

Order Information in Working Memory: fMRI Evidence for Parietal and Prefrontal Mechanisms

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Abstract

■ Working memory is thought to include a mechanism that allows for the coding of order information. One question of interest is how order information is coded, and how that code is neurally implemented. Here we report both behavioral and fMRI findings from an experiment that involved comparing two tasks, an item-memory task and an order-memory task. In each case, five letters were presented for storage, followed after a brief interval by a set of probe letters. In the case of the item-memory task, the two letters were identical, and the subject responded to the question, “Was this letter one of the items you saw?”. In

the case of the order-memory task, the letters were different, and subjects responded to the question, “Are these two letters in the order in which you saw them?”. Behaviorally, items that were further apart in the sequence elicited faster reaction times and higher accuracy in the Order task. Areas that were significantly more activated in the Order condition included the parietal and prefrontal cortex. Parietal activations overlapped those involved in number processing, leading to the suggestion that the underlying representation of order and numbers may share a common process, coding for magnitude. ■

INTRODUCTION

Working memory is involved in much of human cognition (e.g., Baddeley, 1992; Baddeley & Hitch, 1974). It has been implicated as a major contributor to such critical higher-order cognitive skills as reasoning (Salt-house, 1993; Carpenter, Just, & Shell, 1990; Larson, Merritt, & Williams, 1988), language comprehension (Just & Carpenter, 1992), and problem-solving (Atwood & Polson, 1976; Simon & Newell, 1971). There is evidence from behavioral studies of patients and from neuroimaging studies that working memory for different kinds of information, such as verbal, spatial, and object, is at least partly separable in its neural signature (e.g., Smith, Jonides, & Koeppe, 1996; Smith et al., 1995; Logie, Zucco, & Baddeley, 1990). Here we focus on verbal working memory—more specifically, on the maintenance and processing of representations that code for the order and sequence of information in working memory.

The cognitive components of verbal working memory are thought to include at least three sets of mechanisms: storage, rehearsal, and executive processes (Smith, Jonides, Marshuetz, & Koeppe, 1998; Baddeley & Hitch, 1974). Evidence from patients and neuroimaging suggests that rehearsal is articulatory in nature, closely related to speech, and mediated primarily by prefrontal mechanisms: Broca’s area and premotor cortex (Hen-

son, Burgess, & Frith, 2000; Awh et al., 1996; Paulesu, Frith, & Frackowiak, 1993). Storage is presumably mediated by the parietal cortex: Brodmann’s areas (BA) 7 and 40 (D’Esposito & Postle, in press; Smith & Jonides, 1999; Smith et al., 1998; Paulesu et al., 1993). Finally, the ventrolateral and dorsolateral prefrontal cortex (DLPFC) are thought to mediate executive processes (e.g., Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; Smith et al., 1998; D’Esposito et al., 1995; Milner, 1964).

Executive processes seem to be of critical importance in performing higher-order cognitive tasks such as reading. For example, Daneman and Carpenter (1980) showed that, whereas performance on a simple maintenance task does not predict reading comprehension, reading comprehension is well-predicted by performance on a task that requires maintenance of some information while processing other information. By presumption, this is because this more complex task recruits executive processes to control and coordinate the component-processes. Furthermore, patients with prefrontal damage are often unimpaired on simple maintenance tasks (e.g., D’Esposito & Postle, in press), whereas they experience difficulty on tasks requiring the inhibition of a prepotent response (inhibition is often cited as an executive process). An example of the latter would be the incompatible condition of the Stroop task,

in which the subject must report the ink color of a color word (e.g., the word “red” printed in green ink), when the word and ink color are different (Vendrell et al., 1995; Perrett, 1974). Thus, there is a distinction between tasks requiring the storage and rehearsal of information, as opposed to those that recruit executive processes in addition (Smith & Jonides, 1999; Smith et al., 1998).

A number of distinct executive processes have been proposed. Among them are attention-and-inhibition (Jonides et al., 1998; Fuster, 1997; Chao & Knight, 1995; Cohen & Servan-Schreiber, 1992; Milner, Petrides, & Smith, 1985), task-management (Geva et al., 1999; Meyer et al., 1998; D’Esposito et al., 1995), monitoring (Petrides, Alivisatos, Meyer, & Evans, 1993), and coding for the order or sequence of information in memory (Smith, Marshuetz, & Geva, in press; Cabeza, Nichole, Houle, Mangels, & Nyberg, 2000; D’Esposito, Postle, Ballard, & Lease, 1999; Collette et al., 1999; Cabeza et al., 1997). Coding for order or sequence is the focus of this report.

The issue of how order information is processed has a significant history in cognitive psychology. For example, Sternberg tested subjects on two tasks. In one task (Sternberg, 1967), a paradigm called “Searching-For-Next”, subjects received a series of digits followed by a probe item and were required to produce the next item in the sequence. For example, given the memory set of items “7 1 9 3”, and a probe item, “9”, subjects were required to say “three”. In a comparison Item-Recognition task (Sternberg, 1966), subjects received a similar series of digits and a single item. They had to respond “yes” if the probe item was contained in the memory set of digits, and “no” if it was not. Sternberg examined the slopes relating memory-set size to reaction times in the Item-Recognition task, and found that the slopes for negative and positive items were parallel. Furthermore, he noted an absence of serial position effects (different reaction times for items depending on their position in the memory set). In contrast, the slope relating reaction times to set-size was seven times greater in the Searching-For-Next task than in the Item-Recognition task and pronounced serial position effects were observed. These findings taken together imply that a different process occurred in the two tasks.

In another experiment that contrasted order and item information in working memory, McElree and Doshier (1993) applied a speed/accuracy procedure to item-recognition and order tasks. In the Order task, they presented subjects with a series of six consonants, one at a time (e.g., “Q B F L X K”), followed by a probe item consisting of two letters (e.g., “X B”). Subjects had to indicate which probe item was the more recent. McElree and Doshier examined serial position effects in both tasks, and found that serial position in the memory set affected reaction time in the Order, but not Item, task. By manipulating the subjects’ speed/accuracy trade-off, they were able to conclude that rates at which item and order information accumulated in memory were differ-

ent. Therefore, behavioral experiments suggest separable processing of item and order.

Prior behavioral research suggests that there are several possible means by which order information may be represented: inter-item associations, direct discrete coding, and magnitude coding. Because each of these mechanisms has different behavioral consequences, we might expect different underlying neural processes. Thus, we shall describe the three mechanisms and their behavioral consequences in some detail.

The first possibility is that items are coded with respect to other items on the list via *inter-item associations* (e.g., Henson, 1999; Sternberg, 1967; Yntema & Trask, 1963; Young, 1961). In the simplest case, given a set of items, “F G P L T”, subjects code the order of the items in the following way: “F precedes G, G precedes P, P precedes L, L precedes T”. When probed with two items that were on the list and asked to make a judgment about whether the items appear in the same order as they were presented in the list, this inter-item associative mechanism predicts that reaction time will increase with the number of intervening items. That is, if you must memorize the list of items “F G P L T” and respond to the question, “are these two items in the correct order?”, it should take longer to respond to the item “F T” than the item “L T”, because in the former case you must traverse all the inter-item associations whereas in the latter case you have only to consider the L–T association.

The second possible mechanism for coding order information is the explicit association of temporal or ordinate position to each item (e.g., Anderson & Matesa, 1997; Ebenholtz, 1966). We refer to this possibility as *direct coding*. In this case, subjects given the same set of items above, “F G P L T” code the items as “F-first, G-second, P-third” and so forth. The behavioral prediction for a direct coding model differs from that of an inter-item association model: If response time is measured to a pair of probes (e.g., “F G” or “F T”), it may not vary with the distance between the letters in the list because subjects can access the associated position for each item and then compare which of those position codes is larger.¹

The third possible order-coding mechanism is one in which order information is coded according to a continuous scale of a variable, such as an index of item recency, familiarity, or some other code that can be expressed in magnitudes (e.g., McLaren, 1994). We shall call this mechanism *magnitude coding* in contrast to direct coding, order information is represented by a continuous index of magnitude. To the extent that items in memory are coded according to magnitude information, the behavioral data should parallel psychophysical functions, such as size discriminations, which are thought to be coded in terms of magnitude. That is, if items are coded according to a continuum of temporal magnitude, the longer that items are separated in time,

the easier the decision should be about whether they are in the correct order or not. For example, assume that items are coded with respect to magnitude of recency. Given the memory set “F G P L T”, subjects should be faster to respond to “F T” than to “L T” because it is easier to discriminate the recency indices when they are less similar to one another. The phenomenon of faster reaction times to more disparate items is referred to as the *distance effect* (Holyoak, 1977; Holyoak & Patterson, 1981; Moyer & Landauer, 1967). Note that this is the exact opposite of what an inter-item associative mechanism predicts. Furthermore, this prediction is counter to that of a direct-coding mechanism, in which the distance function for reaction time is expected to be essentially flat.

Distance effects are typically noted in tasks requiring subjects to make relative judgments about an aspect of two stimuli that are definable along some dimension, such as physical size. Interestingly, the distance effect holds for a variety of domains. For example, the time to judge the distance between items in perceived spatial arrays is shorter for items that are farther apart (Trabasso & Riley, 1975). The same effect is observed in judgments about imagined real-world objects, for which, for example, a subject’s response to the question of which object is larger is faster the more disparate their sizes (Jamieson & Petrusic, 1975; Paivio, 1975; Moyer, 1973). Also, a robust distance effect is observed in numerical comparisons, in which the question of which number is larger or smaller is answered more quickly for numbers that are farther away numerically from one another (Buckley & Gillman, 1974; Moyer & Landauer, 1967). This phenomenon implies that representations of size and quantity are stored as magnitudes that are easier to discriminate from one another if more disparate.

Little research using neuroimaging or patients has addressed the question of what neural regions may mediate distance effects in the perception or memory domains, but Dehaene, Cohen, and colleagues (e.g., Cohen & Dehaene, 1996; Dehaene, 1996, 2000; Dehaene, Dehaene-Lambertz, & Cohen, 1998) have extensively studied the processing of numerical information both in patients and healthy adults undergoing neuroimaging. They have concluded that some aspects of number processing, particularly those analog representations that give rise to distance effects, are mediated by the parietal cortex.

For example, patients with acalculia suffer damage primarily to the intraparietal sulcus and show a striking degree of category-specificity in their inability to process quantitative information. They can comprehend and produce numbers, do simple math problems learned by rote (e.g., 2×2), but they cannot make quantity judgments, nor can they perform calculations (Dehaene & Cohen, 1997). Also, neuroimaging studies demonstrate activation in this same parietal region during calculation tasks (Chochon, Cohen, van de Moortele,

& Dehaene, 1999; Kiefer & Dehaene, 1997; Dehaene et al., 1996). For example, Chochon et al. (1999) reported intraparietal sulcus activation in three distinct number processing tasks: digit comparison, multiplication, and subtraction. Thus, rather than being specific to any task, parietal involvement seems to be involved in number representation more generally.

If order and number information are both represented according to magnitude, we might expect that sequential order judgments are mediated by similar neural mechanisms in the parietal cortex. Indeed, based on evidence from computational modeling and data from frontal- and parietal-lobe patients, Meyer, Mueller, Seymour, and Kieras (2000) have argued that parietal mechanisms are involved in processing order information.

Despite theoretical reasons for suspecting that parietal mechanisms may be responsible for some aspects of order processing, empirical evidence from neuroimaging and patient studies has emphasized the role of the prefrontal cortex. For example, data from frontal-lobe patients implicates the prefrontal cortex in some forms of sequential or temporal coding in episodic long-term memory. Corsi (cited in Milner, 1971) demonstrated that patients with frontal- but not temporal-lobe damage had difficulty making a judgment about the relative recency of two items in episodic long-term memory. Furthermore, Corsi established a double-dissociation between the two processes: Patients with temporal- but not frontal-lobe damage had difficulty making a yes/no recognition judgment about items in the memory set and vice-versa. More recently, Shimamura, Janowsky, and Squire (1990) demonstrated that patients with damage to the prefrontal cortex have difficulty remembering the order of 15 items that they had previously seen, even though they performed normally in tasks requiring information about the content of the items.

In addition to evidence from patients, several neuroimaging experiments have demonstrated prefrontal activation in tasks that require processing of order information. In a positron emission tomography (PET) study, Cabeza et al. (1997) compared memory for order information in episodic long-term memory with a task requiring only the processing of item information. In both conditions, subjects studied lists of words prior to scanning. During scanning, subjects were given a series of memory probes that consisted of two words. In the Item task only one of the probe words had appeared on the list of to-be-remembered words and subjects responded to the question, “Which of these two words appeared on the study list?”. In the Order condition, both words had appeared as target items, separated by eight words on the studied list. In this case, subjects responded to the question, “Which of these two words is the more recent?”. Interestingly, when Cabeza et al. compared the Order and Item tasks, they observed both prefrontal and parietal activation in the Order task. However, it is difficult to determine the mechanism by

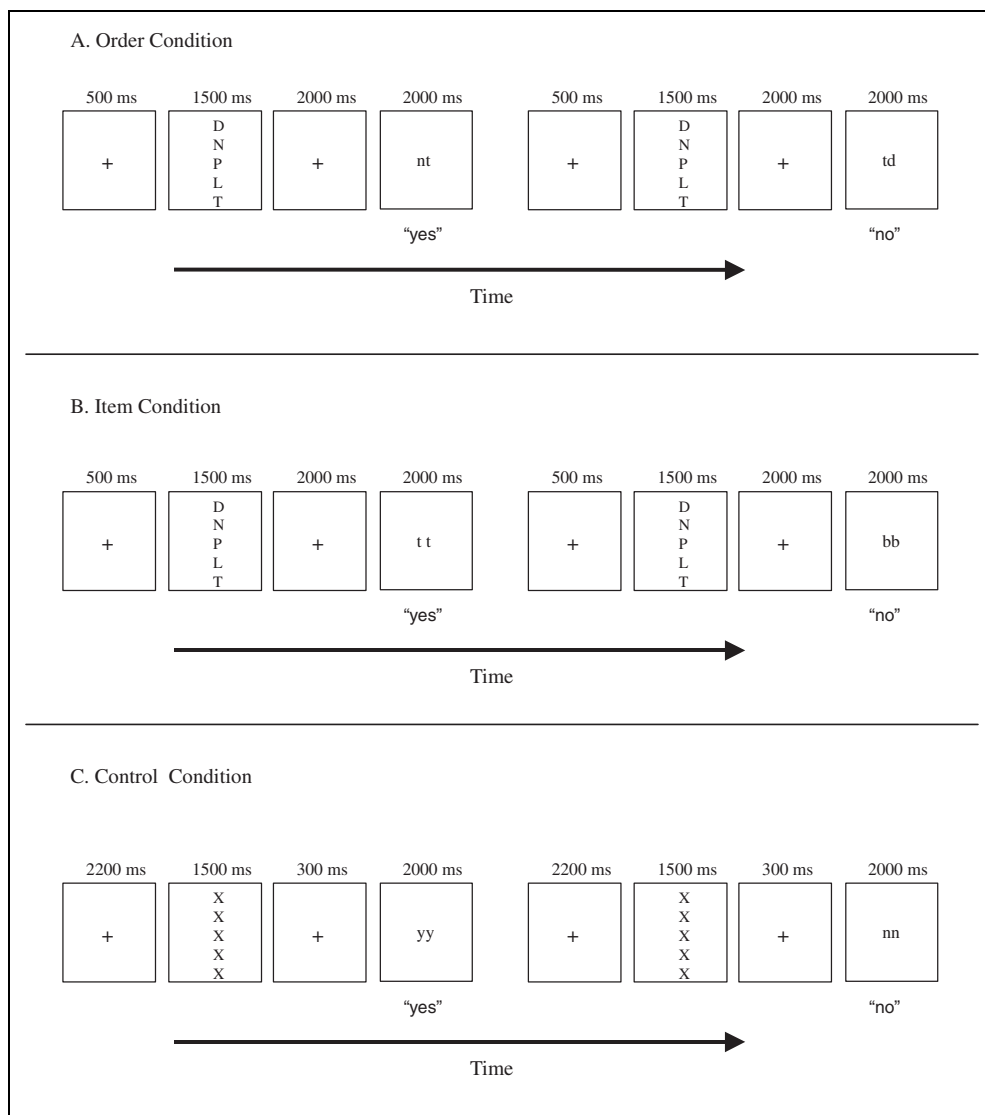
which order was coded in this experiment because the paradigm did not allow for the examination of behavioral distance effects (target items were always separated by eight other items). Furthermore, as in those tasks used in the experiments with frontal-lobe patients, the Cabeza et al. task was a long-term episodic memory task and may have recruited different mechanisms for the coding and retrieval of order information than would a working memory task.

We sought to isolate the neural circuitry involved in order processing in working memory by contrasting two tasks (Figure 1), one requiring mainly the storage and rehearsal of verbal information (Item task) and one requiring subjects to make judgments of the order of two items (Order task). In the Item task, subjects were required to remember five items for 2 sec and respond (manually) to a probe-item either positively if the item appeared in the target set, or negatively if it did not. In the Order task, we required subjects to remember the

items in the order that they appeared from top to bottom of the screen, and respond positively if the two probe items were in the same order, and negatively if they were not. To allow for the examination of distance effects, positive probe items did not need to be adjacent. For example, given the sequence “B F G H J”, a positive response would be required to the probe item “F H” or to the probes “F G” or “F J”. Negative probe items were items from the target set that were transposed, for example, “H F”. Distance was coded from zero (adjacent items) to 3 (three intervening items between probes).

Subjects were also tested in a control condition in which they were presented with a series of five Xs, which they were not required to remember. After a brief delay, they were required to respond to a positive or negative probe when it appeared. This task was designed to control for perception and response selection and execution.

Figure 1. Cognitive tasks. Sequence of events and timing parameters for the (A) Order condition, (B) Item Condition, and (C) Control condition. Figures depict two trials for each condition, the first in each schematic depicts a positive trial, and the second a negative trial.



To the extent that our Order paradigm creates distance effects in reaction time and is mediated cognitively by a magnitude-coding mechanism, we expect activation in the intraparietal sulcus, much like that observed by Chochon et al. (1999) in several number-processing tasks. Furthermore, we might expect prefrontal activation as well, as in previous studies with patients or using neuroimaging methods.

RESULTS

Behavioral Findings

As expected from prior behavioral studies (e.g., Sternberg, 1967), overall accuracy was higher in the Item task (92%) than the Order task (84%), $t(10) = 4.06, p < .001$. Furthermore, mean response times were significantly faster on the Item task (808 msec) than the Order task (1168 msec), $t(10) = 8.01, p < .001$.

A summary of the data can be found in Table 1. There was a marginally significant difference in accuracy between positive probe items in the Item (89%) and Order (86%) tasks, $t(10) = 1.64, p = .06$. In the case of negative responses, the difference between the Item (94%) and Order (81%) tasks was substantial and significant: $t(10) = 5.93, p < .001$. Similarly, the mean response time for positive probes was significantly faster in the Item condition (780 msec) than the Order condition (1083 msec), $t(10) = -12.61, p < .001$. The same pattern held true for negative responses: Response time in the Item condition (836 msec) was significantly faster than for the Order condition (1253 msec), $t(10) = -17.39, p < .001$.

For both tasks, positive responses were faster than negative responses. For the Item condition, positive and negative reaction times were 780 and 836 msec, respectively, $t(10) = -2.30, p = .015$; for the Order condition, positive and negative reaction times were 1083 and 1253 msec, respectively, $t(10) = -7.08, p < .001$.

Table 1. Response Times and Accuracies—Along with Standard Errors—for Each Type of Trial in the Three Conditions

Type of probe	Condition		
	Order	Item	Control
<i>Response times, msec</i>			
Positive	1083±57	780±44	497±24
Negative	1253±42	836±54	505±25
<i>Accuracy, percent</i>			
Positive	86±2.51	89±2.27	99±0.3
Negative	81±2.55	94±1.49	99±0.3

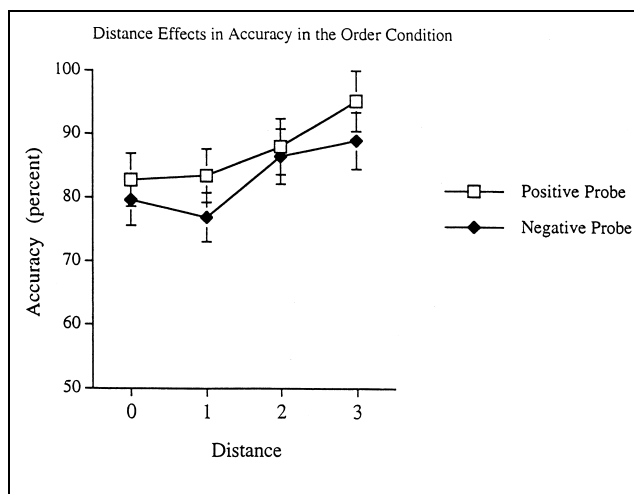


Figure 2. Distance effects in accuracy. Depicts average accuracy at each probe distance in the Order condition. Note that accuracy is greatest when the probe letters are separated by three items.

.001. For the Order task, the same pattern held for accuracy: Average accuracy for positive responses (86%) was greater than for negative responses (81%), $t(10) = 1.95, p = .033$. The pattern did not hold for the Item condition, however. Mean accuracy was lower for positive items (89%) than for negative items (94%), $t(10) = -2.34, p = .017$.

We were particularly interested in assessing distance effects in the Order condition which would suggest the use of magnitude representations. We examined distance effects for both positive and negative probes by taking the following steps: For each subject, we calculated the slopes relating accuracy and reaction time to the distance between the two probe items. We then entered the slope-values into a one-tailed t test to assess the hypothesis that the slopes were significantly greater than zero. In the case of reaction times we expected the slopes to be negative (i.e., shorter reaction times as the distance between the two probe items increased); in the case of accuracy, we expected the slopes to be positive (i.e., greater accuracy as the distance between the two probe items was increased).

The average slope relating accuracy to distance was 4% per intervening item for the positive probes, $t(10) = 4.69, p < .001$. For negative probes, the average slope was also 4% per intervening item, $t(10) = 2.94, p = .007$. That is, for each additional intervening target item, both positive and negative probes yielded responses with 4% greater accuracy (Figure 2). For reaction time, the average slope for positive probes was -49 msec per intervening item, $t(10) = -2.20, p = .026$. Corresponding slope for negative probe items was -26 msec per intervening item, $t(10) = -1.86, p = .046$ (Figure 3). Note that all tests of the distance effect are significant even with a more conservative two-tailed test, with the exception

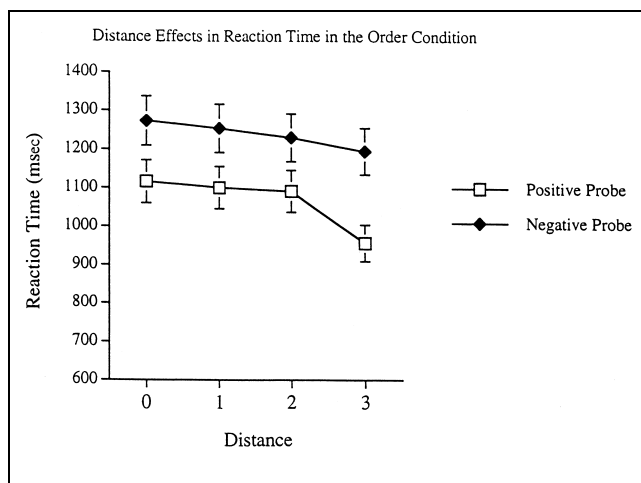


Figure 3. Distance effects in reaction time. Depicts average reaction time at each probe distance in the Order condition. Note that reaction time is fastest when the probe letters are separated by three items.

test for the slope relating reaction times to negative probe distance ($p = .092$).

Brain-Imaging Findings

We report five different types of analyses. The first is a standard exploratory statistical parametric mapping

(SPM) random-effects analysis. The second is a region-of-interest (ROI) analysis to assess how well the Item and Order task activations matched those found in a related paradigm (Jonides et al., 1998). Third, we report data from a test of the hypothesis that the DLPFC is significantly more activated in the Order than the Item condition, by restricting our analysis to the frontal cortex (with the appropriate correction for the number of multiple comparisons). Fourth, we tested the hypothesis that the observed parietal activation occurs in areas that overlap those observed in number processing (Chochon et al., 1999). Finally, we applied an anterior cingulate ROI to the Item versus Order contrast to examine the possibility that the more difficult Order task simply leads to higher activation in every relevant brain region.

Random-Effect Group Analysis

We first determined which areas are involved in both the Item and Order tasks separately relative to the control task. Activation peaks, together with their t score, Talairach coordinates, and Brodmann's area designations are listed in Table 2. The activations were in regions that we (and others) have previously identified as being implicated in verbal working memory tasks (e.g., Jonides et al.,

Table 2. Significant Activation Foci in Random-Effects Analysis

<i>Stereotaxic coordinates</i>	<i>Number of voxels</i>	<i>t value</i>	<i>p value</i>	<i>Anatomical region</i>
<i>(A) Order versus Control</i>				
-46 6 33	713	6.61	.0001	Broca's Area (BA 44)
-38 29 11	139	6.51	.0001	Left dorsolateral prefrontal (BA 46)
-4 20 45	602	10.13	.0001	Left anterior prefrontal (BA 8)
-36 -48 50	2087	12.09	.0001	Left posterior parietal (BA 7/40)
34 -54 47	1345	12.30	.0001	Right posterior parietal (BA 7/40)
-8 -18 2	398	12.55	.0001	Left thalamus
<i>(B) Item versus Control</i>				
-48 8 40	485	6.31	.0001	Left Broca's area/premotor (BA 44/6)
-30 -44 46	1154	7.36	.0001	Left posterior parietal (BA 7/40)
36 -56 47	542	10.19	.0001	Right posterior parietal (BA 7/40)
-8 -18 2	349	13.15	.0001	Left thalamus
-10 16 40	625	9.37	.0001	Anterior cingulate cortex
<i>(C) Order versus Item</i>				
-34 -46 46	357	6.98	.0001	Left posterior parietal (BA 7)
26 -56 52	569	8.00	.0001	Right posterior parietal (BA 40/7)
28 2 56	144	6.06	.001	Left SMA (BA 6)

SMA=Supplementary motor area.

Table 3. ROIs Based on the Recency Condition in Jonides et al. (1998)

<i>ROI number</i>	<i>Stereotaxic coordinates</i>	<i>Anatomical region</i>
1	-24 -62 40	Left posterior parietal cortex (BA 7/40)
2	-46 -4 32	Left premotor cortex (BA 6)
3	-37 8 25	Left premotor/Broca's area (BA 6/44)
4	-26 -6 43	Left motor/premotor cortex (BA 4/6)
5	26 -60 34	Right superior Parietal cortex (BA 7)

1998; Schumacher et al., 1996). In both the Item versus Control and the Order versus Control contrasts, we observed activation in parietal regions on the left and right (BA 7 and 40), typically thought to be involved in item-storage operations (e.g., D'Esposito & Postle, in press; Jonides et al., 1996). In the Item versus Control condition, we also observed activity in Broca's area/premotor, which is an area thought to mediate subvocal rehearsal (e.g., Awh et al., 1996; Paulesu et al., 1993). In the Order versus Control contrast, we also observed Broca's area (BA 44) activation. Additionally, we observed

activation in the left thalamus in both the Item and Order versus Control contrasts. In only the Item versus Control contrast we observed activation in the anterior cingulate cortex (BA 32). Unique to the Order versus Control contrast, we observed activation in the left DLPFC (BA 46).

In the direct comparison of the Order versus Item conditions, we observed greater activation of the left and right parietal regions (BA 7/40) and the left supplementary motor area (BA 6, superior).

Item-Recognition ROIs

To confirm that the areas observed in our two memory tasks matched those observed in other working memory studies, we conducted an ROI analysis on the Order and Item tasks contrasted with the control task. We limited the search for significant voxels to spheres with a 10-mm radius. The regions applied to our data were based on a similar four-target item-recognition task that had similar timing parameters, but that differed from the current tasks in its inclusion of some negative probes that had appeared in the previous target set (the "Recency" condition in Jonides et al., 1998). These regions can be found in Table 3 (note that we excluded cerebellar ROIs because we did not image the cerebellum in the current experiment due to technical constraints).

In the Item versus Control contrast, we observed significant activation in each of the regions reported in the comparable contrast in Jonides et al. (1998). The

Table 4. Coordinates of Significant Activation Foci in ROIs from Jonides et al. (1998)

<i>ROI number</i>	<i>Stereotaxic coordinates</i>	<i>Number of voxels</i>	<i>t value</i>	<i>p value</i>	<i>Anatomical region</i>
<i>(A) Order versus Control</i>					
1	-28 -60 43	440	8.05	.0001	Left posterior parietal cortex (BA 7/40)
2	-52 0 35	246	5.45	.0001	Left premotor Cortex (BA 6)
3	-46 -6 29	246	6.40	.0001	Left premotor/Broca's area (BA 6/44)
4	-30 0 37	125	5.57	.001	Left premotor cortex (BA 6)
5	26 -56 40	285	7.00	.0001	Right superior parietal cortex (BA 7/40)
<i>(B) Item versus Control</i>					
1	-28 -66 40	352	6.32	.0001	Left posterior parietal cortex (BA 7/40)
2	-42 2 27	302	5.55	.0001	Broca's area (BA 44)
3	-40 0 28	56	4.69	.016	Left premotor cortex (BA 6)
4	-28 2 39	142	5.16	.0001	Left premotor cortex (BA 6)
5	26 -56 40	224	6.52	.0001	Right superior parietal cortex (BA 7/40)
<i>(C) Order versus Item</i>					
2	-24 -60 42	122	4.38	.001	Left posterior parietal cortex (BA 7/40)
5	30 -62 42	67	5.41	.005	Right posterior parietal cortex

Table 5. Coordinates of Significant Foci in Prefrontal ROIs

<i>Stereotaxic coordinates</i>	<i>Number of voxels</i>	<i>t value</i>	<i>p value</i>	<i>Anatomical region</i>
<i>(A) Order versus Control</i>				
6 24 42	178	6.01	.021	Anterior cingulate cortex (BA 32)
26 12 50	148	4.37	.05	Right SMA (BA 6/8)
-37 29 11	1229	6.51	.0001	Left dorsolateral prefrontal cortex (BA 46)
<i>(B) Item versus Control</i>				
6 24 48	292	4.81	.002	Anterior cingulate cortex (BA 32)
-10 16 40	1058	9.37	.0001	Anterior cingulate cortex (BA 32)
<i>(C) Order versus Item</i>				
46 39 7	615	4.28	.05	Right dorsolateral prefrontal cortex (BA 46)

same held true in the Order versus Control contrast. The same regions, placed on the Order versus Item contrast yielded significant activation in the left and right parietal cortex (BA 40 and 7, respectively). Coordinates of peak activation foci, *t* values, and significance levels for each of the five regions can be found in Table 4.

Thus, we found that the current experiment well replicates Jonides et al. (1998) with a significant activation focus in both the Order and Item conditions within 10 mm of each activation focus reported in Jonides et al.

Prefrontal ROIs

Previous research suggested that our Order task might be mediated in part by prefrontal mechanisms, particularly DLPFC (e.g., Cabeza et al., 1997). However, because our Order paradigm has not been used in a neuroimaging experiment before, we had no basis for an exact prediction about DLPFC activations. Therefore, we constructed a 30-mm radius spherical ROI roughly in the center of mass in the prefrontal cortex (30, 30, 30 and -30, 30, 30). This region covered most of the prefrontal cortex forward of the precentral gyrus, extending above to cover most of BA 6 superiorly and extending below the most inferior portion of BA 46. This ROI encompassed all of BA 9, 46, 45, and 44, most of inferior and superior 6, and extended into, but did not completely encompass, BA 10. We then corrected for multiple comparisons only in that region via Gaussian random field theory (Worsley, 1997).

The results of this analysis are summarized in Table 5. We observed significant activation in the anterior cingulate cortex in both the Item and Order conditions versus the Control. Furthermore, in the Order versus Control contrast, we observed significant activation in the DLPFC on the left (this was not the case for the Item vs. Control comparisons). In the Order versus Item contrast, we observed significant activity only in the right DLPFC.

The activity that we observed in the prefrontal cortex was not consistent between the Order–Control and Order versus Item contrasts. In particular, the left DLPFC activation in the Order versus Control contrast was not evident in the Order versus Item contrast. We suspect that we do not observe left DLPFC activity in the Order versus Item contrast because there may be subthreshold activity in or near DLPFC in the Item condition. This would be in good agreement with findings that set sizes greater than 4 items engage DLPFC during encoding (Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). To assess this possibility, we placed three reported BA 46 activation foci reported in Rypma et al. [stereotaxic coordinates, (1) -37, 29, 20; (2) -39, 35, 12; (3) -48, 43, 8], on our Item versus Control data. The analysis yielded significant results in BA 46 in the first two ROIs (stereotaxic coordinates = -38, 31, 11, number of voxels = 133, $t(10) = 3.61$, $p = .001$ and stereotaxic coordinates = -36, 27, 6, number of voxels = 137, $t(10) = 3.62$, $p = .001$), but not the third ROI.

Parietal ROIs

We defined ROIs from Chochon et al., 1999 (Table 6) and applied spheres of 10-mm radius to the

Table 6. Parietal Regions Reported in Chochon et al. (1999)

<i>ROI number</i>	<i>Stereotaxic coordinates</i>	<i>Anatomical region</i>
1	42 -29 43	Right postcentral sulcus/ anterior intraparietal sulcus
2	42 -38 38	Right intraparietal sulcus (middle part)
3	39 -41 41	Right intraparietal sulcus (middle part)
4	33 -46 44	Right intraparietal sulcus (posterior part)
5	-45 -41 38	Left intraparietal sulcus (middle part)
6	-39 -64 42	Left intraparietal sulcus (posterior part)
7	-27 -64 42	Left intraparietal sulcus (posterior part)

Order–Item contrast to test the hypothesis that we would observe greater activation in parietal regions implicated in number processing. As summarized in Table 7, the activations that we observed in the Order condition were larger (i.e., affected more voxels and more separate activated sites) and greater (i.e., more significant) than in the Item condition, confirming the hypothesis that the parietal activations in the Order condition are in close agreement with those involved in number processing. It should be noted that some of these sites do reach significance in the Item versus Control contrast, suggesting as in previous work that some parietal foci of activation are due to storage-related mechanisms (Jonides et al., 1997), rather than magnitude coding mechanisms. Since the memory load was the same in both the Order and Item conditions, additional parietal activation observed in the Order versus Item

contrast should be due to the coding of order, rather than storage operations.

Anterior Cingulate ROI

We were concerned about the possibility that the additional activity we observed in the parietal and prefrontal cortex was the result of simply more processing in same circuit of regions in the Order task, due to its increased difficulty, rather than to a qualitative change in processing. The anterior cingulate cortex is thought to be activated by increases in task difficulty (e.g., MacDonald, Cohen, Stenger, & Carter, 2000; Barch et al., 1997), and so we applied an ROI reported in MacDonald et al. (2000) in the anterior cingulate to the contrast of the Item versus Order conditions (stereotaxic coordinates 4, 1, 43; 2). The analysis yielded significant results—indicating more activation in the Item than the Order

Table 7. Coordinates of Significant Activation Foci in ROIs from Chochon et al. (1999)

<i>ROI number</i>	<i>Stereotaxic coordinates</i>	<i>Number of voxels</i>	<i>t value</i>	<i>p value</i>	<i>Anatomical region</i>
<i>(A) Order versus Control</i>					
1	42 –37 39	163	5.07	.001	Right intraparietal sulcus, anterior part (BA 40)
2	38 –44 43	391	6.26	.001	Right intraparietal sulcus, middle part (BA 40)
3	36 –46 43	433	6.92	.001	Right intraparietal sulcus, middle part (BA 40)
4	34 –54 47	473	12.30	.001	Right intraparietal sulcus, posterior part (BA 40)
5	–36 –46 39	325	8.28	.001	Left intraparietal sulcus, middle part (BA 40)
6	–36 –48 50	430	12.09	.001	Left intraparietal sulcus, posterior part (BA 40)
7	–32 –58 45	479	8.69	.001	Left intraparietal sulcus, posterior part (BA 40)
<i>(B) Item versus Control</i>					
1	44 –31 38	211	4.56	.001	Right intraparietal sulcus, anterior part (BA 40)
4	36 –56 47	327	9.49	.001	Right intraparietal sulcus, posterior part (BA 40)
5	–36 –39 39	286	5.39	.001	Left intraparietal sulcus, anterior part (BA 40)
6	–35 –50 48	347	6.65	.001	Left intraparietal sulcus, posterior part (BA 40)
7	–28 –66 40	424	6.32	.001	Left intraparietal sulcus, posterior part (BA 40)
<i>(C) Order versus Item</i>					
1	44 –35 48	166	4.54	.001	Right intraparietal sulcus, anterior part (BA 40)
2	36 –44 39	289	4.45	.001	Right intraparietal sulcus, middle part (BA 40)
3	32 –44 45	378	4.79	.001	Right intraparietal sulcus, middle part (BA 40)
4	28 –42 48	431	5.18	.001	Right intraparietal sulcus, posterior part (BA 40)
5	–36 –44 43	206	6.25	.001	Left intraparietal sulcus, anterior part (BA 40)
6	–34 –46 46	278	6.98	.001	Left intraparietal sulcus, posterior part (BA 40)
7	–24 –60 42	189	4.38	.001	Left intraparietal sulcus, posterior part (BA 40)

condition (stereotaxic coordinates = 6, -2, 46, number of voxels = 57, $t(10) = 3.35$, $p = .009$). These results imply that the greater activation that we observe in the Order task in other brain regions does not simply represent an increase in difficulty.

DISCUSSION

Many of the results that we observed in the Item and Order conditions were typical of working memory experiments. In common to both conditions (vs. the Control), we observed activation in rehearsal-related regions (Broca's area/left premotor cortex). We also observed activation in posterior parietal areas in both conditions, which are thought to mediate storage operations.

The DLPFC was more active in the Order task than in the Item task. This finding is not surprising, given that DLPFC has been implicated in executive processing operations (e.g., Smith et al., 1996; D'Esposito et al., 1995). In particular, DLPFC has been implicated in ordering operations in the patient literature (e.g., Shimamura et al., 1990; Milner, 1964, 1971). We note that the region we observed was dorsal, not ventral, and that our findings are consistent with D'Esposito et al. (1999).

Much as distance effects have been observed for size judgments, perceptual distance judgments, quantities, and other dimensions, we observed significant distance effects for the order of items in memory. The critical additional executive process that occurs during the Order task may belong to a family of operations that have to do with magnitude, or analog, representations.

What is interesting about these results is the substantial degree of activation in posterior parietal regions, especially when compared with the relatively small degree of activation found in DLPFC. However, parietal activation in ordering tasks is not without precedent. Recall the task employed by Cabeza et al. (2000), in which subjects had to make recency judgments about two items that had appeared on a list of to-be-remembered words. Cabeza et al. observed activity in the parietal cortex, and pointed out that some researchers have tied parietal regions to memory for temporal relationships (e.g., Harrington, Haaland, & Knight, 1998; Petrides, 1994), which might be coded by magnitude. Indeed, the activations we observed in the posterior parietal cortex are similar to those observed in number comparison and number calculation, as seen in our ROI analysis. We note that Chochon et al. (1999) report activity in the intraparietal sulcus in three different number processing tasks (digit comparison, multiplication, and subtraction), and that every site they report as active in their three tasks is active in ours. To the extent that number coding, temporal coding, and order coding in memory

can be linked to the same underlying neural mechanisms, and to the extent that they share some similar behavioral properties, these operations may share an underlying computational similarity.

The idea that the parietal cortex may be involved in executive processes, particularly in order coding operations, is not without precedent (e.g., Meyer et al., 2000). Some aspects of attention also considered to be executive processes (c.f. Smith & Jonides, 1999) are linked to the parietal cortex (e.g., Sathian et al., 1999; Corbetta, 1998; Corbetta, Kincade, Ollinger, McAvooy, & Schulman, 2000; Posner, Walker, Friedrich, & Rafal, 1984). Furthermore, the parietal cortex has been implicated in tasks requiring sequencing, in particular, motor sequencing (Harrington et al., 2000; Catalan, Honda, Weeks, Cohen, & Hallett, 1998; Dassonville et al., 1998).

Lastly, it is not surprising that the dorsolateral prefrontal cortex and the parietal cortex are implicated in the same task. Rich interconnections exist between the prefrontal (particularly dorsolateral prefrontal) and parietal regions (e.g., Petrides & Pandya, 1984; Pandya & Seltzer, 1982; Mesulum, Van Hoesen, Pandya, & Geschwind, 1977). Furthermore, these two regions have common cortical and subcortical target regions (Selemon & Goldman-Rakic, 1988), and primates show coactivation of these regions while performing working memory tasks (Friedman & Goldman-Rakic, 1994).

The Order task yields lower performance than the Item task, as indicated by the error data. This raises the question of whether the activation differences between item and order are simply due to the greater difficulty of the Order task. There have been several suggestions that differences in task difficulty are indexed by differences in anterior cingulate cortex activation (e.g., MacDonald et al., 2000; Barch et al., 1997). If the increased activity we observe in the Order task is due to a simple increase in task difficulty, the Order task should lead to greater activity in all working memory regions, especially those sensitive to task difficulty. However, when we examined anterior cingulate activity in the Item versus Order contrast (regions activated more in the Item task), we found the reverse. Furthermore, Barch et al. demonstrated that neither the DLPFC nor the parietal cortex are sensitive to all types of increased difficulty; in fact, in their experiment, degrading the stimuli caused no increase in activation in either of the above regions, despite decreases in behavioral performance. So, together with the arguments from the behavioral data suggesting that the tasks do not just differ in difficulty but in strategic processes as well, we conclude that the areas that are more active in the Order than the Item condition do not simply represent a harder task; they represent different processing mechanisms for the Order task.

Follow-up work using single-trial fMRI paradigm should serve to clarify two issues. The first issue is

common to most, if not all, blocked designs: We cannot be certain that changes in activation are due to the process of interest (order coding) as opposed to a more global change in strategic processing. The second issue is that of the specific role of the parietal cortex in supporting order processing operations.

We have suggested that coding for order involves the use of a magnitude code similar to that employed in number processing tasks (e.g., Chochon et al., 1999). Another possibility is that posterior parietal cortex is involved in specifically coding items for their position in the rehearsal loop (Meyer et al., 2000; Kieras, Meyer, Mueller, & Seymour, 1999). A third possibility is that the posterior parietal cortex is involved at the retrieval stage in the serial scanning process suggested in other behavioral work (McElree & Doshier, 1993). Alternatively, sequential order judgments may involve selectively attending to positions in the memory representation, and this may be the relevant function of the parietal cortex. Lastly, the parietal cortex may be involved in some sort of counting operation that may determine the distance of two items relative to one another. Future experimentation will help determine which stage or stages of processing are mediated by both parietal and prefrontal mechanisms, which will be a step toward an understanding of how order information is represented and processed.

METHODS

Procedure

Twelve normal, right-handed subjects (six male and six female) participated in two sessions: one practice session to gain familiarity with the task, and one scanning session on a separate day.

Practice Session

In the practice session, subjects received both written and oral instructions that placed equal emphasis on speed and accuracy. Subjects each received two blocks of practice that consisted of twenty trials each. If they did not reach 80% accuracy, they received additional blocks of practice until they reached the 80% criterion.

Following the initial learning phase, subjects participated in the behavioral equivalent of six fMRI runs to stabilize strategy, to become familiar with the brief instructions between blocks, and to become comfortable with the timing of the task. The practice session lasted approximately 1.5 hr.

fMRI Session

Subjects participated in eight runs, resulting in a total of 16 blocks of data for each condition. Runs lasted almost 7 min each. Each run consisted of two blocks of each condition: Control, Order, and Item, with 10 trials per

block. Blocks were presented in pseudo-random order. Prior to the functional runs, both T1- and T2-weighted structural images were acquired. In total, the fMRI session lasted approximately 2 hr.

Cognitive Tasks²

Stimuli were consonants, and were presented on a Macintosh IIci with a 15-in. color monitor using PsychoScope (Cohen, MacWhinney, Flatt, & Provost, 1993) during practice, and projected on to a screen viewed by the subject via a mirror positioned above the eyes during scanning.

For all conditions, the proportion of positive and negative probes was 50%, and each trial lasted 6000 msec. In both the Item and Order tasks, subjects saw five consonants in a vertical array for 1500 msec, and were instructed to read them silently from top to bottom. Following the encoding interval, there was a retention delay of 2000 msec, following which two probe letters appeared for 2000 msec; and subjects had to respond positively or negatively by keypress with either the index finger or the second finger, respectively, of the right hand.

In the Order condition, the probes consisted of two consonants, presented horizontally, that were contained in the target set, either in the same order as the input order, or transposed. Probe items did not have to be adjacent in order for the item to be a positive probe. Subjects responded to the question "Are these items in the correct order?". In the Item condition, probes consisted of two identical consonants (to equate for the visual display in the Order condition), presented horizontally, which either had been contained in the target set or were new. In the latter condition, subjects responded to the question "Was this one of the letters you just saw?". In both the Order and Item conditions, a 500 msec inter-trial interval followed the probe.

The control condition differed from both the Item and Order tasks in timing and task demands. In this condition, subjects saw five Xs in the display, arrayed in the same positions (vertically) as in the Item and Order conditions. After 1500 msec, the Xs disappeared, and were replaced by a blank screen, which lasted for 300 msec. Two letters then appeared, arrayed horizontally, either the letter Y to which subjects were to respond with the index finger, or N, to which subjects responded with the middle finger. In order to keep the trial length consistent with the other two conditions, the inter-trial interval was lengthened to 2200 msec, yielding a trial length of 6000 msec.

Image Acquisition and Analysis

Subjects participated in eight fMRI runs (1.5 T GE LX gradient-echo EPI, TR = 2000, TE = 40, FOV = 240 ×

150) while performing the cognitive tasks, for a total of 528 scans per condition. Slices were 7 mm thick, 128×80 matrix (in-plane resolution 1.875×1.875 mm), acquired at 14 contiguous locations parallel to the anterior commissure-posterior commissure line. Slices covered all of the cortex but did not cover the cerebellum for most subjects.

All fMRI data were analyzed using SPM99 (Wellcome Department of Cognitive Neurology, London) implemented in Matlab (Mathworks, Sherborn, MA), and consisted of: (1) Intra-subject registration to correct motion between scans. (2) Transformation of each image to a stereotaxic system (Talairach & Tournoux, 1988)³ resampling to 2-mm isotropic voxels. (3) Spatial smoothing using a 4-mm FWHM Gaussian filter. (4) Creation of a *t* statistic map for each relevant contrast (Order vs. Control, Item vs. Control, and Order vs. Item). (5) Averaging of contrast sets across subjects (random-effects analysis; Holmes & Friston, 1998).

The random effects analysis employs *t* tests for a contrast of interest and produces estimates of the size and intensity of activations using Gaussian random field theory (Worsley, 1997). The threshold for voxels to enter the analysis was set to a *p* value of .001 for all contrasts. In all cases, *p* values reported (Tables 2, 3, 4, 5, 6, and 7) reflect *p* values corrected for multiple comparisons.

A priori hypotheses were tested using a correction for multiple comparisons in the ROI that were defined based on (1) significant peak areas of activation observed in a similar verbal working memory task (Jonides et al., 1998), (2) region-based, restricted to the prefrontal cortex, (3) significant peak areas observed in number processing tasks (Chochon et al., 1999), and (4) anterior cingulate activity reported in a task designed to study cognitive control (MacDonald et al., 2000). For all ROIs, the threshold to enter the analysis was set to *p* = .01. All ROI analyses were performed via the small volume correction function in SPM99. These ROI analyses are centered on regions reported in the experiments mentioned above and function to restrict the volume search size to a sphere with a user-specified radius. What is produced is the peak activation focus within the region in question (so the activation focus on which the ROI is centered typically differs from the peak voxel reported). Reported here separately are: (1) the center of the sphere, as defined from regions reported in the literature, and (2) the most active voxel in our data within the specified region. These two will differ slightly from one another, due to the nature of the analysis.

Our literature-based ROIs were 10 mm in radius and were placed according to the stereotaxic location of the peak voxel reported. In our region-based prefrontal analysis, we placed a spherical ROI with a 30-mm radius

roughly in the center of mass in the prefrontal cortex (stereotaxic coordinates on the right, 30, 30, 30 and left, -30, 30, 10).

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The data reported in this experiment have been deposited in National fMRI Data Center (<http://www.fmridc.org>). The accession number 13-2-2000-1117M.

Notes

1. With additional assumptions, though, direct coding can predict distance effects. One possibility is that the comparison of positions (e.g., first vs. third) is easier the greater the ordinal difference in positions (see the following arguments about distance effects). Another possibility is that each temporal position is itself represented by multiple features, and adjacent temporal positions share more features than nonadjacent ones.

2. One subject's behavioral data from the fMRI session were lost due to an equipment malfunction.

3. For the purpose of this report, SPM (Montreal Neurological Institute) coordinates were translated into Talairach coordinates (Talairach & Tournoux, 1988) using the following algorithm supplied by Matthew Brett: Where X' , Y' , and Z' indicate Talairach coordinates and X , Y , and Z indicate MNI coordinates:

Above the anterior commissure ($Z \geq 0$):

$$\begin{aligned} X' &= 0.9900X \\ Y' &= 0.9688Y + 0.0460Z \\ Z' &= -0.0485Y + 0.9189Z \end{aligned}$$

Below the anterior commissure ($Z < 0$):

$$\begin{aligned} X' &= 0.9900X \\ Y' &= 0.9688Y + 0.0420Z \\ Z' &= -0.0485Y + 0.8390Z. \end{aligned}$$

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