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M.A., Emory University, 2014
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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

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Humans think about order and number using a spatial representation, and the orientation of this representation is influenced by learning to read and count in a particular direction. For example, people who read and count from left to right represent small/early items on the left side of space and large/late items on the right side of space. Evidence that pre-verbal children organize order and number spatially raises the possibility that humans are predisposed to organize magnitude and order using space without explicit language training. Nonhuman animals also represent magnitudes and order. I tested the hypothesis that nonhuman primates use spatial representations to code order. I reasoned that if ordering depends on spatial representation then performance on an ordering task would be more impaired when performed concurrently with a spatial memory task than when performed concurrently with a non-spatial visual matching task. Across species and tasks I found that concurrent cognitive load impaired performance, but I did not find that this impairment was especially large with concurrent spatial and ordinal processing. In Manuscript 1, orangutan and chimpanzee performance was generally impaired in all concurrent cognitive load conditions, suggesting that spatial memory, visual memory, and ordering are all supported by a general working memory resource. In Manuscript 2, I tested rhesus monkeys on a similar set of experiments in which an ordering task was embedded within a spatial memory task and a non-spatial visual matching-to-sample task. I again found that spatial memory was impaired under all concurrent cognitive load conditions. Taken together, this set of experiments suggests that there is a domain general working memory resource supporting spatial and visual cognition in apes and monkeys, rather than a resource supporting spatial and ordinal processing specifically.

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General Introduction

As someone reading English, you are probably inclined to visualize B to the left of D if told to imagine the alphabet. If I asked you to remember a list of words, you would probably imagine items earlier in the list on the left side of your mental representation and the items later in the list toward the right (Previtali, de Hevia, & Girelli, 2010). There is accumulating evidence that the mechanism underlying these visualizations is a spatial representation that is shared across species.

Humans use a spatial representation when performing numerical cognition and when performing tasks based on ordered representation of novel and familiar stimuli (Dehaene, Bossini, & Giraux, 1993; Gevers, Reynvoet, & Fias, 2003; Prado, Van Der Henst, & Noveck, 2008; Previtali et al., 2010). Nonhuman animals can differentiate items of different numerosity (for a review see Brannon, 2006), and order stimuli (e.g. Merritt & Terrace, 2011) in ways that are similar to humans (e.g. Cantlon & Brannon, 2006). Human infants also associate magnitude with space (e.g. de Hevia, Girelli, Addabbo, & Cassia, 2014; Rugani & de Hevia, 2016). Similar cognitive mechanisms have been proposed to support both numerical and ordinal cognition in humans and nonhuman animals (e.g. Gevers et al., 2003). Neurological studies indicate that similar regions in the brain support spatial and numerical cognition in humans (Hubbard, Piazza, Pinel, & Dehaene, 2005), and these brain regions are also activated when nonhuman primates are performing numerical and spatial cognition tests (Nieder, Diester, & Tudusciuc, 2006; Nieder & Miller, 2004). Here I will discuss studies that find that the ability to remember sequences is widely shared across humans and nonhumans animals. Because similar patterns of results have been observed from ordinal and numerical experimental paradigms and across species a parsimonious explanation for the parallels is that humans' and nonhuman animals' behavior is controlled by the same mechanism. Evidence from nonhuman animals suggests that a predisposition to associate space and order is an evolutionarily ancient feature of cognition, and is an efficient organizing principle. I will argue that the cognitive mechanism supporting the ability to order is a mental representation that is spatial.

Spatial representations of magnitude and order in humans

A mental number line

A leading theory in human numerical cognition is that humans represent numbers and magnitudes spatially (Dehaene et al., 1993). Specifically this spatial representation has been described as a mental number or magnitude line (Cheung & Lourenco, 2016; Holmes & Lourenco, 2011; Longo & Lourenco, 2007; Wood, Willmes, Nuerk, & Fischer, 2008). The mental number line hypothesis proposes that our representation of number goes, for Westerners, from left to right with small numbers on the left and large numbers on the right. Magnitude difference is represented by spatial distance. Much of the evidence for spatial-numerical associations in humans comes from the spatial-numerical association of response codes, or SNARC, paradigm (Dehaene et al., 1993). In this paradigm participants are asked to categorize a numeral presented on a screen as odd or even by responding on the left or right side of space. Participants are not asked to respond on the basis of the magnitude of the number presented, yet there is an interaction between the side of space and the magnitude of the stimulus. English speaking participants respond more quickly on the left when presented with a small number, and more quickly on the right when presented with a large number. These response facilitations suggest that the simple act of viewing a number causes spatial attention to shift in the direction in which the viewed number is represented on the mental number line (Wood et al., 2008).

Even before learning language, humans represent magnitude spatially. Evidence from human infants supports the idea that magnitude and space share a representational system (de Hevia & Spelke, 2010; Rugani & de Hevia, 2016), and that this representation is preferentially represented from left to right (de Hevia, Girelli, et al., 2014). Young infants generalized their habituation for increasing or decreasing numerosities to increasing or decreasing lengths. This indicates that the infants already associated number with space (de Hevia & Spelke, 2010). Additionally, infants looked longer at novel increasing numerosities that were presented left-to-right, even if they had been habituated to decreasing numerosities presented from left-to-right. They did not show differential looking time to numerosities presented right-to-left (de Hevia, Girelli, et al., 2014). This suggests that humans are predisposed to organize number in a left-to-right orientation. Even neonates who are under 3 days old associate number with space especially when number and space are positively related (de Hevia, Izard, Coubart, Spelke, & Streri, 2014). Four month old infants are also able to represent sequences that do not involve numerical stimuli (Macchi, Picozzi, Girelli, & de Hevia, 2012). These results indicate that number and order are represented spatially in humans who have not yet learned language.

In addition to being present independent of language, there is also evidence that the mental number line may be functionally isomorphic with physical lines, i.e. the mental representation of the number line shares the same metric and is processed as though it were a physical line. Patients with right parietal damage and subsequent left hemispatial neglect bisect physical lines right of center. They also misstate the midpoint of a numerical interval as greater than the actual midpoint (Zorzi, Priftis, & Umiltà, 2002). A displacement toward the larger number in the numerical interval suggests a corresponding bias to the right of center of a physical line that aligns with their perceptual neglect (for a review see Umiltà, Priftis, & Zorzi, 2009; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006). These patterns do appear to be unique to number representations. Neglect patients do not bisect letter or month intervals with the same biases observed for numbers (Zorzi et al., 2006). These results suggest that numbers are represented differently than other ordered series, and the number line is functionally isomorphic with physical space in a way that other non-numeric sequences are not. However, evidence from experiments with sequences contradicts the proposal that series are not represented spatially and suggests that order is associated with space (Prado et al., 2008).

Spatial representations of order

Another explanation for the SNARC effect proposes that there is not a spatial representation of order stored in long-term memory as a mental number line. Rather, the representation is much more flexible than a functionally isomorphic line and is a temporary relational representation formed in working memory for task completion (Abrahamse, van Dijck, & Fias, 2016; Abrahamse, van Dijck, Majerus, & Fias, 2014; Ginsburg, van Dijck, Previtali, Fias, & Gevers, 2014; van Dijck, Abrahamse, Acar, Ketels, & Fias, 2014; van Dijck, Abrahamse, Majerus, & Fias, 2013; van Dijck & Fias, 2011; van Dijck, Gevers, & Fias, 2009). This hypothesis suggests that the SNARC effect is driven by items earlier in the sequence being associated with the left side of space and items later in the sequence being associated with the right side of space all of which happens online in working memory. If spatial-numerical associations are due to a mental number line representation stored in long-term memory, then even when numerals are put in a new order, their magnitude will drive the SNARC effect, rather than their recently learned random order. Participants who had to memorize a random order of numerals and were then asked to respond to whether the sample numeral was odd or even, as in the typical SNARC task, did not show a SNARC effect for the magnitude of the number, but rather showed a SNARC effect for the position within the sequence (van Dijck & Fias, 2011). This suggests that the order of the series drives the representation, rather than a long-term mental number/magnitude line generating the results.

Working memory for order also interacts with spatial attention (van Dijck et al., 2013). Again, participants were asked to learn a sequence of numbers. They then completed a visual attention task in which a number was presented at the center of a screen. The number disappeared and a dot would appear to the left or the right of center. Participants had to respond to a button when they saw a dot appear, but only if the number that had just been presented was from the newly learned sequence. Participants were faster to register seeing the target when it was on the left after seeing items earlier in the sequence and on the right after seeing items later in the sequence. There was no interaction between the magnitude of the digit presented and spatial position. A long-term mental number line is unlikely to be flexible or over-ridden when a task puts magnitude and order in conflict (Abrahamse et al., 2016). In this study, the short-term ordered series of numerals was associated with space more strongly than was the magnitude of the numbers. This supports the idea that representations of order are spatial, and the representation may be formulated in working memory. These studies have prompted the criticism that it is keeping the order in mind to complete the task that is driving these results (e.g. Cheung & Lourenco, 2016). In other contexts it is not the order driving the spatial representations but the magnitude. This is a fair criticism, but it does not negate the fact that order can and does drive the spatial representation when task demands require it. Additionally, even numerical representations are flexible and dependent on task demands. The orientation of the “mental number line” is flexible (Bächtold, Baumüller, & Brugger, 1998; Patro & Shaki, 2016; Shaki & Gevers, 2011; Shaki, Petrusic, & Leth-Steensen, 2012). Participants who are told to imagine a clock face show a right-to-left spatial representation, compared to the left-to-right spatial representation observed in participants who imagine a ruler (Bächtold et al., 1998). Therefore, there is flexibility within the spatial representational system, and both order and number representations are susceptible to task demands.

There is also compelling evidence that a spatial organization extends to other ordered stimuli. Sequences such as months of the year, letters of the alphabet, and days of the week all show SNARC effects such that Western participants are faster to respond to months/letters/days that are early in the sequence on the left side of space than the right side, and the opposite side of space for later items in the sequence (Gevers et al., 2003; Gevers, Reynvoet, & Fias, 2004). In one such study, participants were asked to respond based on whether a stimulus, a month of the year, occurred before or after a comparison stimulus, July, in which case the task was *order relevant* and participants had to directly process and respond according to the order of the stimuli (Gevers et al., 2003). Alternatively, participants were asked whether a particular phoneme, R, occurred in the sample stimulus, an *order irrelevant* task, and they may have implicitly processed the order of the stimuli. Spatial-order associations were found when the participant was responding both to the order relevant and the order irrelevant task. The symmetrical performance on both order relevant and order irrelevant tasks indicates that order, like number, is implicitly processed, it can be tested using similar paradigms as numerical stimuli, and it is spatially represented. It is important to note that these findings contradict those found by Dehaene et al. (1993). In this seminal SNARC study, no interaction between ordered stimuli and position was found. However there were several issues with this finding. First, the study only had 10 participants, and therefore had very low power. And second, in no experimental condition was the order of the stimuli activated, which, given the study's low power, may have led to no significant SNARC effect (Dehaene et al., 1993).

In the SNARC tasks described above, the ordinal relations of the stimuli used were very familiar to the participants. One possible explanation for the SNARC results for days of the week and letters of the alphabet is that these are sequences that have extensive directional training from reading direction, timelines, and calendars that go from left to right for Western participants. Yet, significant SNARC results are found for novel lists of everyday words that are learned in the experimental context (Previtali et al., 2010). Participants were faster to report whether the letter R was in a target word on the left side of space than the right side of space for items early in the sequence, and the opposite was true for items at the end of the sequence. Similarly, participants who learned a sequence via transitive reasoning were faster to respond on the left for pairs of items earlier in the sequence and on the right for pairs later in the sequence (Prado et al., 2008). This indicates that these spatial representations are due to a mechanism other than trained associations between a particular sequence and space. These findings have specific relevance for nonhuman animal studies because nonhuman animals do not have extensive experience ordering any particular sequences, but still may represent order spatially.

Animals show patterns that suggest spatial representations across tasks involving ordered stimuli

Box 1. **Weber's Law and ordinal cognition**. Numerical cognition and ordinal cognition share many properties. Numerical cognition relates to one's ability to think about and discriminate items of different numerosity while ordinal cognition relates to thinking about and manipulating sequences that do not necessarily include number. One of the few laws in psychology is related to numerical cognition. Weber's Law states that the discriminability of two quantities depends on their ratio. So it is easier to discriminate one from two than eight from nine and seven to twelve is easier than seven to eight. Two effects are congruent with these findings: distance and magnitude effects. **Distance effects** indicate that the more numerically different two items, the easier they are to discriminate. 3 and 9 are easier to discriminate than 3 and 7. **Magnitude effects** suggest that large numbers are harder to discriminate than smaller numbers. 2 and 3 are easier to discriminate than 8 and 9. Because arbitrary ordered stimuli, unlike numbers, do not have inherent ratio properties, we can dissociate these effects and examine distance and magnitude effects separately rather than applying Weber's law to tests of ordinal cognition.

The mechanisms supporting human ordinal and numerical cognition are likely similar to those supporting the same abilities in nonhuman animals. In truly comparative study designs, in which humans and nonhuman animals are tested with the same procedures, similar patterns for ordinal and numerical cognition result (e.g. Gazes et al., 2014; Merritt & Terrace, 2011). **Distance** and **magnitude** effects are key pieces of evidence supporting the idea that nonhuman animals and humans share numerical cognition mechanisms (See Box 1). Two numerals are easier to discriminate if they are more numerically different. So 2 and 7 are easier to discriminate than 2 and 5. This is the distance effect. Additionally, smaller items are easier to differentiate than large numbers. So 2 and 3 are easier to distinguish between than 6 and 7. These are magnitude effects. The very language used to describe these effects indicates a spatial coding of magnitude. If two items are "distant" from each other, space as well as magnitude can be used to discriminate between them. When rhesus monkeys respond to pairs of items with different numbers of dots, their performance follows Weber's Law (Box 1; Cantlon & Brannon, 2007). These effects are not unique to rhesus monkeys, and similar results have been found across species tested on numerical discriminations (for reviews Brannon, 2006; Feigenson, Dehaene, & Spelke, 2004).

Transitive inference

Transitive inference, or TI, is the ability to determine a novel item's relation to another item based on its shared relation with a third item (Figure 1). For example, Emily is faster than Ryan, and Ryan is faster than Tom. Because of Tom's and Emily's shared relationship with Ryan, we know that Emily is faster than Tom. The ability to make such inferences is shared by many nonhuman animals including rats (Davis, 1992), squirrel monkeys (McGonigle & Chalmers, 1977), rhesus monkeys (Gazes, Chee, & Hampton, 2012), pigeons (Lazareva & Wasserman, 2006), and chimpanzees (Gillan, 1981; for a review see Vasconcelos, 2008). However, the cognitive mechanisms supporting this ability may not be the same across species, and more than one mechanism may control performance in a single species. One hypothesis suggests that when learning TI relations, animals represent the list items spatially leading to results such as the symbolic distance effect, or SDE (for an early description D'Amato & Colombo, 1990; Gazes et al., 2012; Gazes et al., 2014). The symbolic distance effect is similar to the distance effect found for numerical stimuli (Box 1). In this case, it is symbolic because TI stimuli do not have explicit magnitudes, but they may have magnitude-like properties. Stimuli that have more intervening items between them, if represented spatially, should be easier to discriminate.

If we add more people to the example above, and tell you that Tom is faster than Celia and Celia is faster than Sarah, you might have to take an extra second to decide if Ryan is faster than Celia. Ryan and Celia have only one intervening person between them. However, you would be much faster to determine that Ryan is faster than Sarah because they have 2 intervening people, thus more distance (Figure 1B). Symbolic distance effects are found across species performing transitive inference tasks suggesting a shared spatial representation of TI lists (Bond, Kamil, & Balda, 2003; Gazes et al., 2012; MacLean, Merritt, & Brannon, 2008; Merritt & Terrace, 2011).

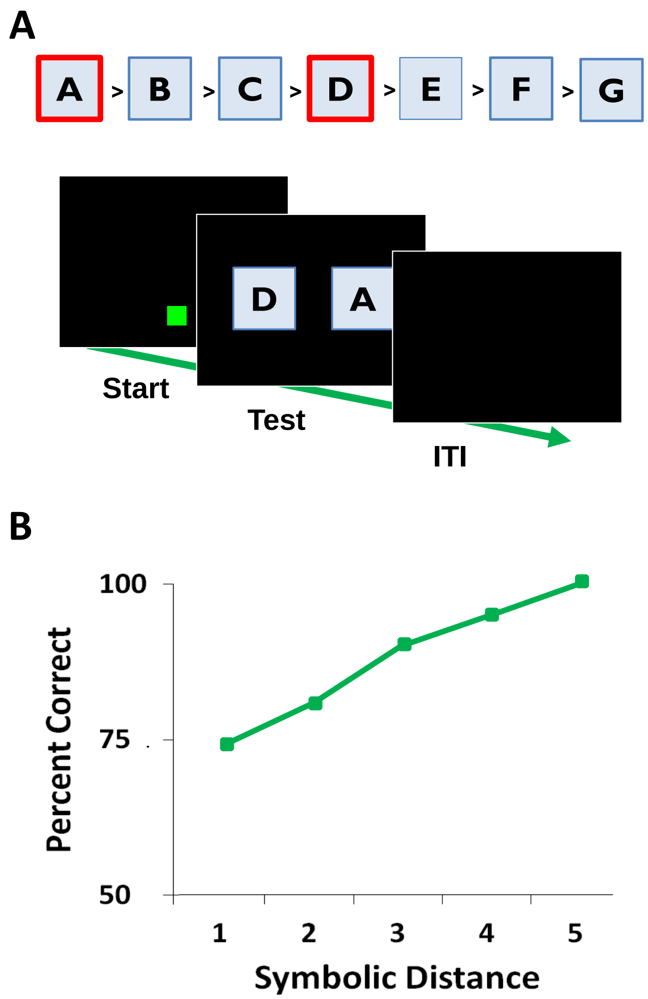

Figure 1. Transitive inference task and performance. A) A typical transitive inference test. Subjects are trained on the list by seeing adjacent pairs (i.e. stimulus C and stimulus D) and learning to touch the stimulus that occurs earlier in the list. So for pair CD, stimulus C is correct. For DE, stimulus D is correct. They are then tested on non-adjacent pairs, like stimulus A and D in the example. B) Symbolic distance effects are found for typical TI performance. As the number of intervening items increases, performance increases. Pair BD has a symbolic distance of 1 and pair AG has a symbolic distance of 5.

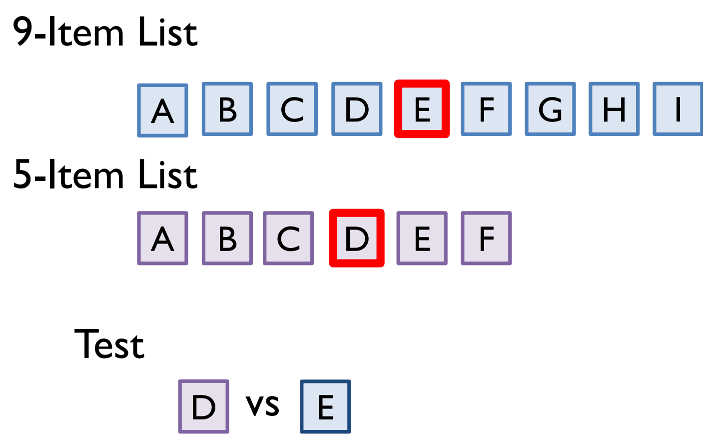

Figure 2. Relative vs. absolute ordinal representation. Monkeys and humans were trained on two lists. One had 9 items and one had 5 items. They were then shown test pairs in which one stimulus was from each list. When stimulus D from the 5 item list was put in conflict with stimulus E from the 9-item list it tested whether the participants were using an absolute rule of or a relative rule. If participants choose item D they are choosing the item that corresponds to an absolute representation: item D is the 4th item in the list. If they choose item E a relative representation is controlling their choice: item E from a 9-item list is closer to the beginning of its list than item D is from the beginning of its 5-item list. Both monkeys' and humans' chose the item relatively closer to the beginning of the list (E in this case), a choice that is based on relative ordinal representations (Merritt & Terrace, 2011).

Monkeys and humans respond similarly to manipulations of the TI test designed to elucidate features of their representations of TI lists (Merritt & Terrace, 2011). Relative ordinal information, rather than absolute ordinal information, controls both monkeys and humans choices when making TI decisions (Figure 2). This means that the length of the list and therefore the relative spatial location of any item from the first or last item of the list influences performance. Monkeys and humans were trained to pick the item closer to the beginning of a list. At test they were presented with the 3rd item of a short list and the 3rd item of a long list. Because the 3rd item of a long list is relatively closer to the beginning of its list it was chosen over the item that is relatively closer to the end of a short list (Figure 2; Merritt & Terrace, 2011). These results are consistent with a spatial representation supporting memory for the lists learned in this context across in humans and nonhuman primates.

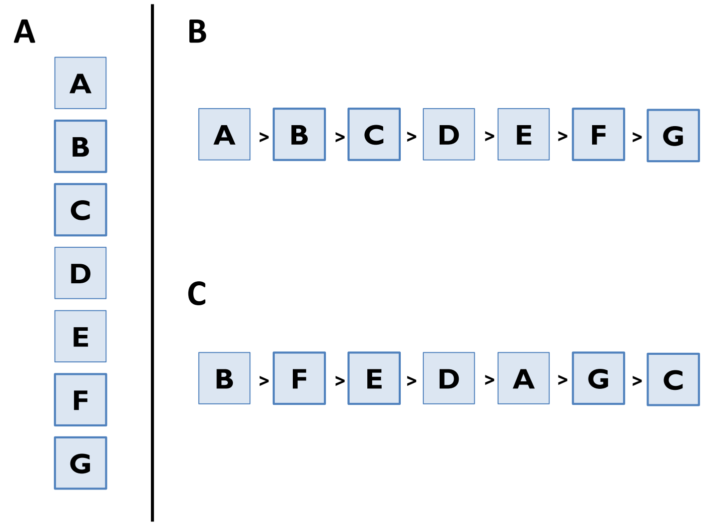

Figure 3. Spatial training is put in conflict with transitive inference performance. A) Monkeys and humans were first trained on a list using space. They learned to associate list items to their spatial location within the vertical presentation of all list items. After reaching criterion on the spatial training, participants moved on to transitive inference training and testing B) Half of the human participants received TI training that was congruent with the spatial training, i.e. in the same order. The TI training and testing was the same as described in Figure 2. In this case the item that had been on the top of the vertical layout was now "A" (always reinforced) in the TI list and the bottom was "G," (never reinforced). B) The other half of the participants received incongruent TI training. In this case the spatial training had no association with the order of the TI list, although the same images were used. All monkeys received both types, but half received congruent first and half received incongruent first (Gazes, Lazareva, Bergene, & Hampton, 2014).

Additionally, explicit spatial training facilitates TI performance in humans and rhesus monkeys (Figure 3; Gazes et al., 2014). Humans and rhesus monkeys learned a list of seven images that were presented vertically (Figure 3A). They were trained that each item had a particular spatial location within the vertical series. After reaching criterion on the vertical list training task, monkeys and humans were then give traditional TI training and tests. Half the participants received spatial training that then corresponded to the list order for TI (Figure 3B) and half received training that did not correspond to the list order for TI (Figure 3C). Adult humans who learned a spatial association of list items that then was congruent to the transitive inference tests that they subsequently received, performed better than participants who received spatial training that was incongruent to the order of items during the transitive inference testing (Gazes et al., 2014). The results from monkeys were more ambiguous. Unlike the human participants, monkeys received both congruent and incongruent training and testing, the order of the tasks counterbalanced across subjects. Monkeys who first received congruent spatial and transitive inference tests, performed better on the TI tasks after the congruent spatial training than after the incongruent spatial training. However, this was not true for monkeys who were first trained with a spatial organization that did not correspond with the order of the TI task. These monkeys did not perform better on the TI test, even after they switched to the congruent condition and received spatial training that did correspond with the TI list order. It is important to note that the monkeys in this experiment were highly trained, and had had previous experience with the TI paradigm. These inconclusive results do not indicate that monkeys are not spatially organizing TI lists. The results do indicate that monkeys may be able to use different strategies depending on task demands, and although a spatial strategy may be most efficient in one case, they can learn to ignore space in another context. Even with ambiguous results, this experiment represents an important test of how space can influence ordinal cognition.

Although similar results were found with humans and nonhuman primates performing TI tasks (Gazes et al., 2014; Merritt & Terrace, 2011), the cognitive mechanism controlling the ability to remember and process sequence information may be different across species. Some species may have an ecological need to readily use ordered information, such as remembering the ranks of members of large complex groups, and may do so differently than species that live in relatively simple social groups. Accordingly, nonhuman animals that live in social groups with more complexity and stricter dominance hierarchies show strong transitive inference abilities (Bond et al., 2003; MacLean et al., 2008), and they do not rely on associative values while animals without this social need do rely on reinforcement based mechanisms. Both ring-tailed lemurs (prosimians that live in large social groups) and mongoose lemurs (prosimians that live in small groups) can learn to pick item A when presented with pair AB and to pick B when presented with BC etc. for all adjacent list items, but at test only ring-tailed lemurs show symbolic distance effects (MacLean et al., 2008). Similarly, corvids that live in socially complex groups performed better on TI tests compared to corvids that are less social (Bond et al., 2003). These results indicate that nonhuman animals that have an ecological need to efficiently remember and process sequence information do so using, as their primary mechanism, a representation that may be spatial.

An alternative explanation to a spatial representation of the whole list is a hypothesis suggesting that, especially in nonhuman animals, successful transitive performance is driven by reinforcement history and accrued associative values. It is not based on a representation of the list as a whole (Vasconcelos, 2008; Von Fersen, Wynne, Delius, & Staddon, 1991; Wynne, 1995). Although these hypotheses can explain nonhuman animals’ ability to choose transitively in many situations, several studies have directly tested and rejected associative values as the mechanism supporting TI, especially in nonhuman primates (Gazes et al., 2012; Gazes et al., 2014; MacLean et al., 2008; Merritt & Terrace, 2011). Associative values cannot account for transitive responding in naturalistic social settings (Paz-y-Miño, Bond, Kamil, & Balda, 2004), nor does it account for the differences between relatively more and less social species (MacLean et al., 2008). Instead, results from TI tests across species indicate that the cognitive mechanism supporting performance is a spatial representation of entire ordered lists.

Evidence for spatial representations in other ordering paradigms

Symbolic distance effects are also found in tasks with trial-unique lists (Templer & Hampton, 2013). Rhesus monkeys were presented with 5 unique images one after the other in succession. At test, monkeys then were presented with pairs of items from the list and they were reinforced for choosing the item that occurred earlier in the list (Figure 4A). Monkeys tested in this way show symbolic distance effects like those described for the transitive inference tasks (Templer & Hampton, 2013). As the number of intervening items between test pairs increased accuracy increased and response time decreased. This pattern is consistent with a spatial representation of the previously presented sequence, rather than image-image associations. If it were image-image associations, response time would increase as the number of intervening items increased because subjects would have to work their way through the entire list. A spatial representation would predict that response time would decrease as symbolic distance (and thus represented spatial distance) increases, and that was what was observed. Additionally, these kinds of distance effects cannot be due to associative values because unlike in TI, list items are not independently rewarded. Therefore, the symbolic distance effects found in this task suggest that monkeys have a spatial representation of the list.

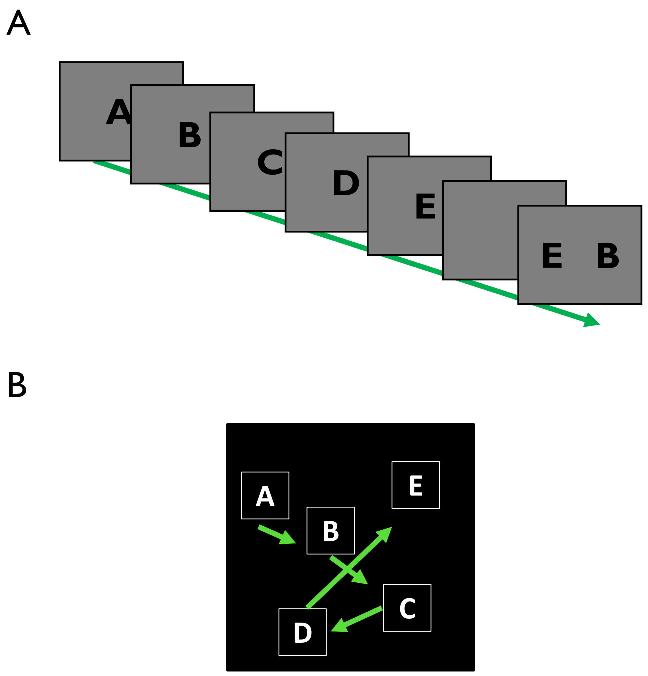

Figure 4. Two order tasks. A) In this order task, subjects are presented with sample images one at a time which they have to touch. After seeing all five items they are presented with a two choice test in which selecting the item earlier in the sequence is reinforced (Templer & Hampton, 2013). The items in the list are trial-unique. B) In the simultaneous chain task, participants are presented with all list items on the screen at once. Participants are reinforced for touching all list items in the correct order, shown here with letters. The spatial arrangement of the list items changes from one trial to the next trials, but the items in the list remain constant across trials.

Results from nonhuman animals tested with another sequence learning paradigm, the simultaneous chain or SC, provide evidence both supporting and refuting the hypothesis that lists learned via this paradigm are represented spatially. In this task, a series of items is presented all at once and subjects have to respond to all items available in the correct order while all previously chosen stimuli remain in view (Figure 4B; Inoue & Matsuzawa, 2007; Kawai & Matsuzawa, 2000; Terrace, 2005; Tomonaga & Matsuzawa, 2000). Subjects are then tested on trials in which only two items from the list are presented, and subjects have to touch the earlier then the later item from the sequence. If animals have a representation in which each item is associated with the preceding item, an associative chain, they would have to work their way through their mental list from the beginning before deciding which item to choose first. This would lead to increased latency to respond to either test item the further those items are from the first item in the series. If items are represented spatially, animals would not have to work their way through the entire list from the beginning, and would not show increased latency when test items are later in the list.

Differences in patterns of responding to the SC test are found across species. Pigeons respond accurately at test only when presented with pairs that include either the first or last item from the list, while monkeys respond with above chance accuracy to all pairs (Terrace & McGonigle, 1994). Marmosets that learn to chain a 4-item list are much faster to respond to test pairs when they contain the first item from the sequence (Koba, Takemoto, Miwa, & Nakamura, 2012). They also show the opposite of distance effects, in that they are slower to respond to the second test item as the number of intervening list items between the two images increases. This heightened latency is indicative of an associative chain supporting performance in this species. Ring-tailed lemurs and capuchin monkeys also show evidence for an associative chain mechanism supporting their performance on SC tasks (D'Amato & Colombo, 1988; Merritt, MacLean, Jaffe, & Brannon, 2007). However, rhesus monkeys, chimpanzees, and humans performing an SC task for arbitrary stimuli, show both distance and magnitude effects (Terrace, 2005; and see Box 1). They perform better when there are more intervening items between the test pair items, and when the distance is kept constant they perform better on items earlier in the sequence than later. This may especially be true when monkeys have extensive list learning experience (Terrace, Son, & Brannon, 2003). These species specific patterns may help elucidate the evolutionary point at which the SC task is controlled by a spatial representational mechanism. Results from SC tasks performed across species suggest that it isn’t until a common ancestor with rhesus monkeys that consistent use of a spatial representation for order evolved in primates.

Direct tests of spatial representations in chicks

Baby chickens also associate space and order (Rugani & de Hevia, 2016; Rugani, Kelly, Szelest, Regolin, & Vallortigara, 2010; Rugani, Regolin, & Vallortigara, 2007; Rugani, Vallortigara, Vallini, & Regolin, 2011). They represent an evolutionarily distant species to humans, and their performance on spatial and ordinal tasks can therefore help to shed light on the evolution of these abilities in nonhuman animals in a convergent context. Chicks are able to learn to pick a specific item in a 10 or 16 item series, showing an ability to discriminate ordinal position within a long series, and this performance is consistent across probe trials in which the spatial layout of the series changes (Rugani et al., 2010; Rugani et al., 2007). These results indicate that the chicks have a representation of the series. Chicks trained to pick the fourth item from the start in a series of food wells oriented along the midline of a testing box also correctly identify the fourth item when the series has been rotated 90 degrees from its original position (for the version with monkeys see Figure 5). When tested on a horizontal arrangement of items, chicks consistently pick the item that is correct if they are scanning in a rightward direction, i.e. the 4th from the left. This is also true of adult nutcrackers, who showed a rightward bias similar to the chicks’ (Rugani et al., 2010). Birds have very strong right hemispheric dominance in visuospatial tasks, so their behavior in this task is controlled by their left visual field. This leads them to start furthest to the left and move towards the right. It also leads them to make more errors to the left of center when trained to peck at the central item in linear array (Regolin, 2006). When ordinal and spatial information are congruent, the lateralized representation, similar to a mental number line, is activated. In contrast, when spatial information is no longer reliable because the distance between test items is different than in training, the right hemispheric dominance is reduced. Instead, the bilaterally represented ordinal information controls behavior, and no leftward bias is observed (Rugani et al., 2011). Thus in the case of avian cognition, the observed directionality is likely due to lateralized visual-spatial processing (Larsson, 2013). Primates process visual information bilaterally, so this suggests that the mechanism supporting chick and primate ordinal cognition may be different, while the predisposition to associate space and order may have evolved convergently.

Chicks also associate space with magnitude (Rugani, Vallortigara, Priftis, & Regolin, 2015). Chicks were trained to find pellets behind an object on which five items were presented. When they were tested with two choice objects on their left and on their right, they searched for food behind the object on the left more often when both objects had two items displayed and they searched for food behind the object on the right more often when both objects had eight items displayed (Rugani et al., 2015). These results suggest that the chicks orient leftward for smaller magnitude items and orient rightward for larger magnitude items, akin to a mental number line. However, critics point out that that chicks have individual biases that are not accounted for in their analyses (Harshaw, 2015), and that the stimuli may elicit left/right biases by their appearance (i.e. amount of background whiteness on the objects) rather than by the numerosity of the stimuli presented (Shaki & Fischer, 2015). Additionally, very few of the chicks showed left biases with small stimuli and corresponding right biases with large stimuli. In many cases, the chicks chose both left and right stimuli more than once for both objects with two and objects with eight numerosities. So although this study provides interesting insight into how chicks' lateralized brains approach a problem with space and numerosity, the results are difficult to interpret. Because a lateralized mechanism is probably driving some of these results, these studies do not provide insight into the evolution of space-magnitude associations in humans. These studies do indicate that in this species space and order/magnitude are associated, suggesting that spatial associations and representations may be an efficient organizing feature of cognition.

Direct tests of space-order associations in nonhuman primates

Evidence is accumulating from an increasing body of directs tests supporting spatial representations for ordered stimuli. One such study was based upon the open field task used with chicks and nutcrackers (Rugani et al., 2010), but was modified to be presented on a computer to test rhesus monkeys (Drucker & Brannon, 2014). Monkeys were trained to touch the fourth item from the bottom (second from the top) in a 5-item vertical series of ovals (Figure 5). They were then tested on whether they had generalized the ordinal rule "touch the fourth from the end of the series" by being presented with trials in which the number of items in the series increased, decreased, were shifted up or were shifted down. Although monkeys continued to choose the 4th from the bottom in the shifted condition, when presented with a 4-item array they chose the 3rd from the bottom significantly above chance, and when presented with a 6-item array they chose the 5th from the bottom significantly above chance. This suggests that they were picking the item

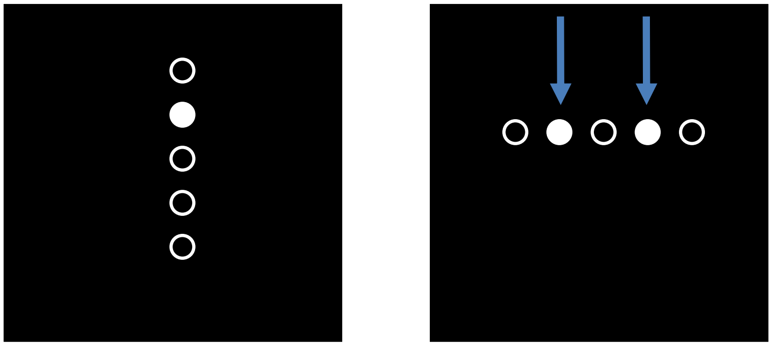

Figure 5. Transfer of vertical order to horizontal order. Monkeys were trained to pick the fourth item from the bottom/second from the top in a series of five (Left). The filled in dot represents the rewarded location. At test the series was rotated 90 degrees and there were now two possible correct locations, the fourth from the left and the fourth from the right (Right). This task was modified from experiments with chicks and longer series of food wells (see Rugani et al. 2010 and Rugani et al. 2011). Monkeys consistently chose the item that was 4th from the left/2nd from the right in the series (Drucker and Brannon, 2014).

second from the top of the series. They were also tested in a horizontal condition in which they had to choose an item within a horizontal series of five circles that were probes within a session including vertical trials. In the horizontal test, monkeys chose the fourth from the left/the second from the right significantly above chance. Space and order were not put in conflict in the horizontal condition. Monkeys could be using a 4th from the bottom or 2nd from the top rule. The probe tests did not eliminate either option. However, the consistency of the monkeys' choices to the 4th from the left/2nd from the right indicates a spatial association with order in primates. If they did not have a consistent orientation, they would have been equally likely to choose the 2nd from the left/4th from the right at least at an individual level. It is also unlikely to be just spatial memory because during training and earlier testing the inter-item distance and the number of stimuli varied. Unlike the results from birds, these results cannot be explained by strong hemispheric lateralization, and it is much more likely that similar mechanisms are supporting rhesus monkey and human spatial representations.

A more ecologically valid test of spatial representation of ordered stimuli also indicates that chimpanzees associate order with space (Dahl & Adachi, 2013). When chimpanzees perform a matching-to-sample procedure in which they have to match faces of familiar conspecifics, they are faster to respond when high ranking individuals are presented above low ranking individuals on a computer screen, than when rank and space are not congruent with each other (Figure 6A). Chimpanzees were not explicitly required to respond to the rank of the faces presented, but results indicate that rank was implicitly processed and is represented spatially. This study provides evidence supporting the idea

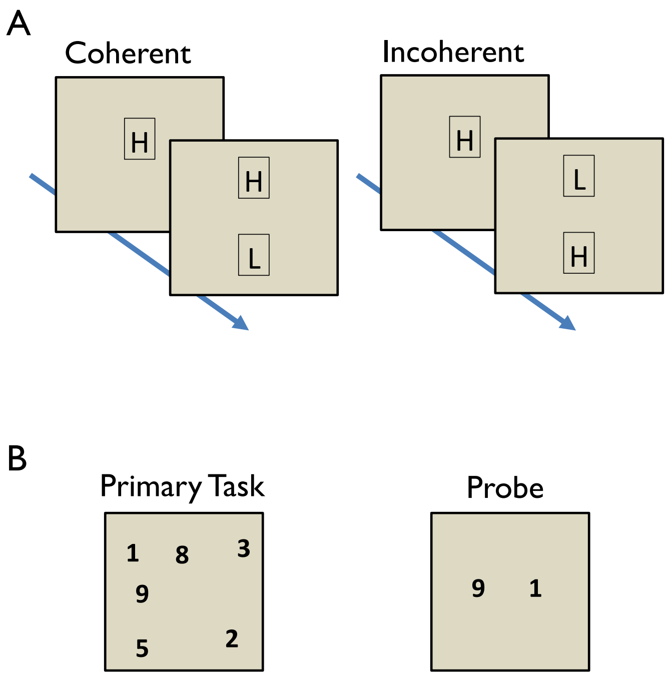

Figure 6. Chimpanzee order-space associations. A) Chimpanzees were trained in a matching to sample procedure. They had to match the identity of a known conspecific from their group when presented with a two choice task in which one stimulus matched the identity and one distractor conspecific were presented in a vertical orientation. In this figure, H represents a high ranking individual and L represents a low ranking individual. Chimpanzees were faster to respond to coherent trials in which the high ranking individual was presented above the low ranking individual, rather than incoherent trials in which the low ranking individual was presented above the high ranking individual (Dahl and Adachi, 2013). B) Chimpanzees were trained to order simultaneously presented numerals 1-9. They were then probed with trials in which only numerals 1 and 9 were presented horizontally. In half the trials 1 was to the left of 9 (LtoR) and in half the trials 9 was to the left of 1 (RtoL). All individuals tested were faster to respond to the left to right condition than to the right to left condition. This is reminiscent of human SNARC results, although only end-items were used in this test (Adachi, 2014).

that an ordered sequence, such as rank, is represented spatially. Chimpanzees associate high rank with the top of the screen and low rank with the bottom. Although these results support a spatial representation of rank order, they can also be explained by real-life associations developed by these subjects. A high ranking individual might prefer the high ground, or be above a low ranking individual in a fight. Thus, these associations may, in part, provide a model for how spatial associations are culturally developed. However, it is also possible that the spatial associations for rank do not translate to a general representation of other ordered series. Yet, when chimpanzees perform a less ecological task, they also show spatial-order associations (Figure 6B; Adachi, 2014). When chimpanzees, who have experience with ordering numerals 1-9 that had simultaneously been presented (Inoue & Matsuzawa, 2007), as in the simultaneous chaining procedure described above, are probed with trials in which only numerals 1 and 9 were presented horizontally in the same row, they are faster to respond to the stimuli when one is on the left and nine on the right than when the opposite is true. These results indicate that chimpanzees spatially organize sequences from left to right. These results also provide direct evidence that there is a shared spatial representational system for order across species.

The parietal lobe is implicated in both spatial and ordinal cognition across species

Humans and nonhuman primates share similar neural substrates supporting spatial-ordinal cognition, and this, in combination with behavioral evidence, supports the hypothesis that these abilities share a mechanism across species. The parietal lobe, while being important for sensory processing, has also been implicated in spatial representations, numerical cognition, and ordinal cognition in humans and nonhuman animals (Hinton, Dymond, von Hecker, & Evans, 2010; Hubbard et al., 2005; Moeller, Willmes, & Klein, 2015; Prado, Noveck, & Van Der Henst, 2010). Human imaging studies and single cell recordings in nonhuman animals indicate that there is converging evidence across techniques and species suggesting a neurological basis for magnitude/order-space interactions in the parietal lobe.

Human imaging studies

The horizontal portion of the intraparietal sulcus, or hIPS, is implicated in both numerical and spatial cognition in humans (Cutini, Scarpa, Scatturin, Dell'Acqua, & Zorzi, 2012; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Husain & Nachev, 2007; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007). When participants are passively viewing numerical stimuli and are habituated to a specific numerosity, the hIPS has an increased blood-oxygen-level dependent, or BOLD, signal when the numerosity of the presented stimulus changes (Piazza et al., 2004), and this is true across modes of presentation including dot patterns and number words (Piazza et al., 2007). The IPS is also a region implicated in aspects of spatial processing (Hubbard et al., 2005; Husain & Nachev, 2007; Sereno, Pitzalis, & Martinez, 2001). Imaging studies with the SNARC task indicate that both the spatial and numerical components of this task are processed in the same areas of the parietal lobe (Cutini et al., 2012). These findings indicate that similar brain regions are responsible for aspects of spatial and numerical cognition.

Additionally, the distance and magnitude effects observed in many numerical studies may actually have a topographic basis in the parietal lobe. fMRI results indicate that, in humans, there is more cortical surface area devoted to smaller magnitudes and less surface area devoted to large magnitudes in the posterior parietal cortex (Harvey, Klein, Petridou, & Dumoulin, 2013). This helps explain why it is easier to distinguish smaller magnitudes from each other: there is more cortical space devoted to those magnitudes. This topographic structuring is present in the right hemisphere, while the left hemisphere has less clear organization. The spatial layout of this map is not to be taken as evidence for phenomena such as the mental number line, but a more specialized right hemisphere could help explain results in which infants show a left-to-right preference very early in life (de Hevia, Girelli, et al., 2014). The direction of the mental number line is highly flexible even within individuals (e.g. Shaki & Gevers, 2011), so the organization of the mental number line is unlikely to be hard coded in the brain.

Ordered series are also associated with increased BOLD signal in the horizontal portion of the intra parietal sulcus (Acuna, Eliassen, Donoghue, & Sanes, 2002; Fias, Lammertyn, Caessens, & Orban, 2007; Prado et al., 2010). The hIPS is an important region in ordinal letter comparisons (Fias et al., 2007), and when participants perform a TI task, there is increased BOLD in the parietal lobe after participants have learned a list (Acuna et al., 2002; Prado et al., 2010; Van Opstal, Verguts, Orban, & Fias, 2008). These are the same regions and networks associated with numerical cognition, and thus these results corroborate the hypothesis that similar mechanisms support both numerical and ordinal cognition. It is important to note that there are some differences in the systems involved in numerical and ordinal cognition (Prado et al., 2010), so the mechanisms across tasks are not identical. However, some of these differences may be unique to humans, i.e. related to language; therefore, it is likely that the underlying mechanism that is evolutionarily ancient is shared across magnitude and order (and species).

Nonhuman primate single-cell recordings

The same regions indicated in human fMRI studies are activated in single-cell recording studies in nonhuman primates (Grefkes & Fink, 2005; Nieder et al., 2006; Viswanathan & Nieder, 2013). Neurons in the nonhuman primate ventral intraparietal area of the intraparietal sulcus, or VIP, respond selectively to presentations of numerosity (Nieder & Miller, 2004; Viswanathan & Nieder, 2013). Additionally, monkeys who have to match the numerical magnitude of either a visual or auditory sample stimulus, show activations that are numerosity specific in both the prefrontal cortex and VIP (Nieder, 2012). Different populations of neurons are activated depending on whether the numerosities are presented with a spatial or temporal layout, yet a third population of neurons is activated regardless of the initial form in which the numerosity is presented (Nieder et al., 2006). Single cell recording from the posterior parietal cortex in macaques has also shown that neurons in these areas respond to spatial cognition (for a review see Grefkes & Fink, 2005). Area LIP of the parietal cortex in macaques is activated when monkeys have to remember the spatial location of a target stimulus (Grefkes & Fink, 2005). These results indicate that there is a neural network supporting the spatial/numerical/temporal associations found across species, and they directly show that the same network supports both spatial and numerical cognition.

It is important to note that investigators have hypothesized that human and monkey parietal lobe are not completely homologous (for a review see Husain & Nachev, 2007). The inferior parietal lobe may be more expanded in humans than in monkeys, but the actual functional differences have not yet been sufficiently investigated. Additionally, the different techniques used to assess brain activation across species make it difficult to definitively conclude that apparently homologous regions are actually behaving similarly or differently. However, the converging evidence across techniques and species does indicate similar neurological mechanisms supporting number/order and spatial associations across species.

Conclusion

Although much of the evidence described above suggests that many species associate space and order/magnitude, alternative explanations suggest that these results are due to outside experience and training. One model suggests that space and number are supported by separate representations, and it is not until cultural training, in the form of reading and math instruction, that these processes become associated with each other (Chen & Verguts, 2010). This model would predict no association between space and number/order in nonhuman animals because they do not receive formal instruction. This model also does not account for the increasing body of evidence in which very young infants are predisposed to associate space and magnitude (Rugani & de Hevia, 2016). Another account for the SNARC effect suggests that the binary responses required in the SNARC paradigm drive the effect, instead of a spatial representation for magnitude/order (Proctor & Cho, 2006). Rather than conceptual overlap, it is the shared response dimension that produces the effect. This model would suggest that the evidence is only similar for order and number tasks because in both types of SNARC tests binary left-right responding is required. This model can account for adult human SNARC effects, but it does not support the results observed in in human infants (de Hevia, Girelli, et al., 2014). Nor is this explanation sufficient to explain the results from nonhuman primates that do not have outside binary associations between space and the ordered stimuli. So although some results, from adult humans especially, can be explained by these alternative models, all can be explained by a spatial representation of order that is similar across species.

Across experimental paradigms and species, there is consistent compelling evidence suggesting that representing order and magnitude spatially is an evolutionarily ancient mechanism. Humans and nonhuman animals show very similar patterns of results when making numerical judgments, and distance effects are found across tasks and species (e.g. Jordan & Brannon, 2006). Distance effects are found in studies with nonhuman animals and on tasks in which humans are using spatial representations. Additional evidence from chicks (Rugani, Vallortigara, & Regolin, 2014), chimpanzees (Adachi, 2014), and rhesus monkeys (Gazes et al., 2014), provide more direct evidence supporting the association between space and order/magnitude across species. Finally, the presence of homologous regions in the parietal lobe associated with ordered stimuli across species indicates that the most parsimonious explanation for all of these overlapping patterns is that humans and nonhuman animals share a spatial mechanism for representing ordered stimuli. The next years will be critical for more definitively evaluating this hypothesis. Investigators must now work to design experiments that explicitly test this hypothesis and go beyond the suggestive evidence we have presented and weighed in this paper. Future studies with nonhuman animals should focus on order-space interactions across entire sequences, including items with variable reinforcement histories, to provide evidence that observed performance patterns are not due entirely to differential reinforcement of stimuli. These tests should be done across ordered stimuli types including magnitude and list learning paradigms such as TI, and they should be done in a number of different species in order to elucidate the evolutionary trajectory for these abilities. Only after these tests are performed will we be able to better understand the mechanism driving space-order associations in humans and its evolutionary precursors.

Introduction to Thesis

There is almost no question that humans associate magnitudes and order with space (Dehaene et al., 1993; Gevers et al., 2003; Previtali et al., 2010). There is evidence from tasks that induce participants to think about magnitude (Wood et al., 2008), to ignore magnitude (Holmes & Lourenco, 2013), that investigate visuo-spatial attention changes with magnitude priming (Fischer, 2001), and tasks that involve less common magnitudes like emotion and pitch (Holmes & Lourenco, 2011; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006). Days of the week and months of the year also are represented spatially (Gevers et al., 2003, 2004). However, even with evidence from very young infants, it is impossible to dissociate the impact of learning and culture on these associations. To investigate the mechanism that is driving this association, it is important to test a group that is not influenced by language, such as nonhuman primates. Rhesus monkeys diverged evolutionarily from humans 32 million years ago, orangutans 15 million years ago, and chimpanzees 5.9 million years ago (Finstermeier et al., 2013). They do not experience training to organize sequences in any particular direction, but their relative evolutionary proximity suggests that if associating space and order/magnitude is an evolutionarily ancient strategy, we will be able to find evidence of this association in these species.

To investigate whether nonhuman primates associate space and order, I capitalized on the hypothesis that spatial working memory and ordering may utilize a domain specific cognitive resource. Thus, if performance is impaired more when a spatial memory task and an ordering task are performed concurrently than when an ordering or spatial task is performed concurrently with a non-spatial task, this will indicate that nonhuman primates have a spatial representation for order. In the first manuscript we investigate whether chimpanzees and orangutans are impaired when ordering, simultaneous matching-to-sample, or a target detection task are embedded within a spatial memory task. Because we were not able to get access to the chimpanzees for additional follow up experiments and one of the five orangutans was about six months slower than the other four, this manuscript includes a third experiment with only four out of the original five orangutans. In that experiment we embedded the ordering task in the spatial memory task and in a delayed matching to sample task. In the second manuscript we built upon the findings of the first manuscript and tested six rhesus monkeys on similar tasks in which ordering was embedded within both spatial memory and identity matching tasks, and a non-spatial object discrimination task was also embedded in spatial memory and identity matching tasks. We conclude with a discussion of our findings and consider the possibility that rather than a domain specific resource, nonhuman primate working memory is supported by a domain general resource taxed across tasks.

Manuscript 1

Ordering images requires spatial working memory in apes

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Abstract

Humans think about order and quantities using mental representations with spatial characteristics. Few studies provide evidence that nonhuman primates have similar spatial representations of order. We directly tested whether the ability to order lists in chimpanzees and orangutans requires cognitive resources associated with spatial cognition. Apes were trained to remember locations on a touchscreen computer over brief delays. We then embedded two tasks in the delay interval of the location matching test. The order task required apes to touch images in a pre-defined sequence, whereas the equally difficult visual matching task required identifying images that were identical. If processing order depends on a spatial representation of the sequence of images, then performance should be relatively more impaired when the order task is under concurrent spatial memory load because the spatial task competes for a limited spatial processing resource. By contrast, the visual matching task should be less affected by competition with the spatial memory task because it does not compete for spatial processing resources. We found that concurrent spatial cognitive load reduced accuracy on the order task significantly more than accuracy in the visual matching task. However, concurrent cognitive load impacted spatial memory equally across tasks, and when ordering was embedded in a delayed visual matching task, spatial load did not impair ordering accuracy more than visual memory load. Unfortunately, our sample size was cut in half for this second comparison, so we did not have enough power to detect a significant difference if there was one. These findings suggest that our closest living primate relatives use spatial cognition for processing order, but rather than a domain specific resource these results suggest that these tasks are supported by a general working memory resource that are taxed across task types.

Introduction

Humans think about order and magnitude using mental representations that have spatial characteristics (Dehaene et al., 1993; van Dijck et al., 2013). For example, many Western humans visualize a mental number line with small numbers to the left side of space and large numbers to the right (Fischer, 2001; Fischer, Castel, Dodd, & Pratt, 2003; Wood et al., 2008). The orientation of this representation is flexible and appears to be determined both by culturally specific directions of reading and counting and by specific task demands such as instructions to visualize a clock face versus a ruler (Bächtold et al., 1998; Göbel, Shaki, & Fischer, 2011; Shaki & Fischer, 2008; Shaki, Fischer, & Petrusic, 2009). Nonhuman animals do not read or count, but they do represent space, magnitude, and order (Brannon, 2006; Gazes et al., 2012; Hubbard et al., 2005; Rugani & de Hevia, 2016; Rugani et al., 2015; Templer & Hampton, 2013). Tests of nonhuman animals can therefore determine the extent to which spatial representation of order is a product of human culture. If nonhuman animals also represent order and magnitude using representations with spatial characteristics, spatial representation is likely a phylogenetically ancient and fundamental mechanism for representing ordered information. In this study, we evaluated whether ordering stimuli depends on spatial representations in nonhuman primates by testing for interference between ordering and spatial working memory.

Order and number/magnitude are difficult to dissociate in humans because numbers are inherently ordered. Western humans associate small magnitudes with the left side of space, and large magnitudes with the right side of space (Cheung, Ayzenberg, Diamond, Yousif, & Lourenco, 2015; Dehaene et al., 1993; Fischer et al., 2003; Nuerk, Wood, & Willmes, 2005; Wood et al., 2008). For example, when reporting whether a number is odd or even, English speaking participants respond more quickly on the left when presented with a small number, and more quickly on the right when presented with a large number (Dehaene et al., 1993; Nuerk et al., 2005). A similar effect is found when participants make left or right responses to report whether a number is smaller or larger than a reference value (Wood et al., 2008). Additionally, participants are faster to report a target viewed in their left hemifield if they were primed with a small number than if they were primed with a large number (Fischer et al., 2003). These response facilitations suggest that the simple act of viewing a number causes spatial attention to shift in the direction in which the viewed number is represented on the mental number line.

Spatial and numerical cognition depend on overlapping brain networks that include the posterior parietal cortex, and this is true in both humans and nonhuman primates (Hubbard et al., 2005). The horizontal portion of the intra-parietal sulcus (hIPS) has been implicated in both spatial and numerical cognition in humans (Cutini et al., 2012; Eger et al., 2003; Hubbard et al., 2005; Piazza et al., 2007). The hIPS has also been implicated in ordinal cognition for letter comparisons (Fias et al., 2007), and the areas ventral and posterior to the intraparietal sulcus have been implicated in ordered list learning (Acuna et al., 2002; Van Opstal et al., 2008). Increased hemodynamic response to the hIPS was observed in participants who performed odd-even judgments that required leftward or rightward responses (Cutini et al., 2012). The increase in blood flow was particularly strong when participants responded to large numbers with a leftward response and to small numbers with a rightward response. Such experimental conditions required them to respond in the opposite direction to that primed by the magnitude of the number. In addition to imaging studies with humans, single-cell recordings of the intraparietal sulcus in nonhuman primates indicate that this region is activated in both numerical (Nieder, 2012; Viswanathan & Nieder, 2013) and spatial tasks (for a review see Grefkes & Fink, 2005).

The “mental number line” may be one specific example of a more general process by which ordered stimuli and spatial representations interact in working memory (Ginsburg et al., 2014; van Dijck et al., 2014; van Dijck et al., 2013; van Dijck & Fias, 2011; van Dijck et al., 2009). Participants who have memorized a sequence of numbers, for example “8, 2, 7, 4, 3” and then make odd-even judgements with the memorized sequence, are faster to respond to the left when assessing numbers earlier in the sequence and on the right if assessing numbers later in the sequence (Ginsburg et al., 2014; van Dijck & Fias, 2011). Similarly, participants performing a dot detection task react more quickly to a target presented in their left visual hemifield after being primed with items that occur earlier in a memorized sequence than if primed with items later in the memorized sequence (van Dijck et al., 2013). These results suggest that spatial priming effects can result from ordered representations of lists in working memory, with English speakers visualizing earlier items in the list on the left and later items to the right.

Evidence for the spatial representation of ordered sequences in nonhuman primates has been found when order is inferred by transitive inference (Gazes et al., 2014), and when ordered sequences were explicitly trained (Adachi, 2014). Humans and monkeys were taught to arrange images in a specific vertical layout (Gazes et al., 2014). They then learned an inferred rank order of the same images through transitive inference training with premise pairs. For example, if the rank order of the items was A>B>C>D>E>F>G, then when pair AB was presented they were rewarded for picking A, when BC was presented they were rewarded for picking B, and so on for all of the adjacent pairs: AB, BC, CD…FG. This training had no explicit spatial component, but was either consistent or inconsistent with the spatial layout they had learned previously. Humans, and to a lesser extent monkeys, performed better when the trained spatial order was congruent with the order to be inferred by transitive inference. Additionally, chimpanzees that had learned to order images of the numerals 1-9, responded more quickly when the image for “1” was on the left and “9” was on the right than when “9” was on the left and “1” was on the right (Adachi, 2014). The same chimpanzees were not quicker to select images on the left in a matching to sample task, so this effect was not just a bias to start on the left.

To further evaluate the extent to which ordered information is represented spatially in nonhuman primates, we tested whether selecting randomly positioned images according to a memorized sequence requires cognitive resources shared by spatial working memory in chimpanzees and orangutans. Because apes lack the cultural experience humans have with reading and number lines, we cannot know *a priori* how the putative mental representation of order is oriented in these animals. Accordingly, our test does not rely on the assumption of any particular orientation to the spatial representation. Additionally, we are testing whether ordering and a spatial memory task tax a specific shared resource. If both of these tasks draw on this shared resource then performance on one or both of these tasks will likely decrease. To detect this decrement we looked at subjects' performance on these tasks simultaneously. If order is represented spatially and ordering taxes a domain specific spatial memory resource, then performance will be most impaired on trials in which an ordering task and spatial memory task are presented concurrently. This impairment could be driven by errors to the ordering task or errors to the spatial memory task, or errors to both. In each of these cases, increased impairment to these tasks when performed concurrently would indicate that successful performance requires a cognitive resource that is necessary and shared by those tasks. By assessing whether performance is more impaired than would be expected if the two tasks are independent, we were able to test if there are shared resources without assuming the directionality of the apes' allocation of resources. We also did not predict whether the impairment was bi-directional, i.e. impacting both ordering and spatial memory, or uni-directional, i.e. impacting just ordering or just spatial memory. Any impairment would indicate a specific shared resource, regardless of the directionality. We also included trials in which the apes touched a target stimulus during the delay of a spatial memory task to control for the possible impact of touching a new spatial location. Additionally, to control for the non-specific effects that might result from concurrent cognitive load generally, we compared the impact of concurrent spatial load on an equally difficult non-spatial visual matching task and compared the impact of a non-spatial memory load on an ordering task. We also analyzed the impact on the tasks separately to determine the source of the errors contributing to the performance decrement in the earlier analyses.

General Methods

Subjects and Apparatus

Chimpanzees. Four female chimpanzees (*Pan troglodytes*), ages 38, 35, 15, and 15 completed the study. The chimpanzees lived in a group of 14 individuals with access to outdoor (770m^2) and indoor compounds. Animals were fed a wide variety of fresh fruits and vegetables throughout the day supplemented with nutritionally balanced biscuits (fed twice daily) and water available ad libitum. They had participated in a variety of computer-controlled tasks over many years, including a sequencing task that required touching images of Arabic numerals in the conventional order (numerals 1-9; Adachi, 2014; Dahl & Adachi, 2013; Inoue & Matsuzawa, 2007, 2009; Matsuzawa, 2003, 2009, 2013). The stimuli were presented on a 17-inch LCD touch panel display (1024x768 pixels) controlled by custom-written software using Visual Basic 2010 (Microsoft Corporation, Redmond, Washington, USA). Below the display a food tray was installed in which small pieces of apple or raisin were delivered by a custom-designed feeder after every correct trial. The chimpanzees sat in an experimental booth (2.5 m wide, 2.5 m deep, 2.1 m high), separated from the experimenter by transparent acrylic panels. Chimpanzees had access to the computer testing rooms for approximately 4 hours each day, 1 hour of which was for this experiment, five days a week.

Orangutans. Five orangutans completed the study: a 32 year old Sumatran female (*Pongo abelii*), a 9 year old Sumatran male, a 39 year old hybrid (Sumatran/Bornean), a 24 year old Bornean female (*Pongo pygmaeus*), and a 13 year old Bornean male. They lived in two social groups at Zoo Atlanta and were tested while off exhibit. Animals were fed a wide variety of fresh fruits and vegetables throughout the day supplemented with nutritionally balanced biscuits (fed twice daily) and water available ad libitum. Orangutans had learned to order images of the numerals 1-5 in the conventional order prior to this experiment, using similar simultaneous chaining methodology as with the chimpanzees, and had completed a variety of other computerized experiments. The stimuli were presented on a 15-inch LCD color touchscreen monitor (1024x768 pixels) controlled by custom-written software using Visual Basic 2010 (Microsoft Corporation, Redmond, Washington, USA). Their computer systems were also composed of a laptop computer, speakers, and automated reward dispenser (MedAssociates Inc. St. Albans, VT). Below the display a food cup was installed in which nutritionally balanced fruity flavored primate pellets were dispensed after every trial. Orangutans were tested in their indoor housing enclosures, and had access to the indoor computer apparatus for approximately 1 h in the morning 6 days a week before going on exhibit for the day.

Experiment 1

Procedure

Subjects were trained in stages to complete a spatial memory task with other tasks embedded. First they learned the spatial memory task with nothing embedded within it. They then experienced concurrent load when they were trained to touch one stimulus during the delay of the spatial memory task. Finally, they were tested in stages with concurrent spatial and ordering and concurrent spatial and visual simultaneous matching-to-sample loads.

Spatial Memory Training

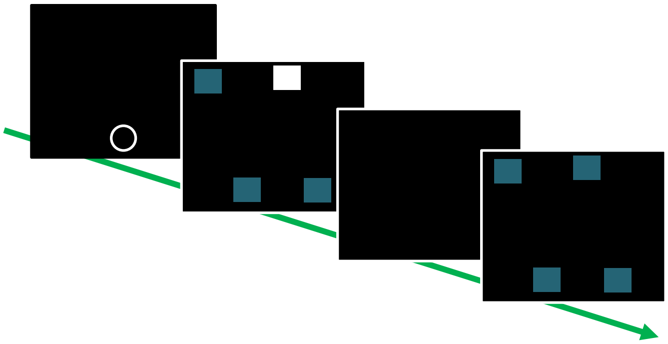

Figure 1. Spatial memory task. Subjects initiated a trial by touching the white circle. They then saw an array of 4 squares: 3 blue and 1 white. After touching the white square the screen went blank for 2000ms. After the delay the four squares appeared again in the same locations, but they were all blue. Apes were rewarded for touching the location previously occupied by the white square.

Subjects were first trained on a spatial memory task. The screen was virtually divided into 48 noncontiguous locations in which stimuli could appear. Each location was 100x100 pixels and was separated from neighbors by 15 pixels. After touching a start circle to initiate a trial, they saw an array of squares (100x100 pixels). At the beginning of training they saw 3 squares: two blue and one white. After they touched the white square, the screen went black for a short delay. After the delay, the squares appeared again in the same screen locations, but all were blue. Subjects were rewarded for touching the square in the location previously occupied by the white sample square. The white square appeared in each of the 48 possible screen locations once in each 48 trial session, and in a random sequence. The blue distractor squares were randomly displayed in other screen locations, with no constraints other than those imposed by the virtual grid of 48 possible locations. The delay between touching the white square and the appearance of the choice screen started at 200ms and increased incrementally up to 2000ms as subjects learned the task. For the chimpanzees, we individually adjusted the delay based on performance. For some individuals the delay length increased by smaller increments than others as they learned the task. For the orangutans, the delay increased incrementally from 200ms to 500ms, to 1000ms, to 1500ms, to 2000ms. When subjects performed above 80% at the 2000ms delay, a third blue distracter square was added to the test arrays (Figure 1). After performing above 80% correct in a 48-trial session with 2000ms delays and 3 distractor squares, subjects moved on to training with concurrent embedded tasks.

Spatial Training with Concurrent Cognitive Load

Subjects continued performing the spatial memory task, but now during the delay period between seeing the sample spatial memory array and the spatial memory test, apes had to touch an intervening item, either a single numeral or a single target shape. Subjects saw the spatial memory array, and after they touched the white square, all of the squares disappeared and either a numeral or a motor control stimulus appeared. The embedded stimuli appeared in one of the possible 48 screen locations, randomly chosen each trial. Apes had to touch the embedded stimulus, after which it disappeared. The time between the spatial memory sample display and test was held constant at 2500ms by adding a black screen delay after the control response before the spatial memory test phase was displayed. If a subject took longer than 2500ms to respond, the trial was tagged in the data as exceeding that length and those trials were removed from spatial memory analyses. Subjects received no explicit reinforcement for touching the embedded stimuli. After the delay, the array of four blue squares appeared and again subjects had to touch the square located in the same location as the white sample location. Subjects had to perform above 65% correct on the spatial memory task for two consecutive 48-trial sessions before moving on to test trials. If subjects failed to reach this criterion within 10 sessions, they were instead required to complete correctly at least 30/48 trials (62.5%) for 3 sessions in a row.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 spatial memory test trials with blank delays (3 distractor items, 2000ms delay). This was intended to remind them of the task and decrease the likelihood of floor level performance on the spatial memory task with intervening items.

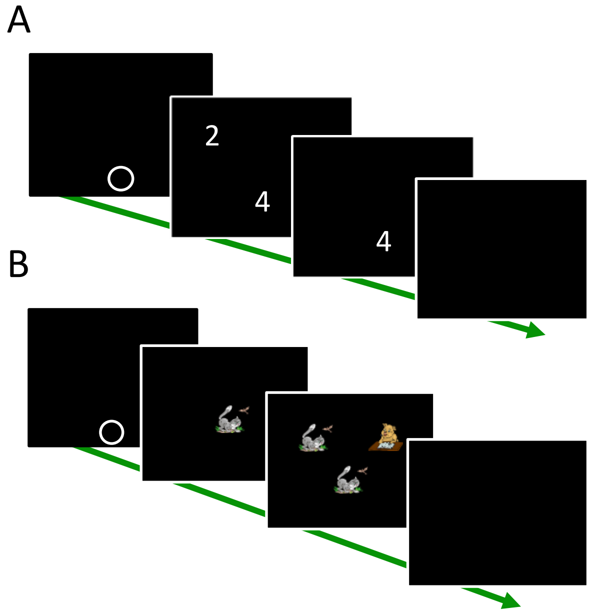

Figure 2. Order task and matching-to-sample control task. A) Ordering. Subjects initiated a trial then were presented with two numerals randomly picked from 1-5 for orangutans and 1-9 for chimpanzees. They had to touch the numerals in ascending order. B) Simultaneous matching-to-sample. After initiating a trial subjects were presented with a sample clipart image. After touching it, two choice stimuli appeared above the sample. Subjects had to touch the new clipart that matched the sample image.

Ordering Training

All subjects had prior experience ordering images of numerals (chimpanzees 1-9, and orangutans 1-5). To proceed to the final phase of testing they had to order two numerals randomly chosen from the sequence and randomly positioned in two of the 48 possible screen locations (Figure 2A) above 90% correct for two consecutive sessions.

Concurrent Cognitive Load Test: Ordering Two Items

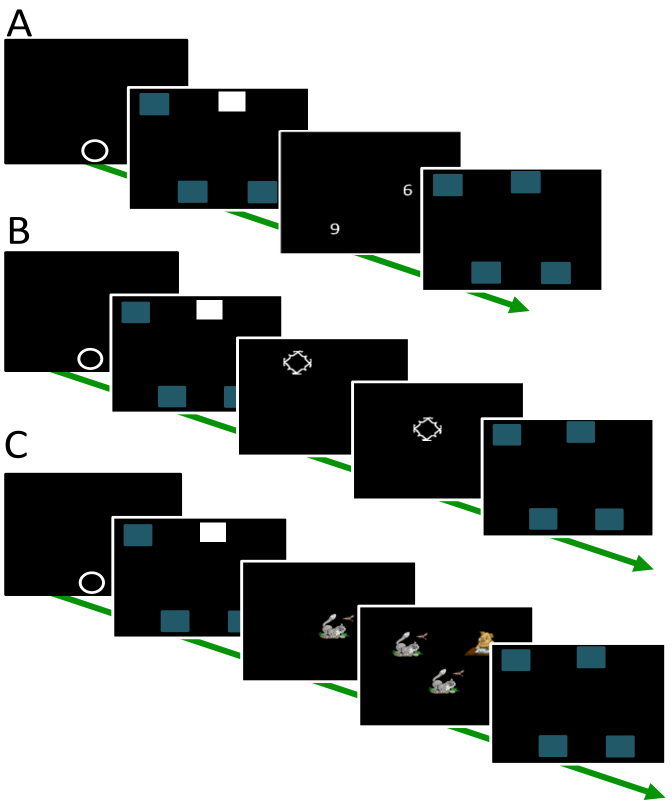

Figure 3. Concurrent cognitive load trials. A) Ordering. Subjects ordered numerals in ascending order while remembering the spatial location of the white square presented at the beginning of the trial. B) Motor control. Subjects touched two randomly located images while remembering the location of the white square presented at the beginning of the trial. C) Matching-to-sample. Subjects matched the identity of the sample clipart image while remembering the location of the white square presented at the beginning of the trial. Incorrect responses in the embedded tasks aborted the trial. Reinforcement was provided following correct responses in the spatial memory task only.

After reaching criterion with one intervening item, and reaching criterion ordering two numerals, subjects were tested with two intervening items inside the spatial memory test. The test phase was identical to training except that instead of one intervening numeral or motor stimulus presented during the delay of the spatial memory task, there were two items. Subjects either had to order two numerals (randomly displayed and randomly chosen; 1-9 for chimpanzees or 1-5 for orangutans; Figure 3A) or touch two motor control stimuli (Figure 3B). In the order task, two numerals were displayed on the screen, and the subject had to touch them in ascending order. The two motor control stimuli were presented one at a time so that there was no chance of the subject attempting to order the stimuli. These trials controlled for the possible impact touching the screen may have had on spatial memory performance. If the subject incorrectly ordered the numerals, the trial was aborted and repeated at the end of the session to ensure the same number of both types of trials were completed and each spatial location was the target at test once each session. Again, subjects received no reinforcement for completing the embedded task. Subjects completed four test sessions. During the same testing session, subjects also received at least two 48-trial sessions of ordering two numerals without the spatial memory component as a baseline (Figure 2A).

Cognitive Effort Control

Because there is no incorrect answer in the motor task (Figure 3B), it is not equivalent to the order task in terms of cognitive difficulty. It does control for the effect of touching the screen in several locations, but it does not control for the general cognitive load that comes from performing a concurrent task that can be incorrect. To address this, subjects performed a second interference test designed to control for cognitive effort: simultaneous visual matching-to-sample. If subjects represent order spatially, concurrent cognitive spatial load will impair performance more when order is embedded than when an equally difficult non-spatial task is embedded.

Simultaneous matching-to-sample training

To ensure that the simultaneous visual matching-to-sample (MTS) task was equal in difficulty to the numerical ordering task, subjects were first tested on MTS alone (Figure 2B). Subjects initiated trials by touching a start circle. They were then presented with a colorful clipart image (100x100 pixels). Immediately after they touched this image, two additional images appeared: one that was identical to the sample image, and the other a distractor. The sample image remained on screen, and subjects were reinforced for touching the choice image that matched the sample. There were 12 clipart images in the set, and each served as target and distractor every 12 trials within a 48-trial session. As with the ordering task, subjects had to perform above 90% correct in two consecutive sessions before moving on to embedded test trials.

Concurrent Cognitive Load Test: MTS

The MTS task was embedded in the spatial memory task as was done with the number image ordering task (Figure 3C). Motor control trials were also included in these test sessions, for a total of 24 MTS trials and 24 motor controls trials in a 48-trial session. Every four trials two MTS and two motor control trials were presented in pseudo-random order, and each incorrect MTS trial was repeated at the end of the session. Again, at the beginning of each testing day subjects received warmup spatial memory trials with blank delays. Subjects completed four test sessions. During the same testing session, subjects also received two 48-trial sessions of MTS without the spatial memory component as a baseline (Figure 2B).

Data Analyses

To assess the extent to which the ordering task and the matching task share cognitive resources with spatial matching, we determined the impact on accuracy on the whole trial resulting from concurrent cognitive load. We calculated the accuracy expected under dual task conditions if performance on the two individual tasks were independent.

This is the simple product of the observed proportion correct on the two tasks when performed independently. For the spatial memory task, we used each individual's performance on the session in which they reached criterion during training. We multiplied accuracy on the spatial memory task by accuracy on the ordering task when it was presented alone and by the MTS task when it was presented alone. This gave us two expected accuracies for the experimental conditions: expected accuracy when spatial memory and ordering were performed together, and expected accuracy when spatial memory and MTS were performed together. We ran a RMANOVA with outcome measure (expected if independent vs observed accuracies) and concurrent load type (ordering vs MTS) as factors. Observed accuracies were the subjects' accuracies on the entire trial the first time it was presented. Because it was not possible to get the motor task wrong, we did not include performance on those trials in this analysis. To assess the source of the error, from the first analysis, we also analyzed subjects' accuracy on the embedded tasks separately from their performance on the spatial memory task. To do this, we ran a RMANOVA on embedded task accuracy with concurrent load type (ordering vs MTS) and embeddedness (alone vs embedded) as within subjects factors and with species as a between subjects factor. We analyzed spatial memory performance using a RMANOVA of spatial matching accuracy with concurrent cognitive load type (order, MTS, motor) as within subjects' factors and species as between subjects factor. We used an alpha of 0.05. Proportion correct data were arcsine transformed prior to analysis to better conform to the normality assumption (Aron & Aron, 1999). Effect sizes are reported as partial eta^2 and Cohen's d.

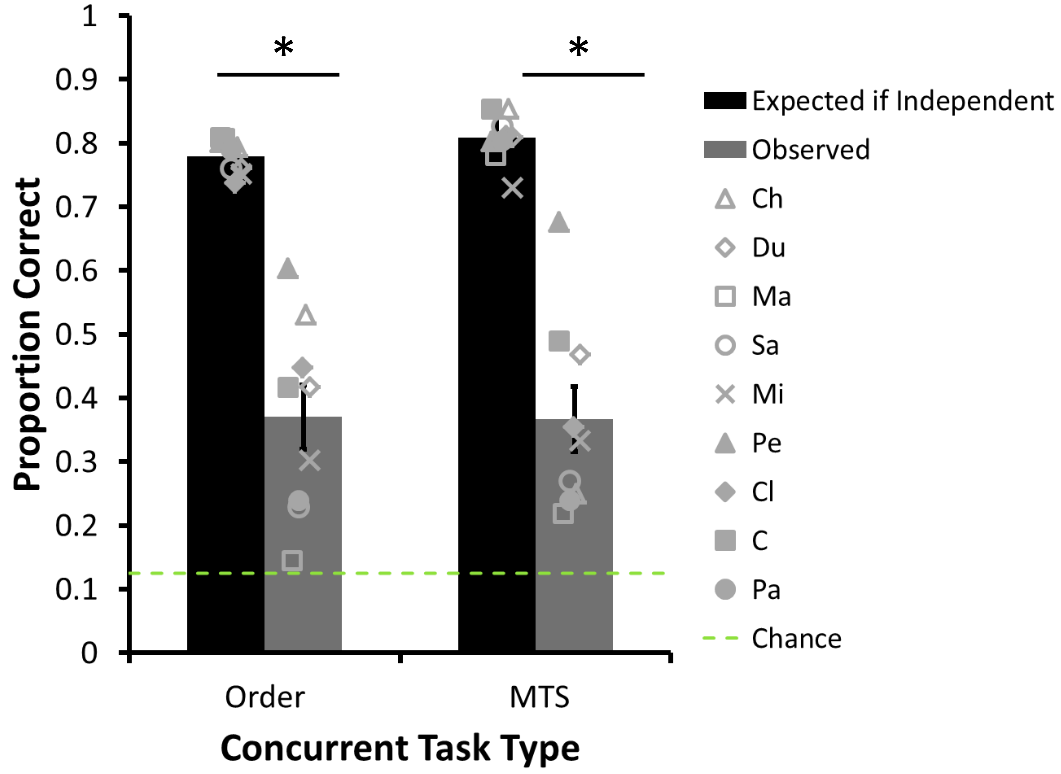

Figure 4. Expected if independent vs observed accuracy, Experiment 1. The bars represent the average proportion correct in the dual task conditions. The points represent accuracy of each animal. The unfilled points represent orangutans and the filled points represent chimpanzees. The black columns represent expected accuracy if the two tasks are independent, and the gray columns represent the observed accuracy in the dual task condition. The left two columns represent accuracy when ordering was embedded in the spatial memory task and the right two represent when the visual matching task was embedded in the spatial memory task.

Results and Discussion

Comparing results from Ordering and MTS Tests

Observed performance in the concurrent load conditions was lower than would be expected if the tasks were independent and did not tax the same cognitive resource. There was a main effect of outcome measure (expected if independent vs observed; $F_{(1,14)}$=133.35, p<0.001, partial eta^2=0.91; Figure 4). There was no effect of species $F_{(1,14)}$=3.42, p=0.9, partial eta^2=0.2), no interaction between species and outcome measure ($F_{(1,14)}$=1.92, p=0.19, partial eta^2=0.12), embedded task type ($F_{(1,14)}$=0.06, p=0.82, partial

eta^2=0.004), or three-way interaction between species, embedded task type, and outcome measure($F_{(1,14)}$=0.012, p=0.92, partial eta^2=0.001). There was also no main effect of inside task type ($F_{(1,14)}$=0.25, p=0.63, partial eta^2=0.02), or interaction between inside task type and outcome measure ($F_{(1,14)}$=0.23, p=0.64, partial eta^2=0.02). Concurrent cognitive load impairs performance generally across tasks. These results suggest that performance on ordering, spatial memory, and MTS are supported by a general cognitive resource. However, we do not know the source of the error driving these results. It is possible that spatial memory performance is generally susceptible to concurrent cognitive load and this is driving the impairment observed in the above analysis. We may observe a differential impact if we look at performance on the embedded task separately from the spatial memory task.

We analyzed subjects' performance on the embedded tasks in the concurrent load conditions and when presented alone. Although graphically it appears that performance on the ordering task decreased more with embedding than did visual matching (Figure 5), the test type (order vs MTS) x embeddedness (alone vs embedded) interaction was not statistically significant ($F_{(1,7)}$=2.95, p=0.13, partial eta^2=0.296). Performance on both tasks suffered from embedding ($F_{(1,7)}$=42.23, $p<0.001$, partial eta^2=0.86; Figure 5), and there was a significant main effect of test type ($F_{(1,7)}$=10.69, p=0.01, partial eta^2=0.6). The pattern of performance by chimpanzees and orangutans was similar. There was a main effect of species ($F_{(1,7)} = 5.66$, p = 0.049, partial eta^2=0.45), but the interactions of species and embeddedness ($F_{(1,7)}$=1.47, p=0.26, partial eta^2=0.17), test type ($F_{(1,7)}$=0.31, p=0.59, partial $eta^2=0.04$), and the 3 way interaction of species x test type x embeddedness ($F_{(1,7)}=0.43$, $p=0.53$, partial $eta^2=0.06$) were not significant.

We do not know how the apes may be allocating their cognitive resources, and it is possible that ordering may impair performance on a spatial memory task more than does the MTS task. To test whether there was a differential impact on the spatial memory task based on the type of task embedded within it, we analyzed accuracy on the spatial memory task. We first compared performance on the spatial memory task following the motor task in both phases of the experiment. There was no difference in spatial memory performance following the motor task across experiments ($t_{(8)}=0.55$, $p=0.6$), so we pooled their accuracy on motor control trials. We excluded trials in which the subjects took longer than 2500ms to complete the embedded task. Subjects performed worse on the spatial memory task following cognitively demanding embedded tasks compared to the less cognitively demanding motor task. There was an effect of concurrent cognitive load type (order, MTS, or motor; $F_{(1,7)}=9.41$, $p=0.003$, partial $eta^2=0.57$). Apes performed significantly worse on the spatial memory task following the ordering task ($M=0.48$) than following the motor task ($M=0.62$; $t_{(8)}=3.16$, $p=0.01$, $d=0.81$), and significantly worse following the MTS task ($M=0.43$) than following the motor task ($t_{(8)}=5.78$, $p<0.001$, $d=1.32$), but there was no difference in their performance on the spatial task following the ordering task compared to following the MTS task ($t_{(8)}=0.93$, $p=0.38$, $d=0.33$). There was no effect of species on the spatial task ($F_{(1,7)}=1.76$, $p=0.23$, partial $eta^2=0.2$).

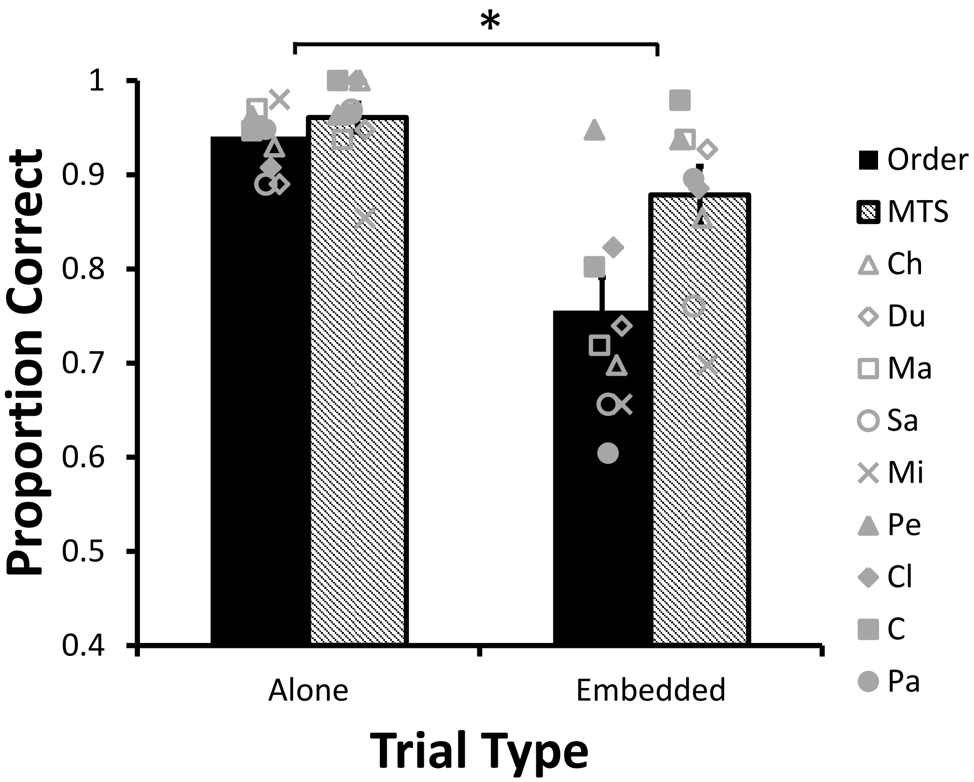

Figure 5. Performance on embedded task types, Experiment 1. The bars represent the average proportion correct in each condition. The points represent accuracy of each animal. The unfilled points represent orangutans and the filled points represent chimpanzees. The black columns represent accuracy on the order task and the striped columns represent accuracy on the MTS task. The left two columns represent accuracy when the tasks were presented alone and the right two represent when the tasks were embedded within the spatial memory task.

Although the interaction of task and embedding was not statistically significant as the spatial representation hypothesis would predict, the data trend toward supporting this hypothesis (Figure 5). Several features of the comparison conducted for test trials with ordering embedded and test trials with MTS embedded may have reduced the power of the comparison. First, testing with the order task and the visual matching task occurred on different days, and after different amounts of training. Subjects' motivation varied drastically across testing sessions due to environmental factors and changing group dynamics, and this could have impacted the results differentially. Second, it is possible that we cannot detect differences in performance on the spatial task following the MTS embedded task from performance following the ordering task because of their near floor level performance in those two conditions. Third, these animals had little experience conducting these tasks simultaneously and this may have contributed to instability in their performance. In an effort to address these issues, we repeated this comparison in Experiment 2, with all test types randomly intermixed within the same testing sessions.

Experiment 2: Intermixed Test

To address issues associated with comparing accuracies on tasks performed across different sessions, and to facilitate direct comparison of the effect of concurrent spatial memory testing on ordering and MTS, we had subjects complete two sessions in which all three trial types (ordering, MTS, and motor control) were intermixed and embedded in the spatial memory task (Figure 2).

Procedure

Each session was 144 trials long and consisted of 48 ordering embedded in spatial memory trials, 48 MTS embedded in spatial memory trials, and 48 motor embedded in spatial memory trials. Each of the three trial types was presented twice every six trials, in a pseudo-random sequence. After initiating the trial, subjects saw the white square spatial sample. During the delay subjects either ordered two number images, matched a sample image to a test image, or touched two motor control stimuli (Figure 3). All other features of the trials were the same as in Experiment 1. At the beginning of each testing day subjects received warmup spatial memory trials with a blank delay. Subjects also completed two 48-trial sessions in which they had to order two numerals and two 48-trial MTS sessions without the spatial memory test to provide a baseline ordering and MTS performance level.

Results and Discussion

Observed performance in the concurrent load conditions was lower than would be expected if the tasks were independent and did not tax the same cognitive resource. There was a main effect of outcome measure (expected if independent vs actual; $F_{(1,14)}=134.65$, $p<0.001$, partial $eta^2=0.91$; Figure 6). There was no effect of species ($F_{(1,14)}=2.57$, $p=0.13$, partial $eta^2=0.2$), no interaction between species and outcome measure ($F_{(1,14)}=3.12$, $p=0.1$, partial $eta^2=0.16$), species and embedded task type ($F_{(1,14)}=0.56$, $p=0.47$, partial $eta^2=0.04$), or three-way interaction between species, embedded task type, and outcome measure ($F_{(1,14)}=0.07$, $p=0.79$, partial $eta^2=0.005$). There was also no main effect of concurrent cognitive load type (order vs MTS; $F_{(1,14)}=1.6$, $p=0.23$, partial $eta^2=0.1$), or interaction between concurrent load type and outcome measure (expected if independent vs observed; $F_{(1,14)}=0.35$, $p=0.57$, partial $eta^2=0.02$). These results again suggest that in the trials with concurrent cognitive load, there is no differential impact between ordering and visual MTS. There does seem to be a general impact of concurrent load on all tasks. This could mean that these tasks are supported by a general cognitive resource rather than a domain specific resource that is taxed during ordering and spatial memory tasks. However, we do not know the source of the error driving these impairments, so we analyzed the results from the tasks separately.

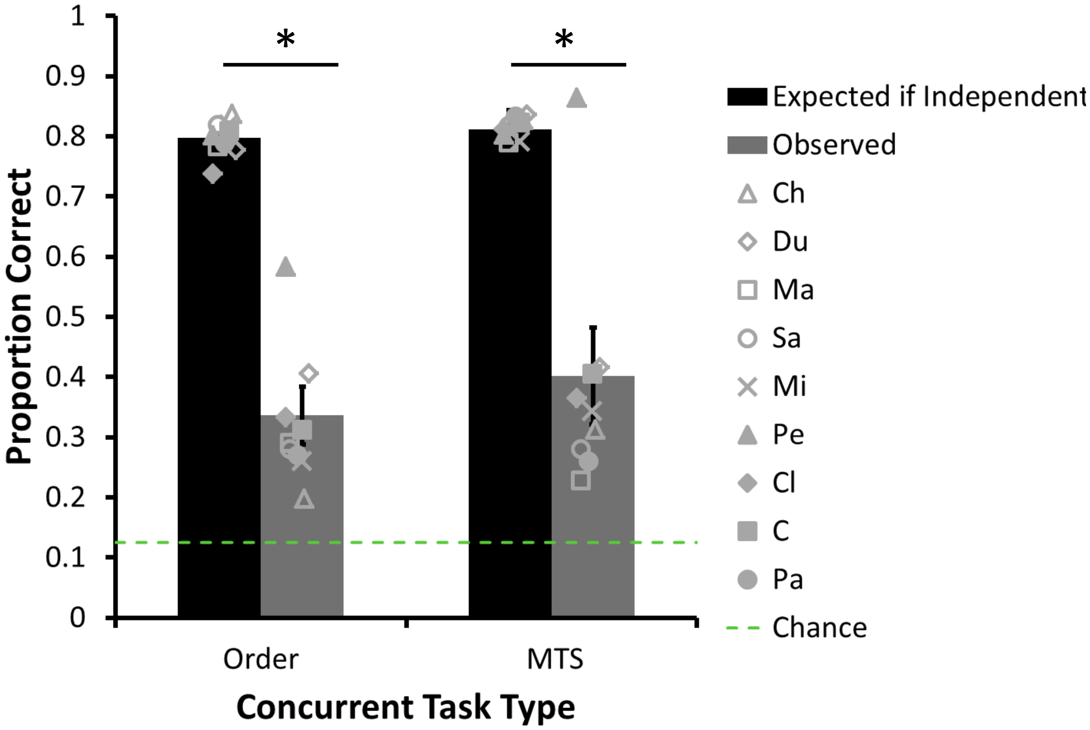

Figure 6. Expected if independent vs observed accuracy, Experiment 2. The bars represent the average proportion correct in the dual task conditions. The points represent accuracy of each animal. The unfilled points represent orangutans and the filled points represent chimpanzees. The black columns represent expected accuracy if the two tasks are independent, and the gray columns represent the observed accuracy in the concurrent cognitive load condition. The left two columns represent accuracy when ordering was embedded in the spatial memory task and the right two represent when the visual matching task was embedded in the spatial memory task.

Consistent with a spatial resource being critical for the order task, accuracy on the ordering task decreased more when it was embedded in the spatial memory task than did performance on the MTS task ($F_{(1,7)}$=13.57, p=0.008, partial eta^2=0.66; Figure 7). This result provides evidence supporting the hypothesis that memory for ordered sequences is controlled by a spatial representation formed in working memory, and this is true across species. Chimpanzees and orangutans performed similarly on both the spatial memory task and the embedded tasks. There was no main effect of species ($F_{(1,7)}$=0.63, p=0.45, partial eta^2=0.08), and no interactions between species and embeddedness ($F_{(1,7)}$=0.03,

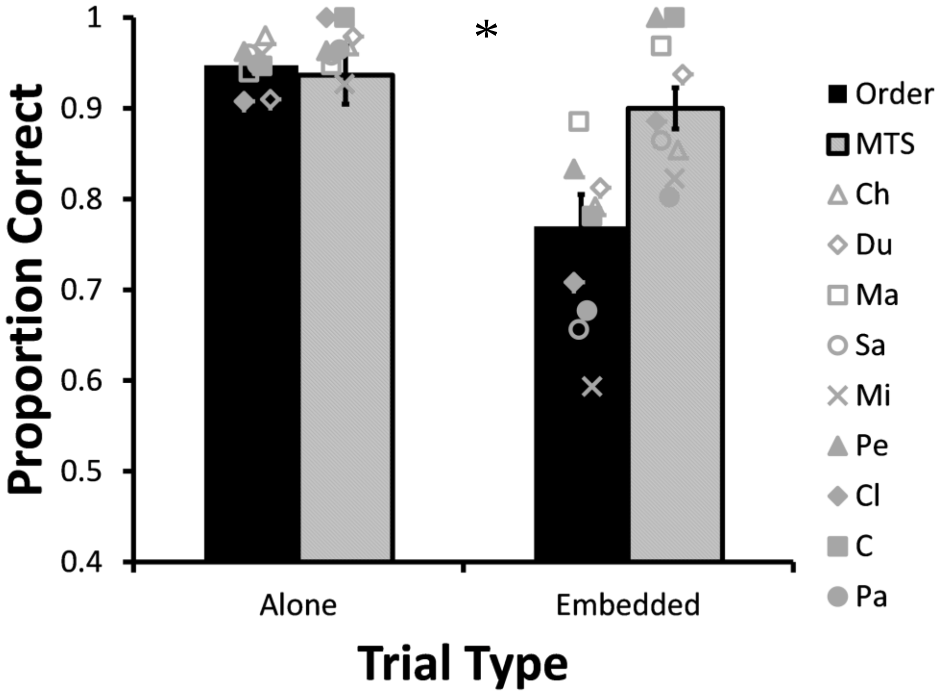

Figure 7. Performance on embedded task types, Experiment 2. The bars represent the average proportion correct in each condition. The points represent accuracy of each animal. The unfilled points represent orangutans and the filled points represent chimpanzees. The black columns represent accuracy on the order task and the striped columns represent accuracy on the MTS task. The left two columns represent accuracy when the tasks were presented alone and the right two represent when the tasks were embedded within the spatial memory task.

p=0.87, partial eta^2=0.004), test type ($F_{(1,7)}$=4.31, p=0.076, partial eta^2=0.38), or 3 way interaction of species x test type x embeddedness ($F_{(1,7)}$=0.008, p=0.93, partial eta^2=0.001) for the embedded tasks.

As in Experiment 1, subjects performed worse on the spatial memory task following cognitively demanding embedded tasks compared to the less cognitively demanding motor task. There was an effect of test type ($F_{(2,14)}$=7.38, p=0.006, partial eta^2=0.51). Apes performed significantly worse on the spatial memory task following the ordering task (M=0.46) than following the motor task (M=0.55; $t_{(8)}$=3.15, p=0.014, d=0.52), and significantly worse following the MTS task(M=0.43) compared to following the motor task ($t_{(8)}$=2.35, p=0.047, d=0.57). There was no difference in their performance on the spatial task following the ordering task compared to following the MTS task ($t_{(8)}$=0.77, p=0.46, d=0.16). There was no effect of species on performance on the spatial task ($F_{(1,7)}$=1.65, p=0.24, partial eta^2=0.24). Unlike the greater impairment on the ordering task compared to the MTS task when both were under concurrent spatial memory load, performing the ordering task did not impair performance on the spatial memory task more than did performing the MTS task. This could possibly be due to the fact that subjects' performance on the spatial memory task was severely impacted by both embedded tasks that required cognitive effort. Apes on average performed just above 40% correct on the spatial memory task following both ordering and MTS embedded tasks. While above chance, this is still very low, and three individuals were at chance level performance for at least one embedded trial type. Because concurrent cognitive load impairs performance across task types, these results provide some support for the hypothesis that there is a domain general resource that supports complex cognition across tasks, and ordering, visual MTS, and spatial memory all tax that resource.

One possible explanation for the larger performance decrement on the ordering task compared to the MTS task when under concurrent spatial memory load is that the MTS task is a perceptual matching task rather than a working memory task. If a general memory resource is taxed across memory tasks, a perceptual matching task is unlikely to tax the same resource, so performance would not be as impaired when under a concurrent memory load. It is also possible that the decrement was due to the fact that ordering is impaired when under any concurrent cognitive load. We did not embed ordering in another task, so the differential decrease could be due to ordering being generally susceptible to interference. Thus we ran Experiment 3 to test whether it is a specific shared cognitive resource driving the performance decrement or if it is a general decrement caused by any form of concurrent load.

Experiment 3: Ordering Embedded in Spatial Memory and Delayed MTS

Because it is possible that our results in Experiments 1 and 2 may be driven by the ordering task being susceptible to impairment in any concurrent cognitive load context, we ran Experiment 3 in which we embedded the ordering task within the spatial memory task and within a delayed matching-to-sample task. If ordering is supported by a domain specific spatial memory resource, performance on the ordering task will be impaired more when it is under concurrent spatial memory load than when it is under concurrent non-spatial visual matching-to-sample load.

Methods

Subjects

Four out of the five orangutans who completed Experiments 1 and 2 completed this follow up study: a 9 year old Sumatran male (*Pongo abelii*), a 39 year old hybrid (Sumatran/Bornean), a 24 year old Bornean female (*Pongo pygmaeus*), and a 13 year old Bornean male. No other features of their environment or the testing apparatus changed. No chimpanzees were available to complete this experiment.

Additional Ordering Training

Because we were concerned that ordering only 5 numerals may not provide sufficient list length, we gave the orangutans additional ordering training with the goal of training them on 9 numerals, as were the chimpanzees. All features of the ordering training were the same. They started by ordering 5 numerals and they again had to reach the criterion of completing two 48-trial sessions in a row with at least 85% of the trials performed correctly. When this criterion was met, another numeral was added to the sequence until they reached 9 numerals. Some orangutans struggled to learn these sequences, so an additional criterion was put in place. After correctly ordering 5 numerals, if orangutans failed to learn to order with an additional numeral after completing at least 10,000 trials, then that orangutan’s top number was the number at which they completed those trials. After these 10,000 trials, the orangutans who reached this point still had to complete one session with an accuracy of 85% at their new “highest” numeral before moving on to the next step in training. One orangutan’s final numeral was six and another’s was seven. Two out of the four orangutans reached criterion with nine numerals.

Visual Delayed Matching-to-Sample (DMTS) Training

After learning the additional numerals, orangutans learned the delayed matching-to-sample (DMTS) task. Although they had all been presented with DMTS trials previously, they had not been systematically trained on this type of task. For these trials, subjects touched a start square to initiate a trial after which an image (100x100 pixels) appeared on the center of the screen. After touching the image the screen went blank for a short delay. Then four choice images appeared in the four corners of the screen (Figure 8A). Orangutans were rewarded for picking the image that matched the image they had seen at the beginning of the trial. They were first trained with a delay of 500ms that was incrementally increased as they correctly responded within a session at least 80% of the time. The delay was increased until they reached a 2000ms delay. There were 8 images from which the sample and distractor choices could be drawn. Every 16 trials each sample was seen twice, and each image was the sample 6 times in a 48-trial session. The correct choice location was pseudo-randomly distributed such that every 8 trials each of the four corners was the correct location twice. The identities of the distractor choices were randomly assigned. After performing above 80% correct in a 48-trial session, subjects moved on to concurrent cognitive load training with one item embedded within the matching-to-sample task.

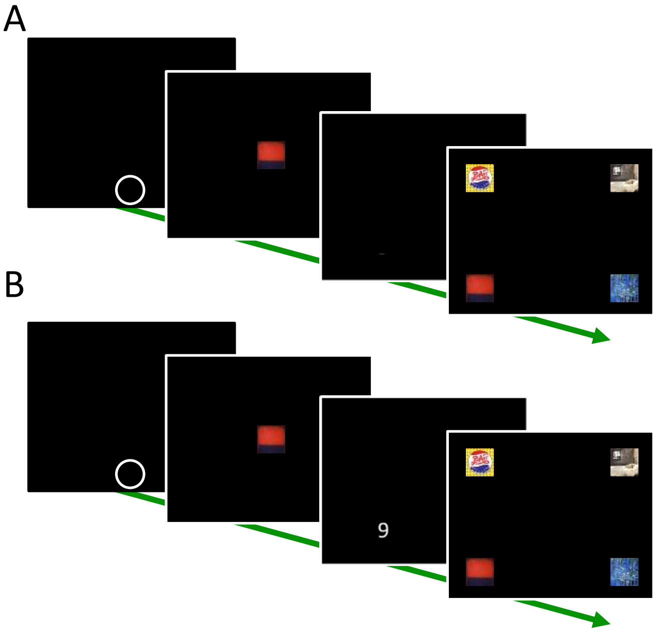

Figure 8. DMTS trials. A) DMTS Alone. Subjects saw a sample image that disappeared for a delay of 2000ms after they touched it. Then four choice images appeared. Subjects were reinforced for touching the matching image. B) DMTS with Ordering Embedded. Subjects touched an embedded stimulus during the delay between seeing the sample image and test images. Subjects were reinforced for touching the matching image.

DMTS Training with Concurrent Cognitive Load

Subjects continued performing the DMTS task, but now during the delay period between seeing the sample image and the test, orangutans had to touch an intervening item, either a single numeral or a single motor control stimulus, just as in the spatial memory training from Experiment 1(Figure 8B). Subjects saw the image, and after they touched it, the screen went blank, and either a numeral or the target stimulus appeared. The embedded stimuli appeared in one of the possible 48 screen locations, randomly chosen each trial. Orangutans had to touch the embedded stimulus, after which it disappeared. The time between the image sample display and test was held constant at 2500ms by adding a black screen delay after the control response before the DMTS test phase was displayed. Subjects received no explicit reinforcement for touching the embedded stimuli. After the delay, the four choice images appeared in the four corners of the screen and again subjects had to touch the image that matched the sample image. Subjects had to perform above 65% correct on the DMTS task for two consecutive 48-trial sessions before moving on to test trials. If subjects failed to reach this criterion within 10 sessions, they were instead required to complete correctly at least 30/48 trials (62.5%) for 3 sessions in a row. This was the same criterion established for the spatial memory training procedures above.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 DMTS trials with blank delays (2000ms delay). This was intended to decrease the likelihood of floor level performance on DMTS with intervening items.

DMTS with Concurrent Cognitive Load: Ordering Two Items

To match the orangutan's prior experience with concurrent load test trials in which they had to order two numerals inside of the spatial memory task, orangutans completed eight sessions in which they had to order two numerals embedded within the DMTS task. This phase was identical to training except that instead of one intervening numeral or motor stimulus presented during the delay of the DMTS task, there were two items. Subjects either had to order two numerals (randomly displayed and randomly chosen; 1-9 for two orangutans, 1-6 for one orangutan, and 1-7 for one orangutan) or touch two motor control stimuli (for the spatial memory equivalent see Figure 3B). In the order task the two numerals were presented on the screen at once and the subject had to touch them in ascending order. The motor control stimuli were presented one at a time so that there was no chance of the subject attempting to order the stimuli. If the subject incorrectly ordered the numerals, the trial was aborted and repeated at the end of the session to ensure the same number of both types of trials were completed and each spatial location was the target at test once each session. Again, subjects received no reinforcement for completing the embedded task.

At this point, the orangutans' experience was matched between the spatial memory task and the DMTS task. We then re-trained every trial type so their experience was matched in time as well.

Ordering Subsets of the Sequence Refresher

Subjects completed trials in which only a subset of the numerals in the sequence were presented. Trials had between 2 and 9 (or 7 or 6 for one orangutan respectively) numerals presented, and subjects again had to touch in ascending order. All other features of the trials were the same as the ordering training. This training was intended to give the subjects experience ordering subsets of the sequence because the final tests did not include ordering all numerals from the sequence. Subjects again had to complete two 48-trial sessions in a row with at least 85% correct to move onto the next step in training.

Spatial Memory Alone and with Concurrent Cognitive Load

Subjects were presented with the spatial memory task with an empty delay, just as in training for Experiment 1. They had to again complete a session with at least 80% accuracy with a 2000ms delay. They then had to again complete trials with one item embedded. The criterion was the same as above: two sessions in a row at or above 65% accuracy, or if they had completed 10 sessions, three sessions in a row at or above 62.5%. All features of these sessions were the same as the training trials above.

DMTS Alone with Concurrent Cognitive Load

Subjects then had to complete DMTS trials with an empty 2000ms delay at 80% accuracy within a 48-trial session. After reaching this criterion, they again had to complete trials with one item embedded in the DMTS task. The criterion was the same as above: two sessions in a row at or above 65% accuracy, or if they had completed 10 sessions, three sessions in a row at or above 62.5%. All features of these sessions were the same as the training trials above.

The purpose of these steps was to ensure that subjects were performing both of these tasks at a similar level. After completing these steps, subjects moved onto test trials.

Concurrent Cognitive Load Test: Spatial Memory and DMTS with Ordering Two Items

We embedded the ordering task in both the spatial memory task and the matching-to-sample task. In a test session there were five trial types: the spatial memory task with nothing embedded, the DMTS task with nothing embedded, ordering two numerals alone, ordering two numerals embedded within the spatial memory task, and ordering two numerals embedded within the DMTS task. The spatial memory task and DMTS task were the same as described above except now the delay between sample and test was 2500ms. Ordering alone was also the same as the non-adjacent task above except that every trial had only two numerals that the subjects had to order. For ordering embedded in spatial memory trials, first subjects touched a start circle to begin a trial. They then were presented with an array of 4 squares, 3 blue and one white, as above. After touching the white square the squares disappeared and two numerals (from the range 1-9 for two orangutans, 1-7 for one orangutan, and 1-6 for one orangutan) appeared randomly arrayed on the screen. Orangutans had to touch the numerals in ascending order. If they touched in the wrong order, they heard a buzz sound and that trial was aborted. To control for the number of trials the orangutans were presented with the spatial memory test, if a trial was aborted, that spatial array was recorded and repeated at the end of the session. If they correctly touched the numerals in ascending order then the sample spatial array was re-presented with all four squares now blue. Orangutans were reinforced for touching the square that had previously been white. Orangutans were not reinforced for correctly ordering the numerals. Each of the possible 48 spatial locations served as the target location once for both the spatial memory alone trials and the spatial memory with ordering embedded trials.

We used a very similar procedure for DMTS trials with ordering embedded. After seeing the sample picture, orangutans saw two numerals to touch in ascending order. Again, incorrect ordering aborted the trial and that trial was recorded and repeated again at the end of the session. After correct ordering, the four DMTS choices were presented in the four corners of the screen and orangutans were rewarded for touching the image that matched the sample image. Each of the five task types was presented 48 times for a minimum session length of 240 trials. Every 10 trials each trial type was presented twice pseudo-randomly. After the original 240 trials were completed, all five trial types continued to be presented pseudo-randomly. If the trial type was to be ordering embedded in spatial memory or ordering embedded in DMTS, rather than a new trial, a trial that had been aborted because of incorrect ordering was presented. This design allowed the animals to continue working without only having the difficult trial types all presented in a row at the end of a session. Subjects completed two testing sessions.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 DMTS trials and at least 8/10 spatial memory trials with blank delays (2000ms delay). This was intended to remind them of the task and decrease the likelihood of floor level performance on DMTS and spatial memory with competing cognitive load.

Results and Discussion

Again, because sharing a limited resource may impair performance on either or both cognitive tasks under concurrent cognitive load, we analyzed accuracy on the whole trial (i.e. encompassing both tasks), and we determined the accuracy expected under dual task conditions if performance on the two individual tasks were independent. This is the simple product of the observed proportion correct on the two tasks when presented separately. We multiplied subjects' proportion correct on the spatial memory task (M=0.94) and the DMTS task (M=0.75) by their proportion correct on the ordering task when it was presented alone (0.90). This gave us two expected accuracies for the experimental conditions: expected accuracy when spatial memory and ordering were performed concurrently (M=0.85), and expected accuracy when MTS and ordering were performed concurrently (M=0.68). We ran a RMANOVA with outcome measure (expected if independent vs actual accuracies) and concurrent cognitive load type (spatial memory vs DMTS) as factors.

Observed performance in the concurrent load conditions was lower than would be expected if the tasks were independent and did not tax the same cognitive resource. There was a main effect of outcome measure (expected vs observed; $F_{(1,6)} = 53.14$, $p<0.001$, partial $eta^2=0.899$; Figure 9). This indicates that the ordering, spatial memory, and DMTS tasks share the same cognitive resource. There was no interaction between outside task type (spatial memory vs DMTS) and outcome measure (expected if independent vs observed; $F_{(1,6)} = 4.75$, $p=0.072$, partial $eta^2=0.44$). There was also no difference between performance on spatial memory tasks and DMTS tasks ($F_{(1,6)} = 1.57$, $p=0.26$, partial $eta^2=0.21$). These results suggest that it is a general resource supporting ordering. Performance on trials in which ordering is under concurrent load with another memory task is impaired, and this seems to be a general impairment across load types. Earlier analyses suggested that it is possible that the spatial memory task is universally impacted by concurrent load but ordering may be a more sensitive measure. However, in the previous experiments ordering was under only one type of concurrent cognitive load. Thus it was important to further test if ordering is differentially impacted when embedded in these different types of trials.

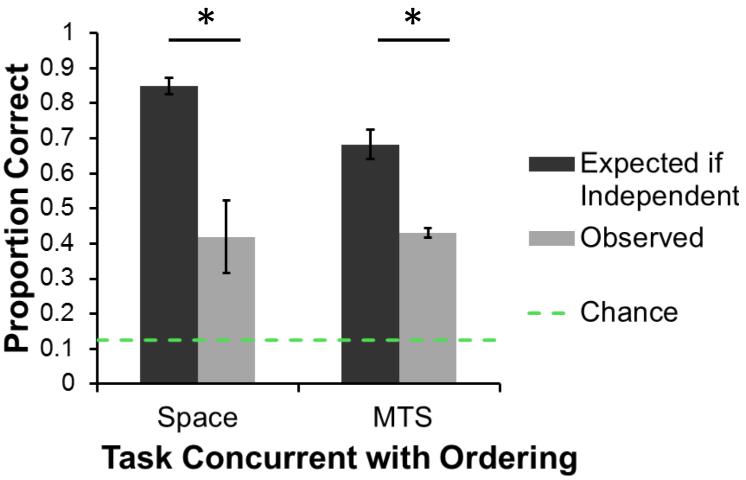

Figure 9. Expected if independent vs observed accuracy, Experiment 3. The bars represent the average proportion correct in the dual task conditions. The dark gray bars represent the expected accuracy on the two tasks if they are independent. The light gray bars represent the observed accuracy in the concurrent cognitive load trials. The left two columns represent accuracy when ordering was embedded in the spatial memory task and the right two represent the orangutans' accuracy when ordering was embedded in the delayed visual matching task (DMTS).

We ran a one-way RMANOVA on the orangutan's accuracy on the ordering task across the three types of outside task (alone, embedded in spatial memory, embedded in

DMTS). Orangutans were not significantly worse on the ordering task when it was embedded within the spatial memory task than when it was alone or embedded in the MTS task. There is no statistically significant difference across these groups ($F_{(2,6)}$=3.28, p=0.109, partial eta^2 = 0.522; Figure 10A). However, these analyses were conducted on a sample size of 4 individuals. Power analysis suggests that with a partial eta^2 of 0.52, we would need at least a sample size of six to observe a significant effect. Thus, although these results are not consistent with the findings from Experiments 1 and 2, our sample size was cut almost in half from these first studies. Given our small sample size it is unlikely that we would be able to find statistically significant differences across these groups. We do see numerical differences

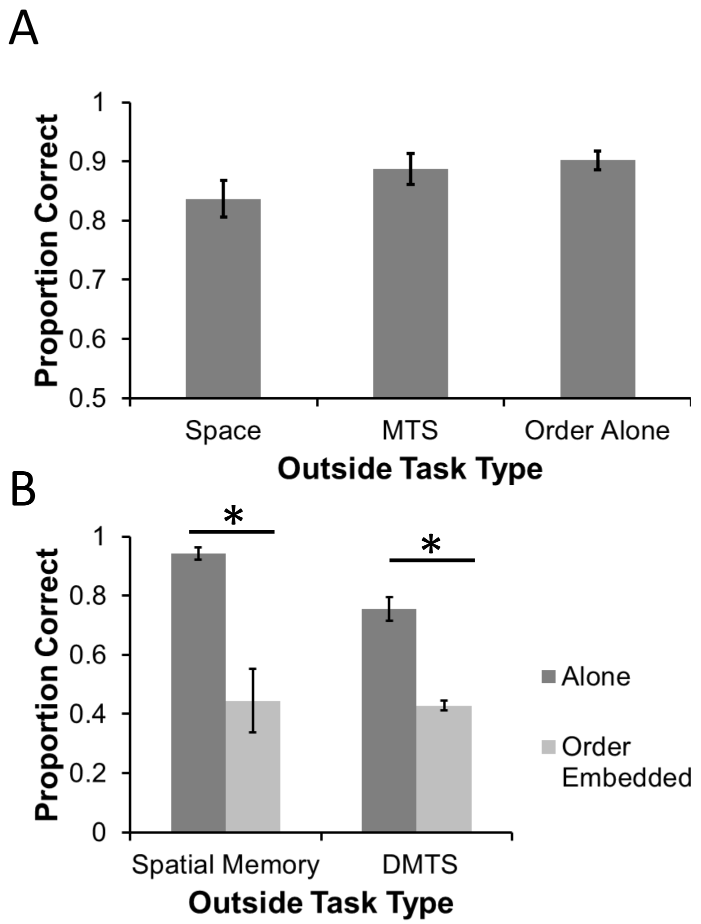

Figure 10.Performance on ordering and outside tasks, Experiment 3. A) Ordering accuracy. The bars represent the average proportion correct on the ordering task when it is embedded in the spatial memory task, embedded in the DMTS task, and when it was presented alone. B) Spatial memory and DMTS accuracy. Dark gray bars represent accuracy on the spatial and DMTS tasks when they were presented alone, and light gray bars represent accuracy on those tasks when they had a concurrent ordering load.

in ordering performance that if maintained with a larger sample size could indicate that ordering is most impaired when embedded within the spatial memory task (embedded in spatial memory M = 0.84, embedded in DMTS M=0.89, alone M=0.9). However, as these results are not statistically significant, we do not have evidence supporting the hypothesis that it is the combination of order and space driving the significant results from Experiment 2, rather than a general impact of load on ordering performance.

To analyze the outside task performance, we ran a 2x2 RMANOVA with outside task (spatial vs DMTS) and aloneness (alone vs order embedded) as factors. Trials that took longer than 2500ms to complete the ordering task were removed from outside task analyses. Orangutans were worse on trials in which the outside task was under a concurrent ordering cognitive load (M=0.44) than when they were performed alone (M=0.85). There was a main effect of concurrent load (alone vs order embedded; $F_{(1,3)}=83.52$, $p=0.003$; partial $eta^2=0.97$; Figure 10B). There was a trending interaction between outside task and aloneness ($F_{(1,3)}=9.53$, $p=0.054$, partial $eta^2=0.76$). There was no effect of outside task type (spatial memory vs MTS; $F_{(1,3)}=3.81$, $p=0.15$; partial $eta^2=0.56$). These results do not support the hypothesis that ordering and spatial memory rely on a domain specific resource that does not contribute to visual memory tasks. Additionally, as described above, spatial memory may be susceptible to concurrent cognitive load across tasks. And although the interaction is trending, we can see that performance on both spatial memory and visual DMTS are impaired by concurrent cognitive load. These results suggest that performance on all tasks tested in these experiments is supported by a general cognitive resource, rather than a domain specific resource that differentially supports ordering and spatial memory.

General Discussion

These results from chimpanzees and orangutans suggest that in apes ordering and spatial memory rely on a general cognitive resource, as performance was impaired across all concurrent cognitive load conditions more than would be expected if the tasks did not tax a shared cognitive resource. Competition from a spatial memory task did impair ordering more than it did visual matching-to-sample, but this may have been due to the MTS task relying on perceptual, rather than memory, resources. Thus, these results do not indicate that spatial representations of order are supported by a domain specific memory mechanism that is evolutionarily ancient. According to phylogenies based on complete mitochondrial DNA genomes, chimpanzees and humans last shared a common ancestor with humans 5.9 million years ago, and humans and orangutans 15.2 million years ago (Finstermeier et al., 2013). Chimpanzees and orangutans did not differ from each other in our tests, suggesting that the mechanism supporting cognition generally in these tasks is conserved evolutionarily in the apes, dating back at least as far as 15 million years.

The interaction between task type (ordering vs MTS) and embeddedness in Experiment 2 could suggest a domain specific resource supporting ordering and spatial memory. However, despite similar baseline performance by the apes on the ordering task and the MTS task in Experiments 1 and 2, it is possible that the ordering task was generally sensitive to a competing cognitive demand, rather than being specifically sensitive to the spatial demands of the competing task. Therefore, we ran Experiment 3 in which we embedded ordering within a spatial memory task and within an identity matching task. We found that ordering performance was not more impaired when under concurrent spatial load then concurrent DMTS load. Unfortunately, only four orangutans were able to complete this experiment. Given our observed effect size, power analysis suggests that we would need a sample size of six to observe a statistically significant result. Thus, to draw further conclusions regarding this pattern of results we would need to test at least two additional individuals. Additionally, completion of the ordering task presumably required retrieval of a memory of the sequence of the number images from memory, whereas the simultaneous MTS task requires retrieval only of the perceptual matching rule. Thus, the general demand on working memory may be greater in the ordering task than the matching task. If ordering and spatial memory tax the same general memory resource that is not taxed in a perceptual task, we would observe this interaction. But this interaction alone is not enough to definitely state whether ordering and spatial memory share a domain specific resource that is not taxed when ordering is under a different concurrent cognitive load. As it stands, our results do not support the hypothesis that a specific shared resource supports ordering and spatial working memory, but we found that concurrent cognitive load impaired performance on memory tasks generally.

We did find that concurrent cognitive load impairs performance across task-types more than would be expected if the two tasks performed together did not tax the same limited cognitive resource. However, in Experiments 1 and 2, the spatial memory task "alone" proportion correct was not matched in space and time to the test trials. Thus the spatial memory performance could have improved or diminished with experience and time, making it difficult to draw further conclusions based upon these results. This problem was attenuated in Experiment 3 because all conditions were performed within two intermixed sessions. We observed impairment with concurrent cognitive load across all task types, and this supports the hypothesis that these memory tasks are supported by a general cognitive resource rather than a domain specific resource between space and order.

If the cognitive tasks included in this study are supported by a general resource rather than a specific resource that supports spatial memory and ordering differently than other tasks, we would expect to see the general impairment when under concurrent cognitive load across conditions as we observed here. The significant interaction in which ordering performance was more impaired than was MTS performance when under concurrent spatial memory load in Experiment 2 might be evidence that the simultaneous matching-to-sample task is supported by a different mechanism, one that is perceptual rather than memory-based. This result does not rule out the possibility that a general resource supports working memory across these concurrent cognitive load conditions, but rather emphasizes that the simultaneous matching task is likely controlled by a different mechanism. We did not have sufficient control trials or sample sizes to definitely determine whether more resources are shared between spatial memory and ordering than other visual memory tasks. Thus in the future it will be appropriate to better control the sources of interference and account for the possibility that it is a general resource that supports complex cognition. In this study we were able to test whether a limited cognitive resource supports ordering and spatial memory specifically in apes without the influence of language training. We found that ordering, spatial memory, and visual memory all rely on a domain general working memory resource. This does not indicate whether apes represent order spatially, but it does suggest that in close primate relatives, domain general working memory resources support cognition.

Introduction to Manuscript 2

I designed the studies described in Manuscript 2 to address the shortcomings from Manuscript 1. I tested six rhesus macaques on a series of experiments built upon the findings from Manuscript 1. I trained them on the ordering task, the spatial memory test, a delayed matching-to-sample task, and an object discrimination task. I then embedded the ordering and object discrimination inside the spatial memory and DMTS tasks. The object discrimination task replaced the simultaneous MTS task from Manuscript 1. Rather than a perceptual matching task, the object discrimination task requires subjects to pull from memory previously learned discriminations. This was intended to more closely model the ordering task that also requires memory for the previously learned sequence. If a domain specific memory resource supports ordering and spatial memory, then performance on trials in which an ordering task and a spatial memory task are performed will be more impaired than performance on trials in which either task is performed concurrently with a non-spatial visual memory task. As in Manuscript 1, I found robust evidence for a domain general resource supporting performance across ordering, spatial memory, and visual memory tasks.

Manuscript 2

Spatial representations for order in monkeys are not supported by a domain specific spatial working memory resource

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Abstract

Humans think about order and number using a spatial representation, with items early in a list represented on the left side of space and later items in a list represented on the right side of space for people who read and count from left to right. The spatial representation of order may be an evolutionarily ancient mechanism supporting ordinal and numerical cognition across species. There is evidence that suggests that nonhuman primates' ability to order relies on a spatial representation mechanism, but there have been very few tests investigating this idea. We tested whether rhesus monkeys' ordering performance is supported by a working memory mechanism in which ordering and spatial memory share a domain specific memory resource that is not taxed in non-spatial visual working memory tasks. We trained monkeys on an ordering task, an object discrimination task, a spatial working memory task, and a non-spatial visual working memory task. We then combined these tasks to test if rhesus monkeys' performance on an ordering task and a spatial memory task was more impaired when they were performed concurrently than when performed concurrently with non-spatial visual memory tasks. We found evidence that concurrent cognitive load of any type impaired performance in monkeys, suggesting that these tasks are supported by a general cognitive resource. We did not find evidence for a domain specific resource supporting ordering and spatial memory in rhesus monkeys.

Introduction

Humans use many spatial metaphors. Politicians are on the left or the right, the past is behind you, the stock market is going up, and sometimes we feel down. The ubiquity of spatial metaphor across contexts raises the question of whether an association between space and other features is dependent on language and culture or if it is an evolutionarily ancient organizing feature of cognition that culture and language have built upon. Humans represent magnitude and order spatially (Cheung et al., 2015; Dehaene et al., 1993; Gevers et al., 2003; Göbel et al., 2011; Previtali et al., 2010; van Dijck et al., 2013; Wood et al., 2008). Additionally, nonhuman animals that do not read or count do represent space, magnitude, and order (Adachi, 2014; Brannon, 2006; Gazes et al., 2012; Hubbard et al., 2005; Rugani & de Hevia, 2016; Rugani et al., 2015; Templer & Hampton, 2013). If nonhuman primates also represent order spatially, then a spatial representation is likely an evolutionarily ancient and fundamental mechanism for ordinal cognition. Thus, in this study we test whether ordering and spatial memory tax the same working memory resource in rhesus monkeys, a species that does not have prior language training and with which we shared a common ancestor 32 million years ago (Finstermeier et al., 2013).

Most of the evidence supporting the hypothesis that spatial representations underlie memory for order and number comes from the Spatial Numerical Association of Response Codes (SNARC) paradigm (Dehaene et al., 1993; Wood et al., 2008). In the SNARC paradigm human participants are presented with numerals that they have to designate as odd or even by touching response keys on the left or right sides of a keyboard. Researchers have consistently found an interaction between space and number such that the majority of Western participants, who read and count from left to right, are faster to respond to small numerals on the left side of space than on the right and vice versa for large numerals (for a review see Wood et al., 2008). The improved speed in the condition that is congruent with a left to right spatial organization for numbers and the reduced speed in the condition that was incongruent with a left-to-right spatial organization is taken as evidence that participants shift their attention along their spatial representation according to the magnitude of the stimulus. The interaction between space and magnitude has also been found across magnitude types including auditory magnitudes (Nuerk et al., 2005), emotional magnitude (Holmes & Lourenco, 2011), and pitch (Rusconi et al., 2006), suggesting that it is not solely numbers and learned spatial associations driving these effects. Ordered series are also represented spatially (Gevers et al., 2003, 2004; Ginsburg & Gevers, 2015; Ginsburg et al., 2014; van Dijck et al., 2013). Days of the week, months of the year, and letters of the alphabet are all associated with spatial representations (Gevers et al., 2003, 2004). Even novel sequences that do not have extensive spatial associations outside of an experimental context are represented spatially (Previtali et al., 2010). There is also evidence that even before formal magnitude and spatial training, infants associate magnitude and space (de Hevia, Girelli, et al., 2014; de Hevia, Girelli, & Cassia, 2012; de Hevia, Izard, et al., 2014; Macchi et al., 2012). Yet, almost from day one, human infants are exposed to cultural practices that could already start to impact their associations between space and magnitude. Thus, studying our primate relatives will elucidate whether a predisposition to associate space and order is an evolutionarily ancient shared characteristic across species, without the influence of culture.

Though found across contexts and cultures, the orientation of the spatial representation of magnitude/order is impacted by language and recent experience (Göbel et al., 2011; Shaki & Gevers, 2011). Western participants who read and count from left-to-right show the left-to-right orientation described above. However, Palestinian participants who read and count from right-to-left show the opposite orientation when tested in an identical paradigm (Shaki et al., 2009). The impact of culture is observable even early in human children's lives. Pre-school children order items in the same orientation as their culture reads (McCrink, Shaki, & Berkowitz, 2014). American (English-speaking) and Israeli (Hebrew-speaking) 3 and 4 year olds learned to label items from left to right or from right to left. When then asked to match the label on a new set of items, American participants performed better after learning to label items from left to right. Israeli children performed better after learning to label from right to left. These results show that the impact of culture on spatial representations is significant before human children start kindergarten. Yet, even within Western participants the orientation of this representation seems to be flexible (Bächtold et al., 1998; Holmes & Lourenco, 2012; Patro & Shaki, 2016; Shaki et al., 2012). People told to imagine numerals as presented on a clock face show a right-to-left orientation for their representation as opposed to when they are told to remember a ruler and their representation goes from left-to-right (Bächtold et al., 1998); people told to imagine floors of a building show a vertical orientation for their representation (Holmes & Lourenco, 2012). These studies show that while there is a consistent association between magnitude and space, the orientation seems to be flexible and very much dependent on culture, language, and recent experience. Additionally, culture impacts these representations even before children have learned to read. Thus in order to understand the underlying mechanism supporting these representations it is important to study populations free of the influence of language and culture, such as nonhuman primates.

Nonhuman animals do seem to associate order and space (Dahl & Adachi, 2013; Drucker & Brannon, 2014; Rugani et al., 2010; Rugani et al., 2011; Vallortigara et al., 2010). Nonhuman primates have long been known to be able to order items (Brannon & Terrace, 1998; Gazes et al., 2012; Kawai & Matsuzawa, 2000; Matsuzawa, 1985; Merritt & Terrace, 2011; Templer & Hampton, 2013; Terrace, 2005; Tomonaga & Matsuzawa, 2000). Findings such as symbolic distance effects, that are consistently found across tasks (Merritt & Terrace, 2011; Terrace, 2005) imply that sequences may be represented spatially. Nonhuman primates who are trained to pick items earlier in a sequence do so more accurately when presented with a pair of items that are further apart within the sequence (i.e. if presented with the second and seventh item they are more accurate than if presented with the second and fourth item). The symbolic difference is represented as spatial distance (Templer & Hampton, 2013; Terrace, 2005). However, these studies have not directly tested whether the mechanism supporting these associations is a spatial representation.

Recent studies have found more concrete evidence supporting spatial representations of order in nonhuman animals (Adachi, 2014; Dahl & Adachi, 2013; Drucker & Brannon, 2014; Gazes et al., 2014; Rugani et al., 2011). Baby chickens and adult nutcrackers trained to pick the fourth item from the bottom of a series presented vertically, consistently pick the fourth from the left when that series is rotated 90 degrees (Rugani et al., 2010). When the spatial distance between items was changed at test, chicks continued to pick the fourth item in the series, but now they picked the fourth from the left and the fourth from the right equally often (Rugani et al., 2011). The chicks' performance seems to be driven by two mechanisms: a spatial representation that is highly lateralized and an ordering mechanism that is bilaterally represented. Therefore, these results suggest that the orientation of the association between order and space seems to be driven by lateralized mechanisms in the avian brain. In nonhuman primates who do not have the same level of lateralization, order also is mapped onto space. Chimpanzees trained to match the identities of other chimps from their group, respond more quickly when images of their high-ranking group-mates are presented on top of a screen and low-ranking on the bottom (Dahl & Adachi, 2013). They are also faster to respond to the first item in a highly trained list on the left side of space than on the right side of space (Adachi, 2014). Monkeys show improved performance on a sequence learning task after receiving congruent spatial training with list-items compared to receiving incongruent spatial training (Gazes et al., 2014). This evidence is suggestive of an underlying spatial representation supporting ordinal cognition. However, these studies all relied on testing a particular orientation of the representation. Because nonhuman primates do not learn to read or count in a particular direction, and they do not have the same level of laterality observed in avian brains, we cannot a priori anticipate the orientation of their representation. Thus we developed a paradigm that did not rely on predicting the orientation of the representation to test whether nonhuman primates represent order spatially.

There is some evidence suggesting that sequences become associated with spatial representations in working memory (for a review see Abrahamse et al., 2016). Evidence suggesting that the spatial representation of numbers actively draws upon spatial working memory resources during task completion comes from a series of studies in which a working memory task and a SNARC task were performed concurrently. If an individual had to remember a series of spatial locations on a screen while also performing a SNARC task, the relation between space and numerical magnitude disappeared (Ginsburg et al., 2014; van Dijck et al., 2009). The spatial working memory load interferes with the spatial association between numbers. Additionally, novel sequences take on spatial associations in working memory (van Dijck et al., 2014; van Dijck & Fias, 2011). These results support the hypothesis that because there are limited spatial memory resources and the spatial memory task taxes those resources, only limited spatial representational resources remain available to support a spatial representation of magnitude.

To test whether nonhuman primates represent order spatially, we presented rhesus monkeys with a series of tests in which two potentially spatial tasks, an ordering task and a spatial memory task, competed for working memory resources. Specifically, we compared monkeys’ performance on trials in which an ordering and a spatial working memory task were performed concurrently to trials in which a non-spatial object discrimination task and a spatial working memory task were performed concurrently. We also compared trials in which the ordering task was performed concurrently with a visual working memory task (delayed matching-to-sample), and the object discrimination task was performed concurrently with a visual working memory task. If ordering and spatial memory share a domain specific working memory resource, performance on trials in which ordering is under a concurrent spatial memory load will be impaired. The magnitude of impairment will be higher than when the ordering task is under a visual memory load. This impairment could be driven by errors to the ordering task or errors to the spatial memory task, or errors to both. In each of these cases, increased impairment to the ordering task or the spatial memory task when performed concurrently, would indicate that successful performance requires a cognitive resource that is necessary and shared by those tasks. By assessing whether performance is more impaired than would be expected if the two tasks are independent, we were able to test if there are shared resources without assuming the directionality of the apes' allocation of resources. We also did not predict whether the impairment was bi-directional, i.e. impacting both ordering and spatial memory, or uni-directional, i.e. impacting just ordering or just spatial memory. Any impairment might indicate a specific shared resource, regardless of the directionality. Similarly, performance on trials in which an object discrimination task is under a concurrent spatial memory load should not be impaired as much, but trials in which an object discrimination task is under a concurrent visual memory load may be significantly impaired as both tasks require visual identity memory resources. To then further assess the source of the errors in the earlier analyses, we also analyzed impairment on each of the tasks separately. In any of these cases, if there is specific impairment when ordering and spatial memory are performed concurrently, it will indicate that those tasks tax a resource that does not support visual memory tasks. If these tasks are all impaired under concurrent cognitive load, it will suggest that these tasks are supported by a general cognitive resource, not specific to spatial memory and ordering.

Methods

Subjects

Subjects were 6 male rhesus macaques (*Macaca mulatta*) aged approximately 8-10 years at the start of testing. Monkeys were pair housed when possible given husbandry constraints and kept on a 12:12 light:dark cycle. Monkeys received full daily food rations and ad libitum access to water. Subjects had prior experience with cognitive testing using touchscreen computers, but five out of the six did not have prior experience ordering numerals or remembering spatial locations. All had prior experience with visual matching-to-sample tasks.

Apparatus

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

Procedure

Pre-Training

Ordering

Monkeys initiated a trial by touching a green square in the lower center of the screen. This ensured that the subjects' hands were in the same position at the beginning of every trial. After touching the green square, white Arabic numerals were presented. Training began with only two numerals presented: 1 and 2. The screen was divided into an 8x6 invisible grid (130x130 pixel squares) with 20 pixel margins between grid locations. The numerals appeared randomly arrayed in two of the 48 possible screen locations. The monkeys had to touch the numerals in ascending order. The numerals disappeared as they were touched in the correct order. If the subject touched all the numerals in the correct order they received positive auditory feedback and a pellet reward. Incorrect touches terminated the trial and were followed by negative auditory feedback and no food reward. Subjects met criterion when they completed two 48-trial sessions in a row with at least 85% of the trials performed correctly. When this criterion was met, another numeral was added to the sequence. If they correctly ordered 1 and 2 then the numeral 3 was added and so on until they reached 9 numerals. Some monkeys struggled to learn these sequences, so an additional criterion was put in place. Because we wanted to ensure sufficient ordering, monkeys had to learn to order at least 5 numerals. However, after correctly ordering 5 numerals, if monkeys failed to learn to order with an additional numeral after completing at least 10,000 trials, then that monkey's top number was the number at which they completed those trials. After these 10,000 trials, the monkeys who got to this point still had to complete one session with an accuracy of 85% at their new "highest" numeral before moving on to the next step in training. One monkey learned to order 7 numerals, 5 others learned to order all 9 numerals.

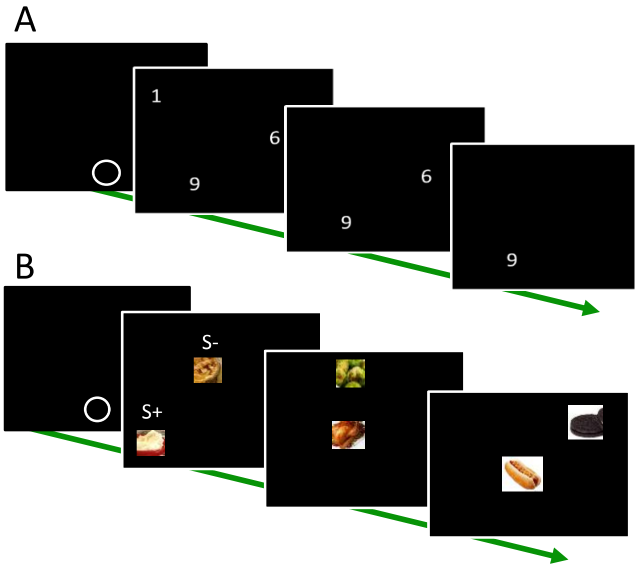

Figure 1.Ordering and object discrimination alone. A) Ordering non-adjacent numerals. Monkeys had to touch in ascending order. Numerals disappeared after correct touches. B) Object Discrimination. In each pair one image was always reinforced and one was never reinforced (S+/S-). Monkeys learned each pair individually, then at test had to respond to three different pairs out of the 9 possible pairs.

Ordering subsets of the sequence

After reaching the final training criterion on the ordering task, subjects were presented with trials in which most trials contained only a subset of the numerals in the sequence (Figure 1A). Trials had between 2 and 9 (or 7 for one monkey) numerals presented, and subjects again had to touch in ascending order. The subsets were randomly determined. All other features of the trials were the same. This training was intended to give the subjects experience ordering subsets of the sequence because the final tests required ordering two or three numerals from the sequence. Subjects again had to perform at least 85% correct on two 48-trial sessions to move onto the next step in training.

Spatial Memory Training

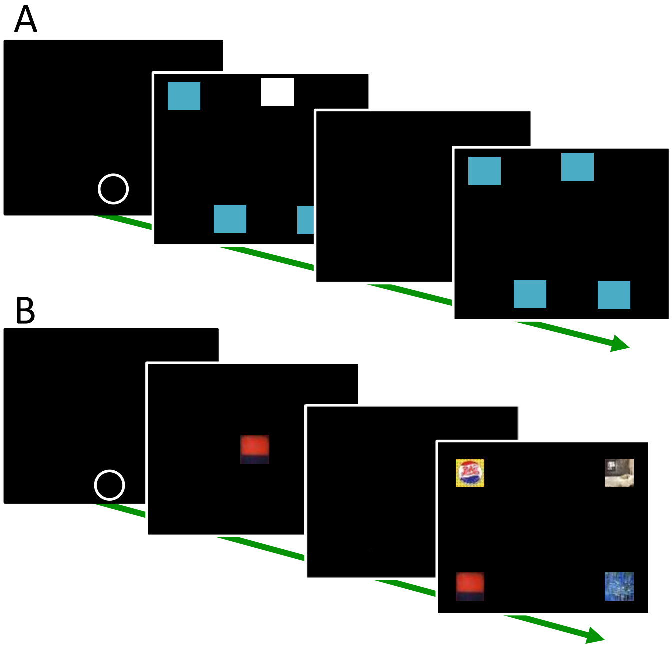

Figure 2. Spatial memory and MTS with empty delays. A) Spatial memory task. Monkeys saw an array of 4 squares, one was white the other 3 were blue. After touching the white square all squares disappeared for the 2000ms delay interval, then appeared in the same locations but all the same blue color. Subjects were reinforced for touching the square that was in the same location as the previously white square. B) MTS. Monkeys saw an image, it disappeared after they touched it. After the 2000ms delay period, they saw 4 images. Monkeys were reinforced for touching the image that matched the sample they saw at the beginning of the trial.

Subjects were first trained on a spatial memory task. The screen was virtually divided in 48 noncontiguous locations in which stimuli could appear. Each location was 100x100 pixels and was separated from neighbors by 15 pixels. After touching a start circle to initiate a trial, they saw an array of squares (100x100 pixels). At the beginning of training they saw 3 squares: two blue and one white. After they touched the white square, the screen went black for a memory delay. After the delay, the squares appeared again in the same screen locations, but all were blue. Subjects were reinforced for touching the square in the location previously occupied by the white sample square. The white square appeared in each of the 48 possible screen locations once in each 48 trial session in a random sequence. The blue distractors were randomly displayed in other screen locations, with no constraints other than those imposed by the virtual grid of 48 possible locations. The delay between touching the white square and the appearance of the choice squares started at 200ms and increased incrementally up to 2000ms as subjects learned the task. When subjects performed above 80% at the 2000ms delay, a third blue distracter square was added to the test arrays (Figure 2A). After performing above 80% correct in a 48-trial session with 2000ms delays and 3 distractor squares, subjects moved on to training with an item embedded within the spatial memory task.

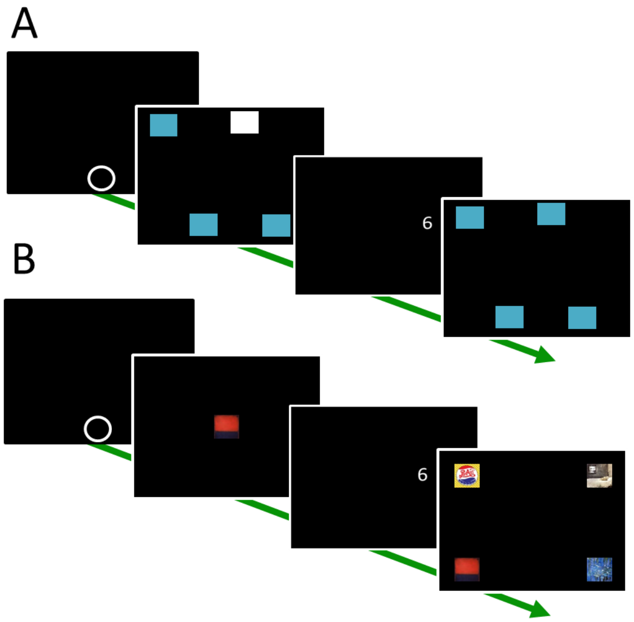

Figure 3. One numeral embedded in spatial memory and MTS. Subjects had to touch one numeral during the delay period of the spatial memory task (A) and the MTS task (B).

Spatial Memory Training with Concurrent Cognitive Load

Subjects continued performing the spatial memory task, but now during the delay period between seeing the sample spatial memory array and the spatial memory test, monkeys had to touch an intervening item, either a single numeral or a single target shape (Figure 3A). Subjects saw the spatial memory array, and after they touched the white square, all of the squares disappeared and either a numeral or the target stimulus appeared. The embedded stimuli appeared in one of the possible 48 screen locations, randomly chosen each trial. Monkeys had to touch the embedded stimulus, after which it disappeared. The time between the spatial memory sample display and test was held constant at 2500ms by adding a black screen delay after the control response before the spatial memory test phase was displayed. Subjects received no explicit reinforcement for touching the embedded stimuli. After the delay, the array of four blue squares appeared and again subjects had to touch the square located in the same location as the white target. Subjects had to perform above 65% correct on the spatial memory task for two consecutive 48-trial sessions before moving on to test trials. If subjects failed to reach this criterion within 10 sessions, they were instead required to complete correctly at least 30/48 trials (62.5%) for 3 sessions in a row.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 spatial memory test trials with blank delays (3 distractor items, 2000ms delay). This was intended to remind them of the task and decrease the likelihood of floor level performance on the spatial memory task with concurrent cognitive load.

Identity Matching-to-Sample (MTS) Training

Monkeys all had extensive prior experience with the matching-to-sample paradigm. For these trials subjects touched a start square to initiate a trial after which an image (100x100 pixels) appeared on the center of the screen. After touching the image the screen went blank for a delay of 2000ms (Figure 2B). Then four choice images appeared in the four corners of the screen. Monkeys were rewarded for picking the image that matched the sample image they had seen at the beginning of the trial. There were 8 images from which the sample and distractor choices could be drawn. Every 16 trials each sample was seen twice, and each image was the sample 6 times in a 48-trial session. The correct choice location was pseudo-randomly distributed such that every 8 trials each of the four corners was the correct location twice, and the identities of the distractor choices was randomly assigned. After performing above 80% correct in a 48-trial session subjects moved on to training an item embedded within the matching-to-sample task.

MTS Training with Concurrent Cognitive Load

Subjects continued performing the MTS task, but now during the delay period between seeing the sample image and the test, monkeys had to touch an intervening item, either a single numeral or a single target shape. Subjects saw the image, and after they touched it, the screen went blank, and either a numeral or the target stimulus appeared (Figure 3B). The embedded stimuli appeared in one of the possible 48 screen locations, randomly chosen each trial. Monkeys had to touch the embedded stimulus, after which it disappeared. The time between the image sample display and test was held constant at 2500ms by adding a black screen delay after the control response before the MTS test phase was displayed. Subjects received no explicit reinforcement for touching the embedded stimuli. After the delay, the four choice images appeared in the four corners of the screen and again subjects had to touch the image that matched the sample image. Subjects had to perform above 65% correct on the MTS task for two consecutive 48-trial sessions before moving on to test trials. If subjects failed to reach this criterion within 10 sessions, they were instead required to complete correctly at least 30/48 trials (62.5%) for

3 sessions in a row. This was the same criterion established for the spatial memory training procedures above.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 MTS trials with blank delays (2000ms delay). This was intended to remind them of the task and decrease the likelihood of floor level performance on MTS with concurrent cognitive load.

Experiment 1: Concurrent Cognitive Load Test Ordering Two Items

After monkeys had reached criterion on all of the tasks individually, they moved onto testing trials. In Experiment 1, monkeys had to order two numerals embedded within both the spatial memory task and the MTS task. If ordering and spatial memory share a domain specific memory resource, then performance on trials when those tasks are performed concurrently will be worse than when ordering and MTS are performed concurrently.

Ordering 2 Items

To test whether ordering and spatial working memory rely on the same domain specific resource, we embedded the ordering task in both the spatial memory task and the matching-to-sample test. In a test session there were five trial types: the spatial memory task with nothing embedded, the MTS task with nothing embedded, ordering two numerals alone, ordering two numerals embedded within the spatial memory task, and ordering two numerals embedded within the MTS task. The spatial memory task and

MTS task were the same as described above except now the delay between sample and test was 2500ms. Ordering alone was also the same as the non-adjacent task above except that every trial had only two numerals that the subjects had to order. For ordering embedded in spatial memory trials, first subjects touched a start circle to begin a trial. They then were presented with an array of 4 squares, 3 blue and one white, as above. After touching the white square the squares disappeared and two numerals (ranging between 1-9 for five monkeys and 1-7 for one monkey) appeared randomly arrayed on the screen. Monkeys had to touch the numerals in ascending order. If they touched in the wrong order, they heard a buzz sound, and that trial was aborted. To control for the number of trials the monkeys made it to the spatial memory test, if a trial was aborted, that spatial array was recorded and repeated at the end of the session. If they correctly touched the numerals in ascending order, then the spatial array was re-presented with all four squares now blue. Monkeys were reinforced for touching the square that had previously been white. Monkeys were not reinforced for correctly ordering numerals. Each of the possible 48 spatial locations served as the target location once for both the spatial memory alone trials and the spatial memory with ordering embedded trials.

We used a very similar procedure for MTS trials with ordering embedded. After seeing the sample picture, monkeys saw two numerals to touch in ascending order. Again, incorrect ordering aborted the trial and that trial was recorded and repeated again at the end of the session. After correctly ordering two numerals, the four MTS choices were presented in the four corners of the screen and monkeys were rewarded for touching the image that matched the sample image. Each of the five task types was presented 48 times for a minimum session length of 240 trials. Every 10 trials each trial type was presented twice pseudo-randomly. After the original 240 trials were completed, all five trial types continued to be presented pseudo-randomly. If the trial type was to be ordering embedded in spatial memory or ordering embedded in MTS, rather than a new trial, a trial that had been aborted because of incorrect ordering was presented. This design allowed the animals to continue working without only having the difficult trial types all presented in a row at the end of a session.

At the start of each day, subjects received warmup trials in which they had to complete correctly at least 8/10 MTS trials and at least 8/10 spatial memory trials with blank delays (2000ms delay). This was intended to remind them of the task and decrease the likelihood of floor level performance on trials with concurrent cognitive load.

Data Analyses Experiments 1 and 2

Because sharing a limited resource may impair performance on either or both cognitive tasks under concurrent cognitive load, we analyzed accuracy on the whole trial (i.e. encompassing both tasks), and we determined the accuracy expected under dual task conditions if performance on the two individual tasks were independent. This is the simple product of the observed proportion correct on the two tasks when presented separately. We multiplied subjects' accuracy on the outside task alone (spatial memory or MTS) by their accuracy on the ordering task when it was presented alone (Table 1). This gave us two expected accuracies for the experimental conditions: expected accuracy when spatial memory and ordering were together, and expected accuracy when MTS and ordering were together. We ran a RMANOVA with outcome measure (expected vs actual accuracies) and concurrent cognitive load type (spatial memory vs MTS) as factors. To further assess the source of the errors, we also analyzed subjects' performance on the ordering and the outside task separately. We ran a one-way RMANOVA on the monkeys' ordering performance when it was alone, embedded in the spatial memory task, and embedded in MTS. To analyze the outside task performance, we ran a 2x2 RMANOVA with outside task (spatial vs MTS) and aloneness (alone vs order embedded) as factors. Trials that took longer than 2500ms to complete the ordering task were removed from outside task analyses. Effect sizes are reported as Cohen's d and partial eta^2. All data were arcsine transformed to better conform to normality assumptions (Aron & Aron, 1999).

Results and Discussion

When ordering and spatial WM were presented concurrently, performance went down more than when ordering and visual MTS were presented concurrently, and this was more than would be expected if the tasks were independent. There was a significant interaction between concurrent cognitive load type (spatial memory vs MTS) and outcome measure (expected if independent vs observed; $F_{(1,10)}=26.28$, $p<0.001$, partial eta^2=0.724; Figure 4). There was also a main effect of concurrent cognitive load type (spatial memory vs MTS; $F_{(1,10)}=38.02$, $p<0.001$, partial eta^2=0.79), and a significant main effect of outcome measure (expected if independent vs observed; $F_{(1,10)}=225.73$, $p<0.001$, partial eta^2=0.958). These results suggest that ordering and spatial memory may share more cognitive resources than do ordering and MTS. Additionally, these tasks are

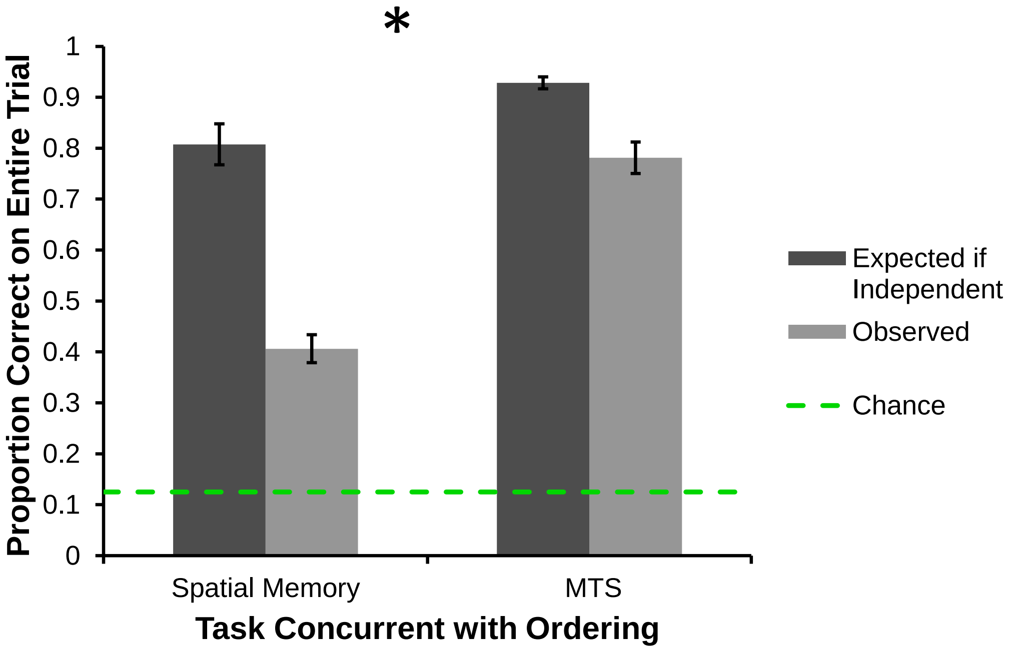

Figure 4. Expected vs observed accuracy on entire trial when ordering two numerals is embedded in spatial memory and MTS. The dark gray bars represent the simple product of the proportion correct on the ordering task and the spatial memory task and the product of the proportion correct of the ordering task and the MTS task when presented independently. The light gray bars represent the average observed accuracies when the tasks were combined. The two bars on the left represent trials with concurrent spatial load and the two bars on the right represent trials with concurrent visual matching load. Error bars represent the standard error of the means.

not independent, and there are shared resources across all tasks that are utilized for task completion. However, we do not know if the errors were made on the outside task itself, or made on the inside task after having seen the sample from the spatial memory or MTS task. This is important because it is possible that the one of the tasks is more impacted than the other. If it is the spatial memory task we do not know if it is impacted because ordering is embedded within it or if it is impacted because it is always impaired in any concurrent cognitive load context.

To assess the source of the error, we separated the monkeys' performance on the outside tasks and the ordering task. Monkeys did perform the ordering task differently depending on the type of task (alone, spatial memory, or MTS) in which it was embedded. There was a main effect of task type ($F_{(1,5)}$=10.70, p=0.02, partial eta^2=0.549; Figure 5). Post-hoc tests showed that accuracy on the ordering task was significantly worse when it was embedded in the MTS task (M=0.91) than when it was alone (M=0.95; $t_{(5)}$= 3.27, p=0.02, d= 1.07). There was a marginally significant difference between ordering alone and ordering embedded within spatial memory (M=0.91; $t_{(5)}$=2.36, p=0.06, d= 1.095), and no difference between ordering embedded in spatial memory and ordering embedded in MTS ($t_{(5)}$= 0.15, p=0.89, d=0.062).

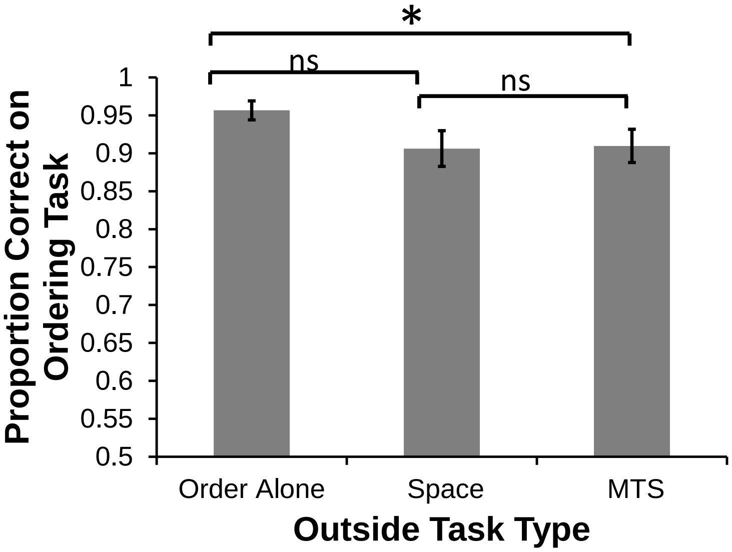

Figure 5. Accuracy on ordering two items embedded in different tasks. This graph represents the monkeys' average accuracy on the ordering task when they had to order two numerals alone, embedded in the spatial memory task and embedded in the MTS task. Error bars represent the standard error.

These results show that monkeys are definitely better at ordering when it is not under concurrent cognitive load. They also show that a very small proportion of the errors observed in the first analysis were due to errors to the ordering task. These results

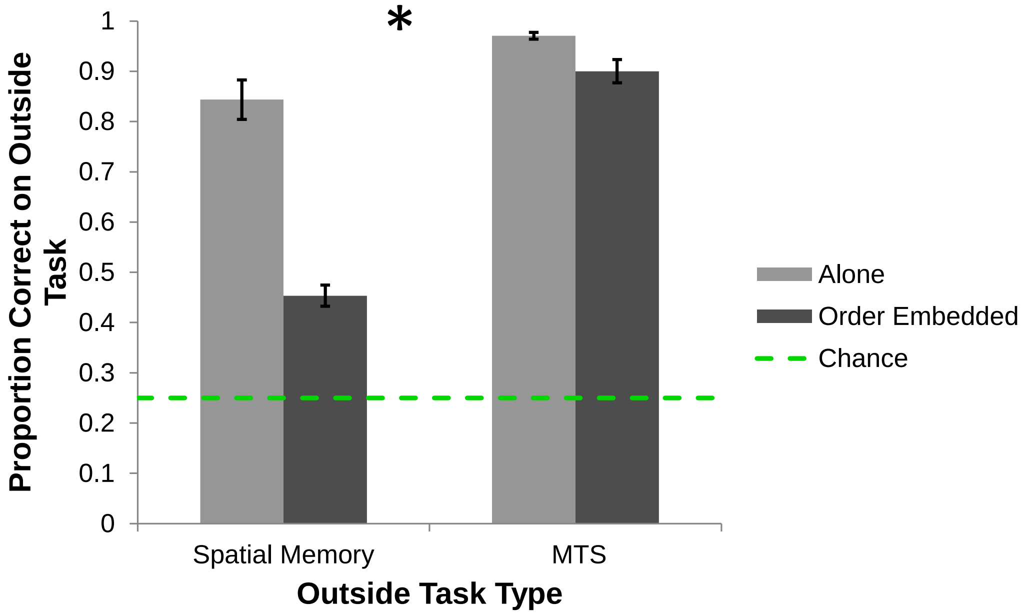

Figure 6. Accuracy on outside tasks when performed alone and with ordering two numerals embedded. The light gray bars represent the average accuracy on the spatial memory task and the MTS task when they were presented with blank delays of 2500ms. The dark gray bars represent the average accuracies when ordering two numerals was embedded within the delay of the two tasks. The monkeys had to get the ordering task correct in order to get to the outside task test, thus these bars represent trials in which monkeys correctly ordered the embedded numerals. The two bars on the left represent trials with the spatial memory task and the two bars on the right represent trials with the visual memory task. Error bars represent the standard error of the means.

suggest that because ordering performance when embedded in the spatial memory task and in MTS is equally impacted there is no evidence for a domain specific resource supporting ordering and spatial memory. However, it is difficult to interpret these findings because monkeys were performing at ceiling levels on the ordering task in all contexts. Thus we ran Experiment 2 and added a third numeral to the ordering task to reduce performance below ceiling level.

When ordering was embedded in the spatial memory and MTS tasks, performance on the outside task went down more when ordering was embedded in the spatial memory task than did performance when ordering was embedded in the MTS task. There was a significant interaction between outside task (spatial memory vs MTS) and aloneness (alone vs order embedded; $F_{(1,5)}=21.59$, $p=0.006$, partial $eta^2=0.812$; Figure 6). There was also a main effect of outside task type ($F_{(1,5)}=83.11$, $p<0.001$; partial $eta^2=0.943$) and a main effect of aloneness ($F_{(1,5)}=47.06$, $p=0.001$; partial $eta^2=0.904$). These results are consistent with the idea that ordering and spatial memory share a domain specific resource that is not taxed in the MTS task. However, as described above, we do not know if spatial memory is just more susceptible to having a concurrent cognitive load, rather than specifically due to shared spatial memory resources. Thus we ran Experiments 3 and 4 to further assess whether these differences are due to a domain specific resource supporting ordering and spatial memory, or if they are due to the spatial memory task being universally disrupted when under any concurrent cognitive load.

Experiment 2: Concurrent Cognitive Load Test Ordering 3 Items

Because of the ceiling level performance on the ordering task in Experiment 1, it was difficult to assess whether ordering was differentially impacted by concurrent spatial memory load. Thus we conducted Experiment 2 to attempt to make ordering more difficult, to move away from ceiling level performance, and to create a more sensitive test. Again, if ordering and spatial memory share specialized resources, performance on trials when those tasks are performed concurrently will be worse than when ordering and MTS are performed concurrently as in Experiment 1. If ordering and spatial memory share a domain specific memory resource and the test is sensitive enough to detect this shared resource when the monkeys perform below ceiling, then performance on trials when those tasks are executed concurrently will be worse than when ordering and MTS are presented concurrently.

Methods

Experiment 2 had identical procedures as Experiment 1, except rather than ordering two items during the delay period of the concurrent cognitive load trials, monkeys were presented with three numerals to touch in ascending order. To accommodate the increased time it might take to touch three items, the delay between sample and test was increased to 3000ms. Trials that exceeded this length were removed from outside task analyses. All other aspects of the trials were the same. Monkeys completed two sessions with the five trial types (the spatial memory task with nothing embedded, the MTS task with nothing embedded, ordering three numerals alone, ordering three numerals embedded within the spatial memory task, and ordering three numerals embedded within the MTS task) intermixed. Again, monkeys completed warm-up trial in which they had to complete correctly at least 8/10 MTS trials and at least 8/10 spatial memory trials with blank delays (2000ms delay).

One monkey completed his two test sessions with this protocol, but he did not perform the spatial memory task above chance levels when it was presented alone (average accuracy of 31%). This indicated that he did not remember how to perform the task, so we gave him additional training on the spatial memory and the MTS tasks. He was again giving 48-trial training sessions with empty delays (described above) until he reached 80% accuracy for both the spatial memory and the MTS tasks. He then completed two more test sessions with the methods described in the above paragraph. In this second round, he performed above chance, so those data were included in the subsequent analyses.

Results and Discussion

We found a very similar pattern of results as in Experiment 1. When ordering was paired with spatial memory, performance went down more than when ordering was paired with MTS and this was more than would be expected if the tasks were independent. There was a significant interaction between concurrent cognitive load type (spatial memory vs MTS) and outcome measure (expected if independent vs observed; $F_{(1,10)}$=7.35, p=0.022; partial eta^2=0.424; Figure 7).There was also a main effect of concurrent cognitive load type (spatial memory vs MTS; $F_{(1,10)}$=7.36, p=0.02; partial eta^2=0.424), and a significant main effect of outcome measure (expected if independent vs observed; $F_{(1,10)}$= 51.42, $p < 0.001$; partial eta^2=0.837). Just as in Experiment 1, these results suggest that ordering and spatial memory may share more resources than do ordering and MTS. Additionally, these tasks are not independent, and there are shared resources across all tasks that support task completion generally. However, we do not know if the errors were made on the outside task itself, or made on the ordering task after having seen the sample from the spatial memory or MTS task, especially because in this experiment we made the ordering task harder. This is important because it is possible that the one of the tasks is more impacted than the other. If it is the spatial memory task we do not know if it is impacted because ordering specifically is embedded within it or if it is impacted because it is always impaired in any concurrent cognitive load context.

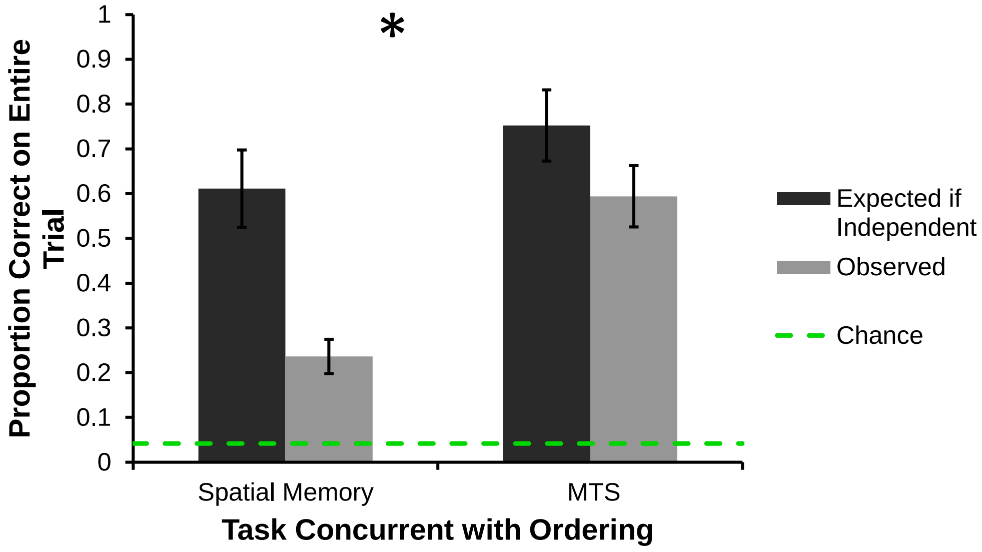

Figure 7. Expected vs actual accuracy on entire trial when ordering three numerals is embedded in spatial memory and MTS. The dark gray bars represent the simple product of the accuracy on the ordering task and the spatial memory task and the product of the accuracy of the ordering task and the MTS task when presented independently. The light gray bars represent the average observed accuracies when the tasks were combined. The two bars on the left represent trials with concurrent spatial load and the two bars on the right represent trials with concurrent visual matching load. Error bars represent the standard error of the means.

To assess the source of the error, we separated the monkeys' performance on the outside tasks and the ordering task. Monkeys performed worse on the ordering task when it was under concurrent cognitive load than when it was alone. There was a main effect of concurrent load type (alone, embedded in spatial memory, embedded in MTS; $F_{(1,5)}=9.61$, p=0.005; partial $eta^2=0.658$; Figure 8). Post-hoc tests showed that accuracy on the ordering task was significantly worse when it was embedded in the MTS task (M=0.77) than when it was alone (M=0.82; $t_{(5)}= 3.22$, p=0.02, d=0.31). Performance was also significantly better when ordering was alone than when ordering was embedded within spatial memory (M=0.72; $t_{(5)}=4.2$, p=0.008, d=0.63), and there was no difference between ordering embedded in spatial memory and ordering embedded in MTS ($t_{(5)}=1.9$, p=0.11,

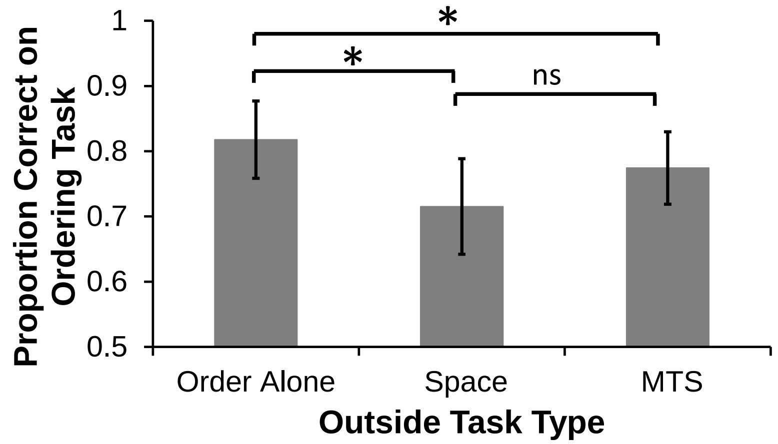

Figure 8. Accuracy on ordering three items embedded in different tasks. This graph represents the monkeys' average accuracy on the ordering task when they had to order three numerals alone, embedded in the spatial memory task and embedded in the MTS task. Error bars represent the standard error.

d=0.37). Monkeys were no longer performing at ceiling, but these results do not show evidence for a domain specific working memory resource supporting ordering and spatial memory differently than ordering and MTS.

We also analyzed outside task performance. One monkey only completed three trials with ordering embedded within the 3000ms delay period. He was removed from further analyses. As in Experiment 1, there was a significant interaction between outside task type (spatial memory vs MTS) and aloneness (alone vs embedded; $F_{(1,4)}$=25.33, p=0.007, partial eta^2=0.86). There was also a main effect of outside task type ($F_{(1,4)}$=28.28, p=0.006, partial eta^2=0.88) and aloneness ($F_{(1,4)}$=20.67, p=0.01, partial eta^2=0.84). These results are consistent with the idea that ordering and spatial memory share a domain specific memory resource, and spatial memory performance goes down more when ordering is embedded than does MTS. However, as discussed in Experiment 1, we cannot assess whether differences in outside task performance are due to specific shared resources with ordering or due to particular sensitivity of the spatial memory task to having anything embedded within it.

Experiment 2 replicates the results of Experiment 1. And we found that ordering three numerals did lower the monkeys' performance on the ordering task, thus ensuring that ceiling effects are not contributing to whether or not we observe differential impacts in the different concurrent cognitive load conditions. Yet, we still do not know if the results we observed are due to spatial memory being generally susceptible to any concurrent load, thus we ran Experiments 3 and 4 to further investigate this possible explanation.

Experiment 3: Object Discrimination

To control for the general impact of concurrent cognitive load on the spatial memory task, we trained monkeys on an object discrimination task that we could then embed in the spatial memory and MTS task. We matched as many features as possible between the ordering and object discrimination tasks, such as the number of touches required, the screen locations in which touches occurred, and the number of to-be-remembered items. The primary difference is the relative amount of spatial memory resource required to perform the tasks. If ordering and spatial memory are both supported by a domain specific memory resource, when ordering and spatial memory are performed concurrently, their performance will be more impaired than when object discrimination and spatial memory are performed concurrently or when ordering and MTS are performed concurrently. Similarly, the MTS task and the object discrimination task may also share specialized visual identity memory resources. If this is the case, performance on trials in which object discrimination and MTS are combined will be impaired more than when ordering and MTS are combined or when object discrimination and spatial memory are combined.

Methods

Object Discrimination Training

Monkeys learned 9 pairs of two-choice image discriminations generated from 18 distinct images. In each pair one image was always reinforced and one image was never reinforced. They were first trained with one pair presented over and over again until they correctly touched the reinforced at image at least 15 out of 18 trials (83% accuracy). After correctly responding to Pair 1, monkeys moved on to Pair 2 and so on until they had learned each of the 9 pairs individually. After touching the start circle, two images (100x100 pixels) appeared on the screen. The two images were randomly arrayed such that they appeared in two of the 48 possible screen locations. Monkeys were reinforced for touching the correct item in the pair. The 9 different pairs were not ordered and had no relation to the other pairs. They then had to complete 2 54-trial sessions in a row above 85% in which all 9 pairs were pseudo-randomly presented such that every 18 trials each pair was presented twice. After reaching this criterion the monkeys moved on to testing with object discrimination embedded in spatial memory and MTS.

Object Discrimination Embedded in Spatial Memory and MTS

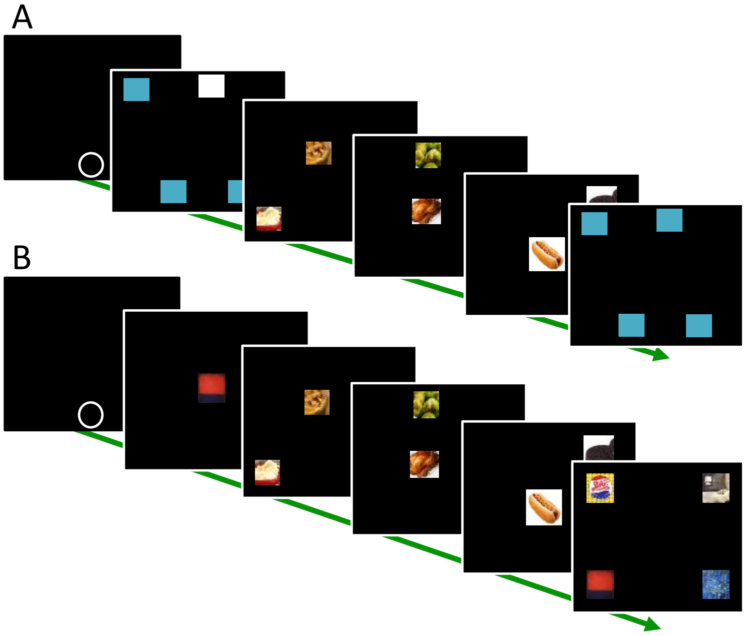

Figure 9. Object discrimination embedded in spatial memory and MTS. A) Object discrimination embedded in the spatial memory task. Monkeys had to correctly identify the S+ stimulus in three image pairs during the delay of the spatial memory task. B) Object discrimination embedded in the MTS task. Monkeys had to correctly identify the S+ stimulus in three image pairs during the delay of the MTS task.

Just as ordering was embedded in spatial memory and MTS trials in Experiment 2, so too was object discrimination (OD) embedded in spatial memory and MTS trials in this experiment. In a test session there were five trial types: the spatial memory task with nothing embedded, the MTS task with nothing embedded, object discrimination with three pairs alone, object discrimination with three pairs embedded within the spatial memory task, and object discrimination with three pairs embedded within the MTS task. The spatial memory task and MTS task were the same as described above with a delay of 3000ms. On the object discrimination alone trials, monkeys had to correctly identify the “reinforced image” across three pairs (Figure 1B). After touching the start circle a pair of images appeared, randomly arrayed on the screen. If the monkey chose the correct image, a second pair appeared again randomly arrayed. If the monkey chose the correct image for this second pair, a third pair appeared randomly arrayed across the screen. If the subject chose the correct image for this third pair they were reinforced with a food reward and positive audio feedback. The pairs were randomly chosen from the 9 possible pairs. Three were chosen to as closely as possible match the touching and cognitive effort required for ordering in Experiment 1.

The same object discrimination procedure was followed on trials in which object discrimination was embedded in spatial memory or MTS. For object discrimination embedded in spatial memory trials, first subjects touched a start circle to begin a trial (Figure 9A). They then were presented with an array of 4 squares, 3 blue and one white as above. After touching the white square the squares disappeared and the first of the object discrimination pairs appeared randomly arrayed on the screen. Monkeys had to correctly choose the reinforced image for three different pairs. If they got any of the pairs incorrect, they heard a buzz sound and that trial was aborted. To control for the number of trials the monkeys made it to the spatial memory test screen, if a trial was aborted, that spatial array was recorded and repeated at the end of the session. If they correctly identified the reinforced image in all three pairs then the spatial array was re-presented with all four squares now blue. Monkeys were reinforced for touching the square that had previously been white. Monkeys were not reinforced for correctly completing the object discrimination portion of the trial. Each of the possible 48 spatial locations served as the target location once for both the spatial memory alone trials and the spatial memory with object discrimination embedded trials.

We used a very similar procedure for MTS trials with object discrimination embedded. After seeing the sample picture, monkeys saw the first object discrimination pair (Figure 9B). Again, incorrectly discriminating a pair aborted the trial and that trial was recorded and repeated again at the end of the session. After correct object discrimination, the four MTS choices were presented in the four corners of the screen and monkeys were rewarded for touching the image that matched the sample image. Each of the five task types was presented 48 times for a minimum session length of 240 trials. Every 10 trials each trial type was presented twice pseudo-randomly. After the original 240 trials were completed, all five trial types continued to be presented pseudo-randomly. If the trial type was to be object discrimination embedded in spatial memory or object discrimination embedded in MTS, rather than a new trial, the previously incorrect trial was presented. Monkeys completed two sessions with these parameters.

Again, monkeys completed warm-up trial in which they had to complete correctly at least 8/10 MTS trials and at least 8/10 spatial memory trials with blank delays (2000ms delay).

Data Analyses Experiment 3 and 4

Again, because sharing a limited resource may impair performance on either or both cognitive tasks under concurrent cognitive load, we analyzed accuracy on the whole trial (i.e. encompassing both tasks), and we determined the accuracy expected under dual task conditions if performance on the two individual tasks were independent. Just as in Experiments 1 and 2, we determined the accuracy expected under dual task conditions if performance on the two individual tasks were independent. We took the simple product of subjects' accuracy on the outside task alone (spatial memory and MTS; Figure 2) by their accuracy on the inside task types when they were presented alone (ordering three numerals and object discrimination with 3 pairs presented sequentially with no concurrent load; Figure 1). This gave us 4 expected accuracies for the 4 experimental conditions: expected accuracy when spatial memory and ordering were presented concurrently, expected accuracy when spatial memory and object discrimination were presented concurrently, expected accuracy when MTS and ordering were presented concurrently, and expected accuracy when MTS and object discrimination were presented concurrently (Table 1). We then ran a 3-way RMANOVA with outcome measure (expected if independent vs actual accuracies), outside task type (spatial memory vs MTS), and inside task type (ordering vs object discrimination) as factors. Because in this experiment ordering trials and object discrimination trials were performed across separate sessions, for the second analysis we ran two paired t-tests on subjects' performance on the spatial memory task alone from the ordering session and the object discrimination session and the MTS task alone from the ordering session and the object discrimination session. Their performance across sessions was not significantly different (spatial memory: $t_{(5)}=0.875$, $p=0.42$; MTS: $t_{(5)}<0.001$, $p=1$), so we averaged the monkeys' performance for the spatial memory alone trials and the MTS alone trials. For the 3-way RMANOVA the expected values were determined by their performance on the two task types within the same sessions. To further assess the source of the errors, we also analyzed inside task and outside task accuracy separately. To analyze inside task performance we ran a RMANOVA with inside task type (ordering vs object discrimination) and outside task type (alone, spatial memory, and MTS) as within-subject factors. To analyze outside task performance, we ran a RMANOVA with inside task type

	Simple Product if Independent			
Experiment	Space*Order	MTS*Order	Space*OD	MTS*OD
1	0.808	0.928		
2	0.611	0.752		
3	0.611	0.752	0.599	0.711
4	0.607	0.719	0.647	0.768

	Observed Accuracy			
	Space*Order	MTS*Order	Space*OD	MTS*OD
1	0.406	0.781		
2	0.236	0.594		
3	0.236	0.594	0.250	0.509
4	0.326	0.561	0.370	0.575

Table 1. Average expected if tasks independent and observed accuracies. These averages represent the average across all 6 monkeys of the simple product between the monkeys' accuracy on the embedded task multiplied by their accuracy on the outside task when the tasks were presented independently. For Experiments 2, 3 and 4, this means they ordered 3 numerals, and for Experiment 3 and 4 they discriminated 3 pairs of images. Their observed performance in the concurrent cognitive load conditions is also presented.

(alone, numeral ordering, object discrimination) and outside type (spatial memory vs MTS) as factors. Effect sizes are reported as Cohen's d and partial eta^2. All data were arcsine-transformed to better conform to normality assumptions (Aron & Aron, 1999).

Results and Discussion

The difference between monkeys' expected performance on the trials that included the spatial memory task and their observed performance was greater than the difference in their expected performance on the trials that included MTS and their observed performance on these trials. There was an interaction between outcome measure (expected if independent vs observed) and outside task type (spatial memory vs MTS; $F_{(1,20)}=16.49$, $p=0.001$, partial eta^2=0.45; Figure 10). There was also a main effect of

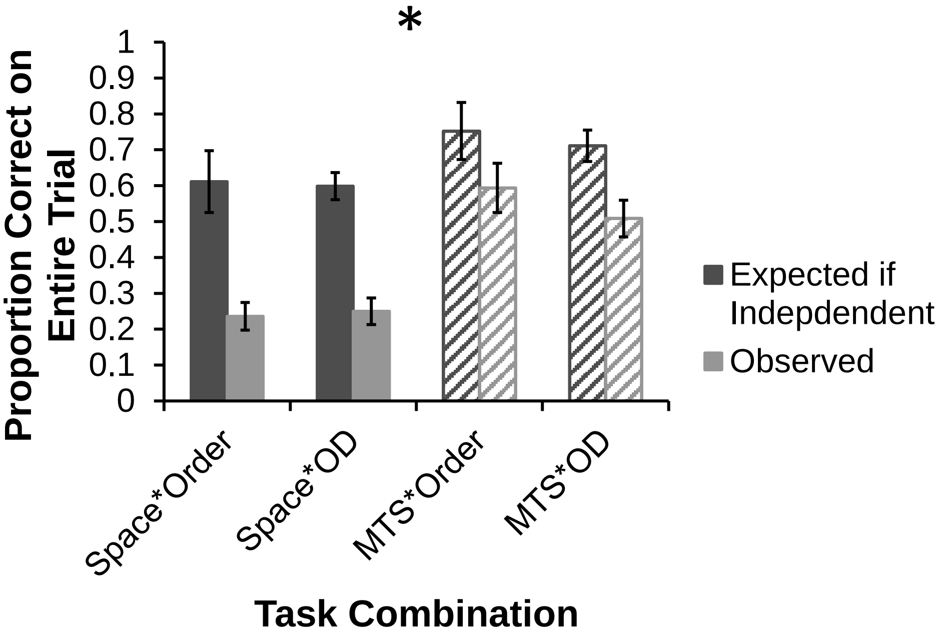

Figure 10. Expected vs observed accuracy on entire trial when ordering and object discrimination are embedded in spatial memory and MTS across separate sessions. This graph represents monkeys' accuracy on the entire trial when ordering and object discrimination are embedded in spatial memory and MTS across separate sessions. Dark gray bars represent the simple product of the accuracy on the internal task and the external task when they were presented independently. The light gray bars represent the average observed accuracies when the tasks were combined. Striped bars represented the tasks in which the external task was the MTS task and the solid bars are the trials in which the spatial memory task was the external task. Error bars represent the standard error. Chance for trials in which the monkeys had to order was 0.04 and was 0.03 for trials in which the monkeys completed object discrimination.

outcome measure ($F_{(1,20)}$=160.43, $p<0.001$, partial eta^2=0.89), with actual accuracies significantly lower than expected accuracies if the two tasks were completely independent (space*order: $t_{(5)}$=5.19, p=0.003, d=2.28; MTS*order: $t_{(5)}$=7.21, $p<0.001$, d=0.94; space*object discrimination: $t_{(5)}$=10.2, $p<0.001$, d=3.77; MTS*object discrimination: $t_{(5)}$=9.72, $p<0.001$, d=1.75; for means see Table 1). This suggests that a general cognitive resource contributes to performance in all concurrent cognitive load combinations. There was also a main effect of outside task type (spatial memory vs MTS; $F_{(1,20)}$=16.24, p=0.001, partial eta^2=0.45). There was no effect of inside type (order vs

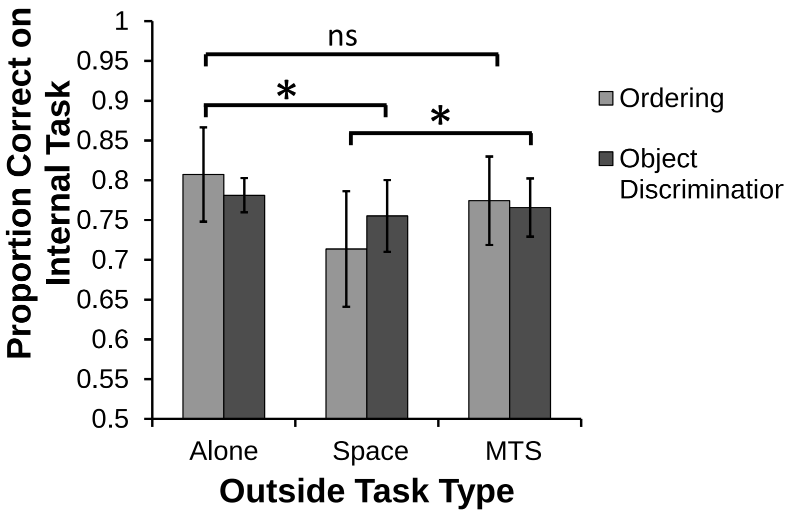

Figure 11. Accuracy on internal task when ordering and object discrimination were performed in different sessions. This graph represents the monkeys' average accuracy on the ordering task and the object discrimination task when they had to order three numerals alone or discriminate three pairs embedded in the spatial memory task and embedded in the MTS task. Light Gray bars represent their ordering performance and dark gray bars their object discrimination performance. Error bars represent the standard error.

object discrimination; $F_{(1,20)}$=0.063, p=0.54, partial eta^2=0.019). There was no interaction with inside task type and outcome measure ($F_{(1,20)}$=0.10, p=0.92, partial eta^2<0.001), no interaction between outside type and inside type ($F_{(1,20)}$=0.378, p=0.55, partial eta^2=0.019), and no 3-way interaction ($F_{(1,20)}$=0.015, p=0.45, partial eta^2=0.03).

After being presented with a spatial memory sample, monkeys perform worse than after being presented with an MTS sample. This does not differ based on what type of concurrent cognitive load is presented. And this difference is larger for the actual accuracies than the expected accuracies. Because there is no impact of inside task type, this suggests that the ordering task and spatial memory task are not supported by a domain specific memory resource that is not taxed in other tasks. It also suggests that there is a domain general resource supporting performance across tasks.

Although this analysis indicates that there is an effect of the outside task type, we do not know if the errors were made on the outside task itself, or made on the inside task after having seen the sample from the spatial memory or MTS task. In order to assess the source of the error, we separated the monkey's performance on the inside tasks and the outside tasks. Ordering and object discrimination are impaired when performed concurrently with the spatial memory task. When comparing performance on the inside task, we found a main effect of outside task type (spatial memory vs MTS; $F_{(2,10)}=9.3$, $p=0.005$, partial $eta^2=0.65$; Figure 11). We collapsed across inside task type and ran a RMANOVA with average performance on each of the outside task types. We found an effect of task type ($F_{(2,10)}=7.22$, $p=0.01$, partial $eta^2=0.59$). Pair-wise comparisons show that average performance on the inside tasks when presented alone (M=0.79) was significantly higher than performance when embedded in the spatial memory task (M=0.73; $t_{(5)}=3.04$, $p=0.03$, $d=0.6$). Performance on the inside tasks when embedded in the spatial memory task was significantly lower than when they were embedded in the MTS task (M=0.77; $t_{(5)}=2.87$, $p=0.03$, $d=0.33$).There was no difference in average performance when the inside tasks were presented alone compared to when they were embedded in MTS ($t_{(5)}=1.72$, $p=0.14$, $d=0.28$). We found no main effect of inside task type ($F_{(1,5)}=0.045$, $p=0.84$, partial $eta^2=0.009$) or an interaction between outside and inside task type ($F_{(2,10)}=2.33$, $p=0.15$, partial $eta^2=0.32$). These results suggest that tasks under concurrent spatial cognitive load are generally impaired. The evidence does not support the hypothesis that ordering and the spatial memory task are supported by a domain specific resource. However, these results do indicate that there is a general resource supporting performance on all of the tasks tested. These results also indicate that

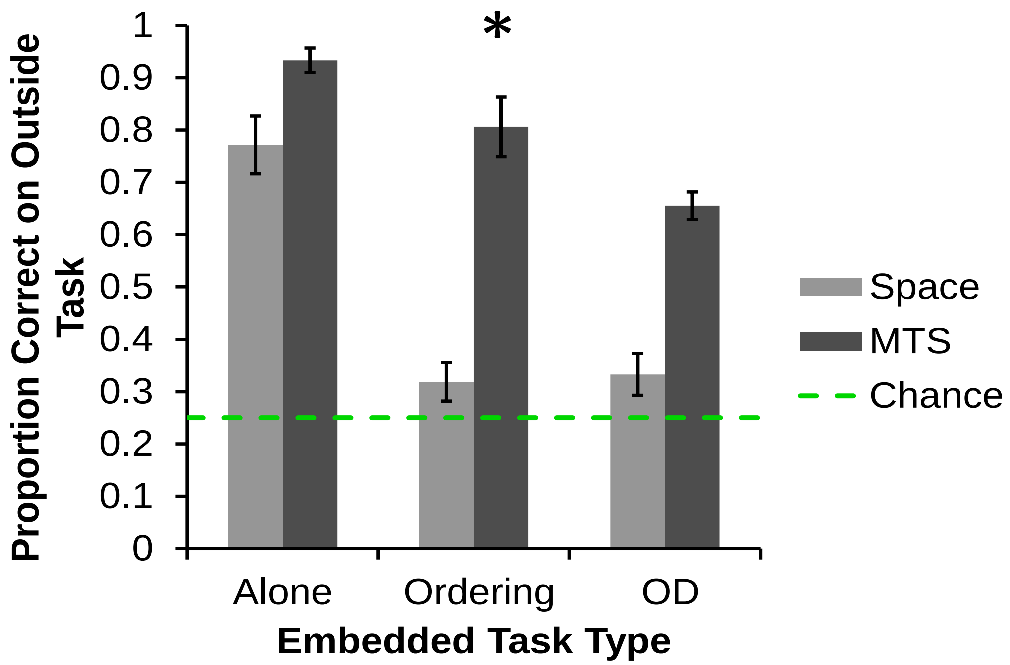

Figure 12. Accuracy on the outside task when ordering and object discrimination were performed in different sessions. The light gray bars represent the average accuracy on the spatial memory task when it was presented with the different internal task conditions (alone, with ordering three numerals embedded, and with object discrimination embedded). The dark gray bars represent the average accuracy on the MTS task when it was presented with the same internal task conditions. The monkeys had to get the embedded task correct in order to get to the outside task test, thus these bars represent trials in which monkeys correctly performed the embedded task.

concurrent spatial memory load impairs performance more than concurrent visual memory load. This could suggest that the general resource supporting performance is a spatial memory resource.

Because one monkey completed a total of three trials in which ordering was embedded in spatial memory and MTS and three trials within the 3000ms range in which object discrimination was embedded in spatial memory and MTS, he was removed from the analyses. The difference between the monkeys' performance on the spatial memory task in the different concurrent load type conditions was greater than the difference between their performance on the MTS task with the concurrent load type conditions. There was an interaction between outside task type (spatial memory vs MTS) and inside task type (alone vs ordering vs object discrimination; $F_{(2,8)}=9.71$, $p=0.007$; partial $eta^2=0.71$; Figure 12). There was also a main effect of outside type ($F_{(1,4)}=35.31$ $p=0.004$; partial $eta^2=0.898$), and a main effect of inside type ($F_{(2,8)}=54.09$, $p<0.001$; partial $eta^2=0.931$). These results suggest that spatial memory is generally impaired by concurrent load regardless of what task is embedded during the delay between sample and test. This argues against a domain specific resource on which ordering and spatial memory rely. It does however argue for a general shared resource supporting all of these tasks. Additionally, because spatial memory is impaired across task types, and because all tasks embedded within spatial memory seem to be more impaired than those same tasks embedded in the MTS task, it is possible that the general resource supporting performance across these tasks is a spatial memory resource.

While these results suggest that there is no specific memory system supporting ordering and spatial memory that does not also support object discrimination and MTS, the two internal task types were presented across different sessions and testing periods. Thus, combining their performance across these tasks for analysis may not be the most valid comparison. Therefore, we ran Experiment 4 in which all trial types were presented within a session.

Experiment 4: Ordering and Object Discrimination Together

Rather than compare across sessions in which many days have passed and changing contexts may have impacted the results, we ran a final test in which all eight trial types were intermixed within one session. In this experiment we controlled for the possibility that ordering is more susceptible to concurrent cognitive load by including trials in which ordering is under concurrent visual memory load, and we controlled for the possibility that the spatial memory task is generally more susceptible to concurrent cognitive load by including trials in which object discrimination is embedded within the spatial memory task. The hypothesis is the same as in Experiment 3: if ordering and spatial memory are supported by a domain specific memory resource, when ordering and spatial memory are performed concurrently, their performance will be more impaired than when object discrimination and spatial memory are performed concurrently or when ordering and MTS are performed concurrently. Similarly, the MTS task and the object discrimination task may also share specialized visual identity memory resources. If this is the case, performance on trials in which object discrimination and MTS are presented concurrently will be impaired more than when ordering and MTS are presented concurrently or when object discrimination and spatial memory are presented concurrently.

Methods

Re-training spatial memory and MTS with 4000ms delay

Because in Experiments 2 and 3 one monkey was not able to complete the internal tasks within the 3000ms set delay length, before the final test we re-trained the monkeys on the spatial memory task and on the MTS task. Everything was identical to the pre-training except that monkeys experienced a 4000ms delay between sample and test for both the spatial memory and MTS tasks. First monkeys had to complete one 48-trial session of the spatial memory task (with nothing embedded) with a 4000ms delay at 80% correct. They then had to complete one 48-trial session of the MTS task with a 4000ms delay at 80% correct. All other features of the trials and sessions were the same as the pre-training for Experiment 1.

Ordering and Object Discrimination in Spatial Memory and MTS Test

A test session included the following task types: spatial memory with nothing embedded, MTS with nothing embedded, ordering three numerals alone, object discrimination with three pairs alone, ordering three numerals embedded in spatial memory, object discrimination with three pairs embedded in spatial memory, ordering three numerals embedded in MTS, and object discrimination with three pairs embedded in MTS. Every 16 trials each of these trial types were presented twice, in pseudo-random order. Each session was a minimum of 384 trials; each trial type was presented at least 48 times. Each of the possible 48 spatial locations served as the target location once for the spatial memory alone trials, the spatial memory with ordering embedded trials, and the spatial memory with object discrimination embedded trials. Similarly, the MTS sample images were controlled such that each was presented an equal number of times as the sample for all trial types with MTS. Again, if monkeys responded incorrectly on the embedded task, that trial was recorded and repeated at the end of the session. All other features of the trials were identical to those described in Experiments 2 and 3, now with a 4000ms delay between sample and test.

Again, monkeys completed warm-up trial in which they had to perform at least 8/10 MTS trials and at least 8/10 spatial memory trials with blank delays correctly (4000ms delay).

Results and Discussion

As in Experiment 3, the difference between monkeys' expected if independent performance on the trials that included the spatial memory task and their observed performance was greater than the difference in their expected performance on the trials that included MTS and their observed performance on these trials. There was an interaction between outcome measure (expected if independent vs observed) and outside task type (spatial memory vs MTS; $F_{(1,20)}$=4.55, p=0.045; partial eta^2=0.1.86; Figure 13). There was also a main effect of outcome measure (expected if independent vs actual; $F_{(1,20)}$= 108.1, p<0.001; partial eta^2=0.844), with actual accuracies significantly lower than expected accuracies if the two tasks were completely independent (space*order: $t_{(5)}$=5.03, p=0.004, d=1.9; MTS*order: $t_{(5)}$=4.67, p=0.005, d=1.03; space*object discrimination: $t_{(5)}$=5.76, p=0.002, d=2.1; MTS*object discrimination: $t_{(5)}$=5.75, p=0.002, d=1.36; for means see Table 1). This means that cognitive resources are definitely shared across these task types; performance on these tasks is not independent. There was also a main effect of outside task type ($F_{(1,20)}$=9.38, p=0.006; partial eta^2=0.319). There was no main effect of inside type ($F_{(1,20)}$=439, p=0.52; partial eta^2=0.21). There was no

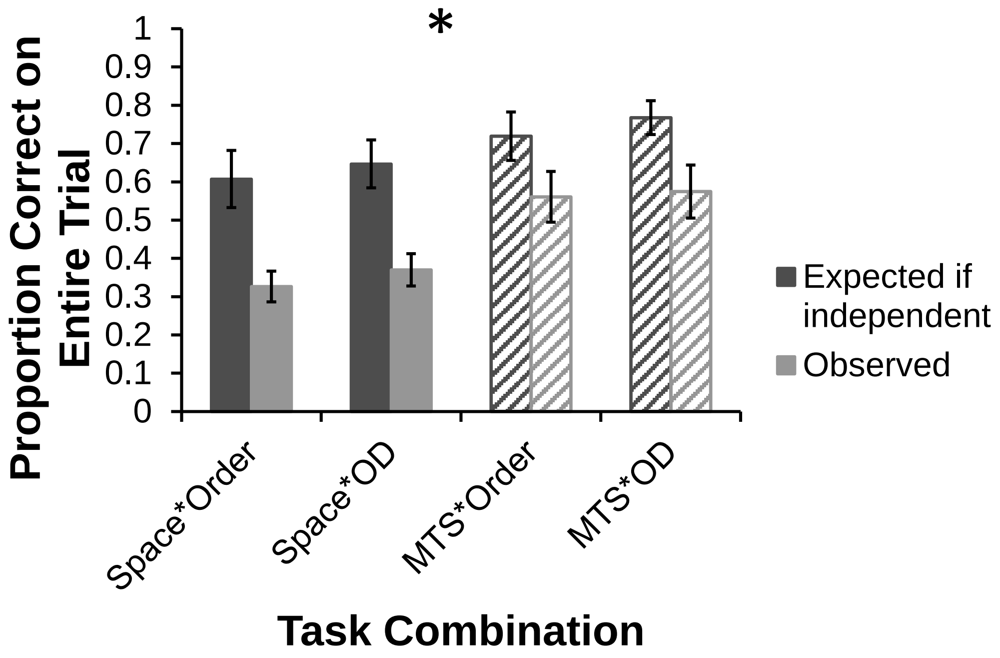

Figure 13. Expected vs observed accuracy on entire trial when ordering and object discrimination are embedded in spatial memory and MTS within a session. This graph represents monkeys' accuracy on the entire trial when ordering and object discrimination are embedded in spatial memory and MTS within one session. Dark gray bars represent the simple product of the accuracy on the internal task and the external task when they were presented independently. The light gray bars represent the average observed accuracies when the tasks were combined. Striped bars represented the tasks in which the external task was the MTS task and the solid bars are the trials in which the spatial memory task was the external task. Error bars represent the standard error. Chance for trials in which the monkeys had to order was 0.04 and was 0.03 for trials in which the monkeys completed object discrimination.

interaction with inside task type and outcome measure ($F_{(1,20)}$=0.104, p=0.75, partial eta^2=0.005), no interaction between outside type and inside type ($F_{(1,20)}$=0.006, p=0.94, partial eta^2<0.001), and no 3-way interaction ($F_{(1,20)}$=0.21, p=0.65, partial eta^2=0.01). Although this analysis indicates that there is an effect of the outside task type, we do not know if the errors were made on the outside task itself, or made on the inside task after having seen the sample from the spatial memory or MTS task. In order to assess the

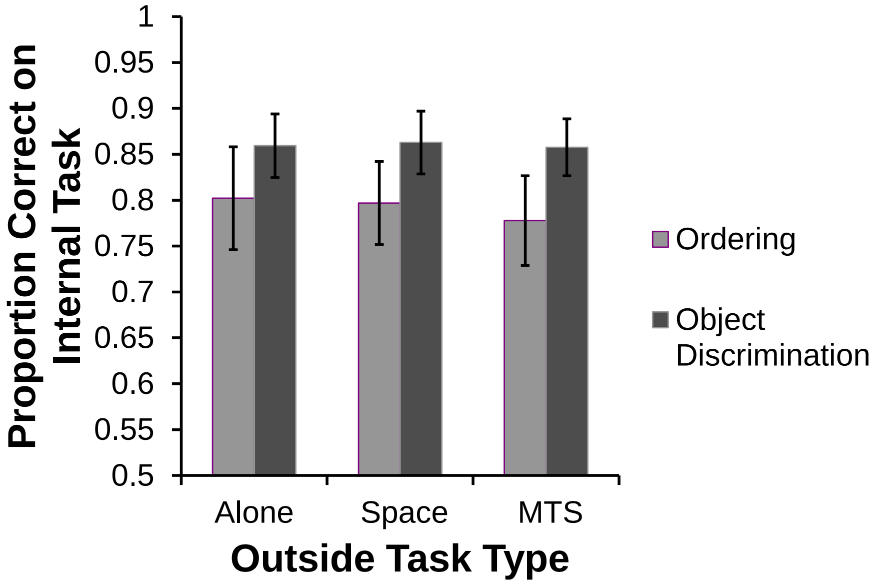

Figure 14. Accuracy on internal task when all trial types were intermixed. This graph represents the monkeys' average accuracy on the ordering task and the object discrimination task when they had to order three numerals alone or discriminate three pairs embedded in the spatial memory task and embedded in the MTS task all within one session. Light gray bars represent their ordering performance and dark gray bars their object discrimination performance. Error bars represent the standard error.

source of the error, we separated the monkey's performance on the outside tasks and the inside tasks.

We analyzed monkeys' performance on the inside tasks. We found no significant differences across any of the groups (outside task type, $F_{(2,10)}$=0.75, p=0.5, partial eta^2=0.13, inside task type $F_{(1,5)}$=3.25, p=0.13, partial eta^2=0.39, or an interaction between outside and inside task type, $F_{(2,10)}$=0.23, p=0.8, partial eta^2=0.04; Figure 14). Performance on the internal tasks was quite high (average performance on ordering was 79% and object discrimination was 85%), thus very little of the impact on the earlier analysis is due to errors on the internal task. This might mean that monkeys are allocating

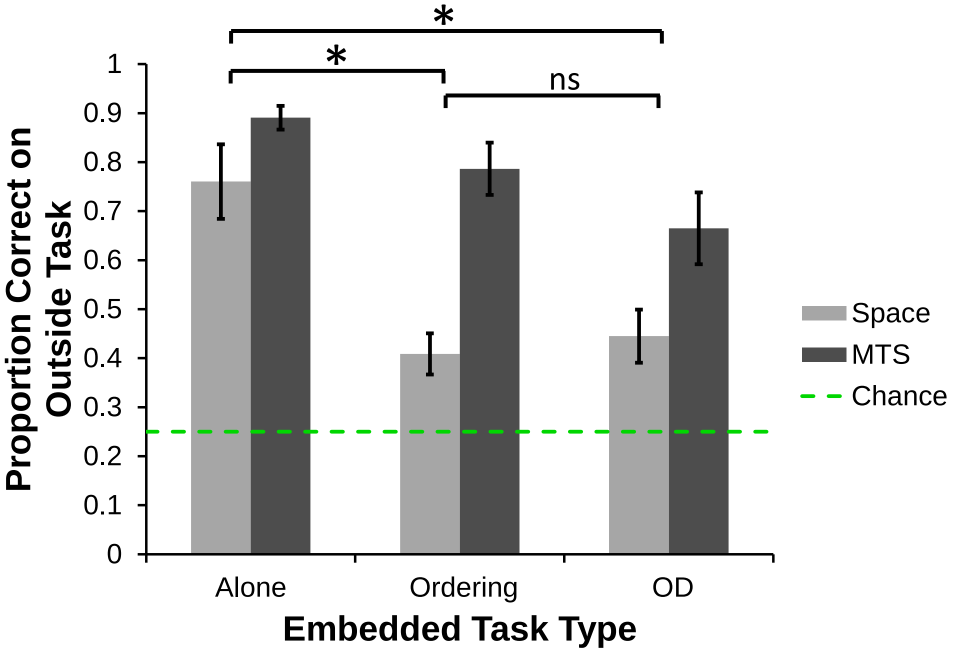

Figure 15. Accuracy on outside task when all trial types were intermixed. The light gray bars represent the average accuracy on the spatial memory task when it was presented with the different internal task conditions (alone, with ordering three numerals embedded, and with object discrimination embedded) all within a session. The dark gray represent the average accuracy on the MTS task when it was presented with the same internal task conditions. The monkeys had to get the embedded task correct in order to get to the outside task test, thus these bars represent trials in which monkeys correctly performed the embedded task.

their resources to the internal task to the detriment of performance on the external tasks as a whole. This is a different pattern than the results from Experiment 3, in which we found a main effect of outside task type. However, monkeys' performance did improve with additional testing experience, so it is possible that this difference is driven by learning.

We also analyzed performance on the outside tasks. Trials in which monkeys took longer than 4000ms to complete the internal task were removed from analysis. There was a main effect of outside type (spatial memory vs MTS; $F_{(1,5)}=8.85$, $p=0.03$, partial

$\text{eta}^2=0.639$; Figure 15) . There was also a main effect of inside type (alone vs ordering vs object discrimination; $F_{(2,10)}=25.18$, $p<0.001$, partial $\text{eta}^2=0.834$). We averaged performance on the outside tasks following each of the inside task types, and pairwise comparisons showed that performance on the outside tasks was significantly higher when presented alone (M=0.83) than when presented following the ordering task (M=0.6; $t_{(5)}=5.65$, $p=0.002$, $d=3.04$) or than when presented following the object discrimination task (M=0.55, $t_{(5)}=5.4$, $p=0.002$, $d=2.98$). There was no difference in outside performance following ordering compared to following object discrimination ($t_{(5)}=1.42$, $p=0.21$, $d=0.69$). There was no interaction between outside type and inside type ($F_{(2,10)}=3.88$, $p=0.057$. partial $\text{eta}^2=0.437$). These results indicate that while there are differences in how the monkeys perform these tasks separately, this difference is not driven by these tasks interacting specifically with each other. Spatial memory performance was not lower following ordering numerals than following object discrimination. These results contribute to the results from Experiments 1-3 suggesting that it is not ordering and spatial memory relying upon a domain specific resource that is not taxed in other tasks, but rather a general cognitive resource controlling performance on these tasks.

General Discussion

The results from these experiments indicate that spatial working memory and ordering are supported by a shared general cognitive resource that also supports visual memory tasks, rather than a domain specific resource only shared between those two tasks. We do not see consistent evidence of differential impacts on the ordering and/or spatial memory task when they are performed concurrently. This is evidenced by the fact that performance on a spatial working memory task was impaired when ordering was embedded within it and when a supposedly “non-spatial” task (object discrimination) was embedded within it. Additionally, performance on the ordering task remained quite high regardless of what type of task it was embedded within. Results from Experiment 2 are suggestive of ordering performance decreasing more when embedded in the spatial memory task, but due to the variability across individuals, we did not observe a significant difference between ordering performance embedded in the spatial memory task and ordering performance embedded in MTS. However, the results from Experiments 3 and 4 suggested instead that this system of shared resources is common across tasks and is not specific to ordering. Results from Experiment 3 also indicated that performance on any internal task is impaired when embedded in the spatial memory task, but by Experiment 4, when all tasks were intermixed in a session, these differences were no longer observed. Overall, the results from these experiments indicate that there is a general cognitive resource that is supporting ordering, spatial memory, and visual memory.

One possible explanation for the general spatial memory impairment caused by concurrent cognitive load may have been due to touching multiple screen locations in the embedded tasks. We strove to control for aspects of the ordering task, such as touching the screen in multiple locations and having the stimuli presented across variable locations, in our design of the object discrimination task. But touching multiple locations in both ordering and object discrimination may have caused significant spatial memory interference. There is evidence that some features of human working memory may be domain specific (Fougnie, Zughni, Godwin, & Marois, 2015), but it is only when two working memory tasks share representational format, i.e. spatial representations, that interference across domains is observed. Thus, our results could be due to the fact that all of our tasks required responses in space, and each of the tasks had spatial components. The observed interference across concurrent load conditions is not evidence for a lack of a spatial representation, but rather evidence for spatial representations supporting features of all of these tasks. Thus, another experiment in which the spatial locations of the embedded tasks are predictable will allow the monkeys to devote more resources to the spatial memory task. If ordering requires more spatial resources because it is controlled by a spatial representation we might then be able to differentiate between task conditions. However, in Experiment 3 we also observed impairments in the embedded tasks when presented concurrently with the spatial memory task. This raises the possibility that the general resource supporting these tasks is a spatial memory resource.

There is evidence that the posterior parietal cortex controls visual working memory generally: memory for objects and memory for locations (Berryhill & Olson, 2008). Participants with parietal lobe damage perform worse than control participants on object memory and location memory tasks. Because memory for order is also supported by the posterior parietal cortex (Hubbard et al., 2005; Prado et al., 2010) the results from our experiments might be explained by the fact that ordering, spatial memory, and visual memory are all supported by the same region in the brain. Thus, concurrent cognitive load will impact these tasks equally. If this is the case, then the experimental design we used in this study will not be able to differentiate between ordering and object discrimination in terms of their shared reliance on spatial memory resources.

Previous experience with other cognitive tasks also may have changed the way that these monkeys complete these tasks. For example, these monkeys have all learned to perform transitive inference tasks (some were subjects in Gazes et al., 2012, and were working on an experiment involving TI at the time of testing). There is evidence that TI performance is supported by spatial representations in monkeys (Gazes et al., 2014). Though the object discrimination pairs are not related to each other as they would be with a TI task, it is possible that the monkeys' prior experience with this type of task may have changed the way that they approach learning pairs of images; specifically being reinforced when utilizing a spatial representation.

In addition to list learning experience, the monkeys in this study are experts at MTS and have relatively less experience with the spatial memory task. The monkeys have been performing versions of MTS since the beginning of their cognitive testing experience. It is the second training task they receive after learning to touch the screen when they start doing cognitive testing. Their strategy for performing MTS may be very different than the strategy they use when performing the spatial memory task. It is possible that these results indicate there is a difference in how visual WM and spatial WM support other cognitive tasks, but it is also possible that these results illustrate differential expertise and do not offer new insights into the cognitive mechanisms supporting each of these tasks separately. Their MTS expertise may also explain why we did not observe increased interference in trials in which object discrimination and MTS were performed concurrently. Both tasks require subjects to remember specific images, and we know that concurrent visual load causes MTS interference (Basile & Hampton, 2013), but it is possible that the monkeys' expertise caused them to be resistant to interference during the MTS trials. Cognitive testing expertise may also have produced the differences between Experiments 3 and 4. Monkeys are experts at learning new tasks, and by Experiment 4, monkeys may have learned a new strategy to complete the tasks.

There is conflicting evidence in humans regarding the underlying mechanism supporting the observed phenomenon of spatial representations across experimental paradigms. It is possible that the mechanism supporting the spatial representations of order observed in humans is not a working memory mechanism (Cheung & Lourenco, 2016). There is evidence for magnitude overriding order, and there is also evidence for order overriding magnitude (Abrahamse et al., 2016; van Dijck & Fias, 2011). There is evidence that well learned lists and novel lists have spatial representations (Gevers et al., 2003; Prado et al., 2010; Previtali et al., 2010). Research with nonhuman primates can help clarify how evolutionarily distant species think about order and number and can elucidate features of the underlying mechanism that are impossible to dissociate in humans. In this study, although we did not find evidence of a domain specific working memory resource supporting ordering and spatial memory performance, clearly ordering and spatial memory do tax a shared memory resource, even if that resource is general and not specific to those tasks.

General Discussion

In this dissertation project I sought to test if spatial representations are an evolutionarily ancient mechanism supporting the ability to order items across species. I tested chimpanzees, orangutans, and rhesus monkeys in a series of experiments designed to test directly whether an ordering task and a spatial memory task compete for a limited domain specific working memory resource not taxed in other memory tasks. These studies extend previous research that found evidence of indirect “space-like” properties, such as symbolic distance effects, in nonhuman primates performing ordering tasks.

The results from Manuscript 1 indicate that chimpanzees and orangutans use working memory resources to perform an ordering and a spatial memory task, but the resource seems to support working memory generally. Performance on trials in which ordering and spatial memory tasks were presented concurrently was impaired. However, performance on trials in which simultaneous matching-to-sample and spatial memory tasks were presented concurrently was also impaired. We did see that performance on the ordering task was more impaired than was performance on the MTS task when under concurrent spatial memory load. It is likely that this performance decrement is due to the MTS task being supported by perceptual resources rather than working memory resources because in our follow up experiment, ordering performance was not statistically more impaired when under concurrent spatial memory load than when under concurrent visual memory load. Although ordering was numerically impaired, power analysis indicates that given our effect size we would need at least six individuals to detect statistical significance with an alpha of 0.05. The results were not significant with the four individuals who completed the third experiment. Therefore, we concluded that working memory tasks, including the ordering and spatial memory tasks, rely upon a domain general resource that is taxed across memory tasks.

In Manuscript 2, we also did not find evidence of a domain specific working memory resource supporting ordinal and spatial cognition. The results were consistent with a general cognitive resource contributing to both spatial memory performance and performance on ordering and object discrimination tasks. Although we cannot know how the monkeys were allocating their resources, their high level of accuracy on the embedded tasks suggests that they dedicated a good portion of their cognitive resources to those tasks. Thus, if both embedded task types tax a general working memory resource that also supports the spatial memory task, allocating resources towards the embedded task would lead to the observed decrease in spatial memory performance. However, in Experiment 3 we also observed that performance on both embedded tasks was impaired when performed concurrently with the spatial memory task. This suggests that both the embedded tasks and the spatial memory were taxing the same resource, but it was not the same resource taxed in the MTS task. It is therefore possible that the general resource supporting these tasks is a spatial memory resource.

All of these tasks require visual working memory, and there is evidence that the same regions in the posterior parietal cortex control memory for objects and memory for locations (Berryhill & Olson, 2008). As discussed at length in the introduction, the intra-parietal sulcus (IPS) supports memory for order across species (Hubbard et al., 2005;

Prado et al., 2010), so if this region is also activated and necessary for object and location memory, we would see interference across object memory and spatial memory tasks that have concurrent ordering loads. This is what we observed. Together the results from Manuscripts 1 and 2 indicate that nonhuman primates use a domain general working memory resource to perform ordering, spatial memory, and visual memory tasks that may have a foundation in the parietal lobe.

Three species and three testing environments

One notable difference between the results from Manuscript 1 and Manuscript 2 was subjects' performance on delayed matching-to-sample (DMTS) trials. Orangutan performance on trials that included a DMTS concurrent load was as impaired as on trials that included a spatial memory concurrent load. However, monkey performance was not as impaired with a DMTS concurrent load as with a spatial memory load, and their results were at ceiling in Experiment 1 of Manuscript 2. One possible explanation for these different findings is the very different testing contexts in which the apes and the monkeys were tested. The rhesus monkeys in this study live in a laboratory environment in which they are given computer tests for 7 hours a day, 6 days a week. They have lived in this environment for at least 4.5 years (most for more than 8) at the time of testing. They also have much more prior experience with the delayed matching-to-sample paradigm than do the orangutans and chimpanzees. DMTS is one of the first cognitive tasks that they learn, and many other studies in which they have been involved rely on a DMTS framework. In addition to the specific DMTS expertise, the monkeys have extensive experience switching between cognitive tests and learning new and challenging tasks. They are experts at detecting changes and modifying their strategies to get rewards. Monkeys may be predisposed to have a spatial representation of order, but their cognitive testing expertise may have uniquely prepared them to adjust how they performed these tasks.

In contrast, the orangutans test for 45 min-1 hour 5 or 6 mornings a week. They have only had consistent computer testing for less than five years, and they have much less experience learning different tasks. They are also generally less motivated than the monkeys because they have the opportunity to interact with their group-mates during testing. Although we did not test them on DMTS, the chimpanzees are also not DMTS experts. They have extensive experience with perceptual cognitive tests but much less experience with memory tasks and tasks that have delays or competing cognitive loads. Thus, some of the differences across studies are likely due to expertise differences rather than a species difference. Yet because these variables are confounded, it is not possible to differentiate between them in these animals. We did find evidence across species for impaired performance on trials in which the spatial memory task was under a concurrent cognitive load, and this indicates that for task types that are not overly trained, a general working memory resource supports performance on these tasks similarly across species.

It is also possible that rhesus monkeys can flexibly adjust their association between space and order. As described in the introduction, rhesus monkeys that learned to associate spatial locations with list items learned a transitive inference (TI) list more quickly when it was congruent with the order of the spatial locations learned previously than when it was incongruent (Gazes et al., 2014). Yet, monkeys that first learned to associate space with list items that was not then congruent with the TI training, did not improve their TI performance on subsequent trials in which their spatial training was consistent with the order of the TI list. These results suggest that the monkeys had several strategies at their disposal. Having learned that the spatial training was not relevant for the following TI task, they continued not to associate those two tasks. This finding might also help us understand the differences between Manuscript 1 and 2. As the monkeys learned that they would see two tasks together, they may have shifted their strategy and where they devoted their cognitive resources to ensure very high performance on the ordering task to the decrement of other tasks. And because of their DMTS expertise, this reallocation did not impact their backup matching strategy, ensuring continued successful matching performance. Rather than species difference, the different results across manuscripts again could be an example of memory test and task switching expertise.

Spatial memory as a general resource

It is also possible that in nonhuman primates, spatial memory resources support cognition generally. We saw performance on the spatial memory task go down when under concurrent cognitive load from ordering, simultaneous MTS, and object discrimination tasks. Performance on the ordering task and the object discrimination task was also impaired when presented concurrently with the spatial memory task, at least in Experiment 3 of Manuscript 2. Chimpanzee and orangutan ordering also was impaired when performed concurrently with the spatial memory task. And although not statistically significant, orangutan ordering was numerically more impaired when performed concurrently with the spatial task than the MTS task. Rather than indicating that ordering is not represented spatially, this could be evidence that spatial working memory is a resource tapped for many different tasks, especially in rhesus monkeys who are cognitive test experts. These experiments were designed to test whether ordering and spatial memory share specific cognitive resources that are not taxed in other tasks. We found that performance was generally impaired when tasks were performed concurrently with the spatial memory task, and this suggests that spatial working memory is a general resource taxed across tasks.

It is also possible that the general decrease in performance across concurrent load trials could be due to the fact that all of the tasks required touching different parts of the screen, and it was this movement in space that contributed to the spatial memory deficit. Touching different parts of the screen shifts spatial attention, and this attentional shift could have disrupted performance generally. However, in chimpanzees and orangutans, spatial memory performance was not as impaired following the motor control task suggesting that all of the decrement cannot be explained by touching across the screen. Thus, there is a shared cognitive resource contributing to the performance decrement observed across concurrent load conditions. In humans, shared representational format, i.e. a spatial representation, causes interference in concurrent load testing conditions. There is evidence that some features of human working memory may be domain specific (Fougnie et al., 2015). Yet, interference is caused when two tasks require responses in the same representational domain. So even if there are domain specific working memory resources supporting different cognitive tasks, our experimental design required specific responses in space to tasks that had spatial components. Rather than providing evidence specifically regarding the mechanism by which working memory supports complex cognition, we have evidence that a shared spatial representation and testing format may have contributed interference across all of the tasks in the above studies.

Other questions this thesis does not address

These studies do not differentiate between the possibility of a mental number/magnitude line (Cheung & Lourenco, 2016; Umiltà et al., 2009; Wood et al., 2008) and the hypothesis that it is order, not magnitude, driving the spatial representation evidenced by the SNARC paradigm in the introduction (Abrahamse et al., 2016; Fias & van Dijck, 2016; van Dijck et al., 2014). We tested whether order learned via the simultaneous chaining paradigm (SCP) is represented spatially in nonhuman primates. It is possible that extensively trained lists, like numbers 1-10, lists learned via SCP, or lists learned via transitive inference (TI) rely on slightly different mechanisms (Jensen, Altschul, Danly, & Terrace, 2013). Most of the evidence for any spatial representations in nonhuman animals has come from the sequence/list learning literature (Gazes et al., 2012; Gazes et al., 2014; Jensen et al., 2013; Merritt & Terrace, 2011; Templer & Hampton, 2013; Terrace, 2005), but this is not how most humans learn sequences or are introduced to magnitudes. It is possible the mechanisms supporting memory for sequences varies depending on how that sequence was learned, and this may contribute to differences we observe across tasks and species. Here I attempted to more concretely test whether nonhuman primates who learned lists via the simultaneous chaining paradigm required a domain specific spatial memory resource to successfully complete trials in which ordering and spatial memory tasks were performed concurrently. I am not drawing further conclusions as to how these results can be interpreted within the larger debate of whether human magnitude/ordinal cognition is supported by a mental number line or a working memory mechanism.

Summary

The results of this thesis indicate that across nonhuman primate species, ordering, spatial memory, and visual memory are supported by a general cognitive resource. In all concurrent cognitive load conditions, across chimpanzees, orangutans, and rhesus monkeys, performance on the spatial memory task was impaired. In some cases, the tasks embedded in the spatial memory task were also impaired, but this was not consistent across experiments. We cannot therefore conclude that nonhuman primates represent order spatially, but we also cannot state with certainty that they do not. Performance on ordering and spatial memory tasks was impaired when performed concurrently, so those tasks are supported by the same memory resource. It is possible that the association between space and order became more specialized in humans, but it is also possible that humans performing these tasks would show similar patterns of performance decrement. Further research controlling for spatial attention and touching across random screen locations would help clarify the sources of this interference. Additionally, comparative research with humans would allow us to determine whether human ordering, spatial memory, and visual memory tasks are supported by the same general resource as they are in nonhuman primates. Here we have found evidence that ordering and spatial memory are supported by a general working memory resource that also supports visual memory in chimpanzees, orangutans, and rhesus monkeys.

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