as the accompanying neural correlates. Indeed, if human laterality is driven by the left-hemisphere asymmetry for language, language trained chimpanzees might also show the quantitative processing biases exhibited by humans. Conversely,

non-language trained chimps should show similar performance to that of the monkeys discussed within.

These findings serve to further elucidate the interspecies similarities and differences between human and nonhuman primates. Once again nonhuman primates have shown themselves to possess complex cognitive abilities far beyond what many would have expected. However small, these cognitive differences do exist, and would appear to be driven by our uniquely human skill with, and propensity for, language. This research leads to the conclusion that human possess an important laterality advantage over nonhuman primates. It is likely this specialization of function that allows us to be so adept at symbolic processing.

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Appendix A.

Symbolic distance effects for human and nonhuman primates on number trials.

(SD)	Humans	Monkeys
One (1)	1460 msec	1360 msec
Two (2)	1310 msec	1280 msec
Three (3)	1190 msec	1140 msec
Four (4)	1160 msec	920 msec
Five (5)	1180 msec	910 msec
Six (6)	930 msec	850 msec
Seven (7)	915 msec	850 msec
Eight (8)	820 msec	860 msec

Appendix B.

Symbolic distance effects for human and nonhuman primates on random-dot trials.

(SD)	Humans	Monkeys
One (1)	1520 msec	1480 msec
Two (2)	1260 msec	1310 msec
Three (3)	1190 msec	1090 msec
Four (4)	1060 msec	1040 msec
Five (5)	1180 msec	1030 msec
Six (6)	910 msec	1070 msec
Seven (7)	940 msec	960 msec
Eight (8)	1240 msec	1070 msec

Appendix C.

Symbolic distance effects for human and nonhuman primates on congruent trials.

(SD)	Humans	Monkeys
One (1)	1200 msec	1030 msec
Two (2)	1090 msec	1030 msec
Three (3)	1040 msec	970 msec
Four (4)	1100 msec	900 msec
Five (5)	950 msec	880 msec
Six (6)	960 msec	930 msec
Seven (7)	960 msec	890 msec
Eight (8)	1050 msec	950 msec

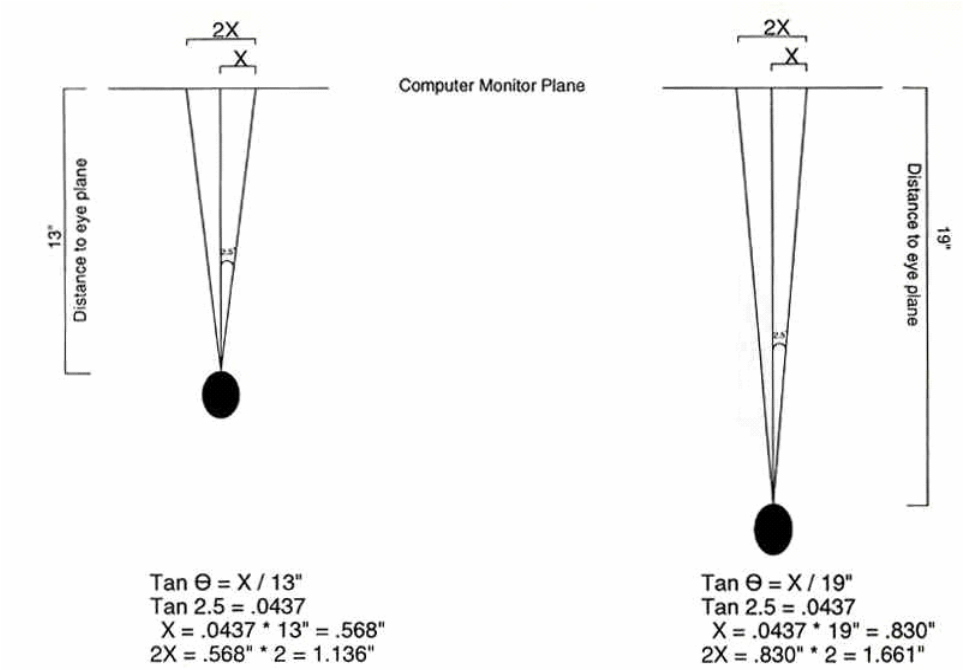
Appendix D.

Symbolic distance effects for humans and nonhuman primates on incongruent trials.

(SD)	Humans	Monkeys
One (1)	1390 msec	1230 msec
Two (2)	1150 msec	1090 msec
Three (3)	1080 msec	1050 msec
Four (4)	1040 msec	1030 msec
Five (5)	1070 msec	990 msec
Six (6)	920 msec	970 msec
Seven (7)	990 msec	980 msec
Eight (8)	840 msec	970 msec

Appendix E.

Coronal view of human brain with left angular gyrus highlighted.



In the first two examples the horizontal lengths of stimuli which subtend 5 degrees at viewing distances of 30 and 50 cm. are determined. First, an imaginary line is projected from the eye to the stimulus. This line is perpendicular to the viewing plane and it establishes two right triangles. The angles measured at the eye are each 2.5 degrees.

The TAN (Tangent) of 2.5 degrees equals .043. The TAN of an angle equals the length of the side opposite the angle divided by the length of the side adjacent to the angle. Therefore, in the example for the 30 cm. viewing distance, X (opposite side length) = (.043) * (30 cm.) = 1.31 cm. (1/2 the horizontal length of the stimulus). Multiply 2 * X to find the horizontal length of the stimulus which subtends 5 degrees at the 30 cm. viewing distance.