Working Memory Delay Activity Predicts Individual Differences in Cognitive Abilities

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Abstract

■ A great deal of prior research has examined the relation between estimates of working memory and cognitive abilities. Yet, the neural mechanisms that account for these relations are still not very well understood. The current study explored whether individual differences in working memory delay activity would be a significant predictor of cognitive abilities. A large number of participants performed multiple measures of capacity, attention control, long-term memory, working memory span, and fluid intelligence, and latent variable analyses were used to examine the data. During two working memory change detection tasks, we acquired EEG data and examined the contralateral delay activity. The results demonstrated that the contralateral delay activity was significantly related to cognitive abilities, and importantly these relations were because of individual differences in both capacity and attention control. These results suggest that individual differences in working memory delay activity predict individual differences in a broad range of cognitive abilities, and this is because of both differences in the number of items that can be maintained and the ability to control access to working memory. ■

INTRODUCTION

Working memory, our ability to actively maintain and use representations for ongoing processing, is a vital component of the broader cognitive system. A great deal of prior research has shown that estimates of an individual's working memory strongly predict performance on a number of other cognitive tasks including measures of inhibitory and attentional control, long-term memory, reading comprehension, performance on the SATs, and learning (Unsworth & Spillers, 2010; Unsworth, Brewer, & Spillers, 2009; Engle & Kane, 2004; Kyllonen & Stephens, 1990; Turner & Engle, 1989; Daneman & Carpenter, 1980). One relation that has garnered a great deal of attention is between working memory and fluid intelligence. Fluid intelligence (gF), which is the ability to solve novel reasoning problems, has been extensively researched and shown to correlate with a number of important skills (Cattell, 1971) and has been found to be an important predictor of a number of real world behaviors (Deary, Strand, Smith, & Fernandes, 2007; Gottfredson & Deary, 2004). A large number of studies have demonstrated a consistent and strong relation between estimates of working memory and performance on measures of gF (e.g., Unsworth, Fukuda, Awh, & Vogel, 2014; Kane et al., 2004; Engle, Tuholski, Laughlin, & Conway, 1999; Kyllonen & Christal, 1990). However, the cognitive and neural mechanisms that account for this important relation are still not very well understood.

Recent research has demonstrated that delay activity during visual working memory tasks provides a neural correlate of working memory capacity (e.g., Todd & Marois, 2004; Vogel & Machizawa, 2004). Specifically, using fMRI, Todd and Marois (2004) found that the delay signal in the intraparietal sulcus increased as set size increased, reaching asymptote around three to four items. Importantly, in a subsequent study, Todd and Marois (2005) found that the delay activity predicted individual differences in behavioral estimates of working memory capacity. Examining ERPs, Vogel and Machizawa (2004) demonstrated that sustained activity over posterior parietal electrodes during the delay of a visual working memory task increased as set size increased and reached asymptote around three to four items. This activity, known as the contralateral delay activity (CDA), reflects a sustained negative wave at posterior electrodes contralateral to the attended hemifield. Importantly, the CDA strongly predicted individual differences in behavioral estimates of working memory capacity. These and other studies suggest that working memory delay activity is a strong predictor of individual differences in working memory capacity.

Despite clear evidence that working memory delay activity is related to behavioral estimates of working memory, it is not clear what this activity represents. Early research suggested that, because the delay activity scaled with the number of items presented and reached asymptotic limits close to behavioral capacity, the neural activity was an online measure of the number of items that individuals could actively maintain (e.g., Todd & Marois,

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2004, 2005; Vogel & Machizawa, 2004). That is, individuals with larger capacities can hold more items leading to increased delay activity compared with individuals with smaller capacities, and these differences likely reflected differences in functioning of parietal areas. However, more recent work has suggested that the delay activity reflects, in part, frontal processes that control which items gain access to working memory and which items are filtered out (e.g., McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005). That is, individuals with more efficient control processes are better able to exclude items from gaining access to working memory than individual with poorer control processes. Evidence in support of this later position comes from studies demonstrating that, for higher working memory individuals, delay activity is sensitive to the number of relevant items (targets), whereas for low working memory, individuals delay activity is sensitive to both the number of relevant and irrelevant (distractor) items (McNab & Klingberg, 2008; Vogel et al., 2005). Furthermore, whereas activity in parietal areas seems to be linked with the number of items that can be maintained, frontal areas are linked with the ability to filter out irrelevant items (Voytek & Knight, 2010; McNab & Klingberg, 2008). Thus, these results suggest that individual differences in working memory delay activity might be related to both individual differences in the number of items that can be maintained as well as the ability to control attention and prevent distractors from gaining access to working memory.

Collectively prior work has shown that individual differences in working memory are related to individual differences in cognitive abilities. However, despite the ubiquity of this behavioral relationship, the evidence linking working memory function at the neural level and the individual's general cognitive ability is scant and somewhat indirect. That is, although there are existing demonstrations of neural activity correlating with gF scores (Burgess, Conway, Gray, & Braver, 2011; Gray, Chabris, & Braver, 2003), these relationships are generally observed only when participants must reject distractors (lure trials) and is not observed for neural activity during which the individual is simply maintaining multiple pieces of information in mind. Prior research has demonstrated that delay activity during working memory tasks is related to behavioral estimates of working memory, but the link between delay activity and broader cognitive abilities has not been well characterized. That is, will delay activity from one working memory task predict performance on other measures of working memory and, importantly, will this activity predict performance on other measures of cognitive abilities? Additionally, if delay activity is shown to predict performance on measures of cognitive abilities, it is important to understand the source of this prediction. It is possible that the relation is because of individual differences in the number of items that can be maintained (capacity), individual differences in controlling access to working memory (attention control), or some combination of both. The overall goal of this study was to examine individual differences in delay activity during visual working memory tasks to determine if this activity is an accurate predictor of an individual's overall cognitive abilities.

To examine these issues, we utilized a unique combination of psychometric and neurophysiological methods in which a large number of participants performed multiple cognitive ability measures thought to index different constructs. Specifically, participants completed multiple measures of capacity, attention control, gF, long-term memory, and working memory span. Participants also completed two change detection tasks, whereas ERPs were recorded providing two measures of CDA. We used latent variable techniques to examine the pattern of relations among the different cognitive ability constructs and CDA. This analytic approach enables clear conclusions about the links between cognitive constructs by ruling out problems with reliability or idiosyncratic task effects that could drive spurious associations between constructs. Therefore, multiple measures of each construct were used to create latent variables. Furthermore, given power issues in neuroscience designs (e.g., Button et al., 2013), we examined these relations with a much large sample size than is typically used. By examining a large number of participants and a large and diverse number of measures, we should be able to better characterize the nature of individual differences in working memory delay activity and its relation with cognitive abilities.

METHODS

Participants

The current data are a subset of data reported in Unsworth et al. (2014). In that data set, 171 participants were recruited from the participant pool at the University of Oregon and from the local Eugene, OR, community and received $10 per hour for their participation. Participants (63% women) were between the ages of 18 and 35 years (M = 21.4, SD = 3.5). Seven participants did not have usable ERP data, leaving a final data set of 164 participants.

Materials and Procedure

After signing informed consent, all participants completed color capacity, operation span, antisaccade, Raven, delayed free recall, shape capacity, symmetry span, and number series in Session 1. In Session 2, all participants completed space capacity, reading span, disengagement, Cattel's Culture Fair Test, paired associates, orientation capacity, picture source recognition, and motion capacity. In Session 3, participants completed the 48 drop task and the change detection task (in which ERPs were recorded). All tasks were administered in the order listed above.

MEASURES

Capacity

Color Task

Six color circles were simultaneously presented on the computer screen for 100 msec. The colors were randomly selected from 180 isoluminant colors that were evenly distributed along a circle in the CIE Lab color space (L = 70, a = 20, b = 38, and radius = 60). This specific color circle was selected to maximize the discriminability of the colors (Zhang & Luck, 2008). Participants remembered as many of them as possible over a 900-msec retention interval. After the retention interval, a gray probe was presented at one of the stimulus locations along with a color ring consisted of the 180 colors. Similar to the shape task, participants reported the color of the stimulus presented at the probe location by clicking the corresponding color on the color ring. The probe and the color ring stayed on the screen until a response was made. Participants completed 180 trials in total.

Orientation Task

Six clock face stimuli consisting of a ring and a radius-long clock hand were simultaneously presented on the computer screen for 100 msec. The orientation of each clock hand was randomly selected from 1° to 360°. Participants remembered as many orientations of the clock hands as possible over a 900-msec retention interval. After the retention interval, a probe ring was presented at one of the stimulus locations. Participants reported the orientation of the clock hand presented at the probe location by clicking on the rim of the ring. The probe stayed on the screen until a response was made. Participants completed 192 trials in total.

Motion Task

Six motion stimuli were simultaneously presented on the computer screen for 1 sec. A motion stimulus was a circular field of moving dots whose motion were 100% coherent (i.e., all the dots moved in one direction). The motion direction for each field was randomly selected from 1° to 360°. Participants remembered as many motion directions as possible over a 900-msec retention interval. After the retention interval, a probe ring was presented at one of the stimulus locations. Similarly to the orientation task, participants reported the motion direction of the stimulus presented at the probe location by clicking on the rim of the ring. The probe stayed on the screen until a response was made. Participants completed 180 trials in total.

Shape Task

Six shape stimuli were simultaneously presented on the computer screen for 1 sec. Shape stimuli were randomly chosen from a stimulus set borrowed from Zhang and Luck (2008). This stimulus set consisted of 180 shapes that vary on a circular continuum. Participants remembered as many shape stimuli as possible over a 900-msec retention interval. After the retention interval, a question mark was presented at one of the stimulus locations along with a shape ring that consisted of 12 shapes that were evenly spaced on the circular shape continuum. Participants reported the shape of the stimulus presented at the probe location by clicking the corresponding location on the shape ring. Note that participants' response was not limited to the locations of 12 shapes, but they were encouraged to click in between the shapes by extrapolation. Participants completed 180 trials in total.

Space Task

Six letter stimuli (A, B, C, D, E, and F) were simultaneously presented on an imaginary circle on the computer screen for 100 msec. Participants remembered as many locations of the stimuli as possible over a 900-msec retention interval. After the retention interval, a probe letter (A, B, C, D, E, or F) was presented at the center of the screen along with a gray ring at the location of the imaginary circle. Participants reported the location of the probe letter by clicking on the gray ring (see Figure 1). The probe and the ring stayed on the screen until a response was made. Participants completed 180 trials in total.

Change Detection Task

At the beginning of each trial, a central arrow cue was presented for 200 msec to indicate which side (left or right) of the screen to pay attention to. Left and right sides were equally likely to be cued. At 500 msec afterwards, either two or six stimuli were presented on each side of the screen for 150 msec, and participants remembered the stimuli presented on the cued side while ignoring the items on the other side. The minimum distance between the objects was 2°, each as at least 2.5° from fixation, but not more than 6.5° from fixation. After a 900-msec retention interval, one stimulus was presented on each side, and participants indicated if the stimulus on the cued side is identical to the original stimulus presented at that location. It was the same for a half of the trials. After responding, participants were allowed to blink or make eye movements until they initiated the next trial by a button press. The stimuli were colored squares (i.e., red, blue, green, magenta, cyan, yellow, white, and black) for a half of the trials and geometric shapes (rectangular or oval frames with two lines inside, borrowed from Fukuda, Vogel, Mayr, & Awh, 2010) for the other half. All the conditions were randomly intermixed, and participants performed 800 trials in total. Performance for set size 6 condition for each stimulus type was separately converted to a standard capacity estimate (K) by Cowan's (2001) formula as a dependent measure (shape K and

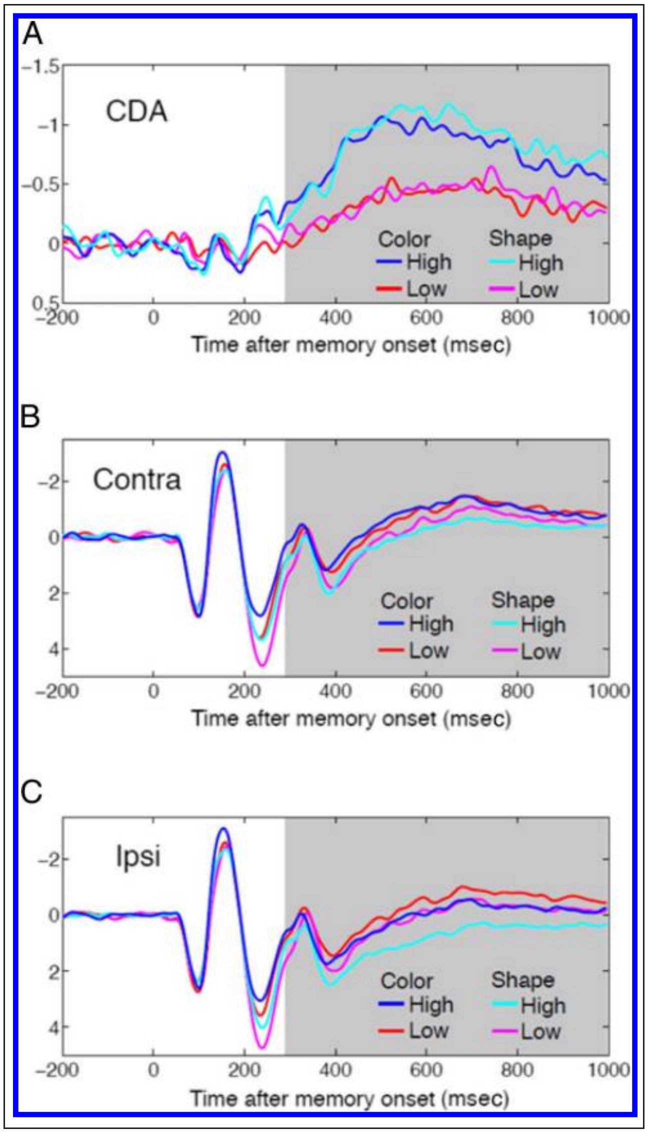


Figure 1. (A) CDA for high (top quartile) and low (bottom quartile) working memory participants for both the color and shape change detection tasks. (B) Contralateral waveforms high (top quartile) and low (bottom quartile) working memory participants for both the color and shape change detection tasks. (C) Ipsilateral waveforms high (top quartile) and low (bottom quartile) working memory participants for both the color and shape change detection tasks. The gray area indicates the time window with which the CDA amplitude was calculated.

color K). Specifically, $K = N \times (H - \mathrm{FA})$, where N is the relevant set size, H is the hit rate, and FA is the false alarm rate (Cowan, 2001). ERPs were recorded during these tasks (see below).

Attention Control

48 Drop Task

Participants were presented with either four or eight colored squares (set size 4 and set size 8 conditions) on the computer screen for 150 msec. Participants remembered as many colors as possible over a 900-msec retention interval. After the retention interval, one test colored square was presented at one of the original stimulus locations, and participants indicated if it was the same color as the original stimulus presented at that location. The test square had the same color in a half of the trials, and it was different for the other half of the trials. Participants completed 80 trials for each condition. On the basis of the performance, the number of the items held in working memory (K estimate) was calculated for each set size using a standard formula (Cowan, 2001). Prior research has shown that, when participants' capacities are overloaded, attention control is needed to regulate attention to prevent being captured by the overloading information (e.g., Cusak, Lehmann, Veldsman, & Mitchell, 2009). The dependent measure (48drop) was the difference between the K estimates for set size 4 and set size 8 (i.e., K for set size 4 − K for set size 8).

Antisaccade

Participants stared at a fixation point that was onscreen for a variable amount of time (200–2200 msec). A white "=" sign was then flashed either to the left or right of fixation (at 11.33° of visual angle) for 100 msec. This was followed by a 50-msec blank screen and a second appearance of the cue for 100 msec, making it appear as though the cue ("=") repeatedly flashed onscreen. Following another 50-msec blank screen, the target stimulus (a B, P, or R) appeared on screen for 100 msec, followed by masking stimuli (an H for 50 msec and an "8" that remained onscreen until a response was given). The participants' task was to identify the target letter by pressing a key for B, P, or R (the keys 1, 2, or 3) as quickly and accurately as possible (based on the original study by Kane, Bleckley, Conway, & Engle, 2001). Participants received, in order, 10 practice trials to learn the response mapping, 15 practice trials, and 40 test trials. Proportion correct was the dependent measure.

Disengagement Task

The disengagement task consisted of two parts. In the first part, the threshold target exposure duration was individually obtained. In this phase, participants were presented with four place holders for 500 msec. Then, a red square frame with a gap on one side was presented as a target in one of the place holders along with three more differently colored square frames (blue, green, or magenta) filling in the other place holders. After a target exposure duration (initially set to 500 msec), color patch masks were presented over all the place holders. Participants' task was to report the direction of the gap on the target. The exposure duration was titrated every trial to establish a threshold target exposure duration with which each individual can perform the task with about 75% accuracy (Fukuda & Vogel, 2011). Participants completed four blocks of 60 trials, and the average exposure duration for the last

20 trials in the last three blocks was used as the threshold target exposure duration.

In the second part, attentional disengagement was assessed. In this phase, participants performed essentially the same task with the fixed target exposure time defined for each individual. The difference however, was that, on one third of the trials, a colored square frame (distractor) was briefly presented on a periphery of a place holder before the target onset. A half of the distractors were red (contingent), and the other half were green, blue, or magenta. Participants completed 720 trials in total. The dependent measure was the difference in the accuracy for no distractor condition and contingent distractor condition (distractor to target SOA = 150 msec).

Long-Term Memory

Picture Source Recognition

During the encoding phase, participants were presented with a picture (30 total pictures) in one of four different quadrants onscreen for 1 sec. Participants were explicitly instructed to pay attention to both the picture (item) as well as the quadrant it was located in (source). At test, participants were presented with 30 old and 30 new pictures in the center of the screen. Participants were required to indicate if the picture was new or if it was old and what quadrant it was presented in via key press. Thus, on each test trial, participants pressed one of five keys indicating new, top left, top right, bottom left, or bottom right. Participants had 5 sec to press the appropriate key to enter their response. A participant's score was the proportion of correct responses.

Paired Associates

Participants were given three lists of 10 word pairs each. All words were common nouns, and the word pairs were presented vertically for 2 sec each. All word pairs were associatively and semantically unrelated. Participants were told that the cue would always be the word on top and the target would be on bottom. After the presentation of the last word, participants saw the cue word and "???" in place of the target word. Participants were instructed to type in the target word from the current list that matched cue. Cues were randomly mixed so that the corresponding target words were not recalled in the same order as they were presented. Participants had 5 sec to type in the corresponding word. A participant's score was proportion of items recalled correctly.

Delayed Free Recall

Participants recalled six lists of 10 words each. All words were common nouns that were presented for 1 sec each. After list presentation, participants engaged in a 16-sec distractor task before recall: Participants saw 8 three-digit numbers appear for 2 sec each and were required to write the digits in ascending order. After the distractor task, participants typed as many words as they could remember from the current list in any order they wished. Participants had 45 sec for recall. A participant's score was the total number of items recalled correctly.

Fluid Intelligence

Raven Advanced Progressive Matrices

The Raven is a measure of abstract reasoning. The test consists of 36 items presented in ascending order of difficulty. Each item consists of a display of 3 × 3 matrices of geometric patterns with the bottom right pattern missing. The task for the participant is to select, among eight alternatives, the one that correctly completes the overall series of patterns. Participants had 10 min to complete the 18 odd-numbered items. A participant's score was the total number of correct solutions.

Number Series

In this task, participants saw a series of numbers and were required to determine what the next number in the series should be. That is, the series followed some unstated rule, which participants were required to figure out to determine which the next number in the series should be. Participants selected their answer out of five possible numbers that were presented. Participants had 4.5 min to complete 15 test items. A participant's score was the total number of items solved correctly.

Cattell's Culture Fair Test

This task is composed of four separate and timed paper-and-pencil subtests. Participants were allowed 2.5–4 min to complete each subtest. In the first subtest (*Series*), participants saw 13 incomplete, progressive series of abstract shapes and figures, along with six alternatives for each, and selected the alternative that best completed the series. In the second subtest (*Classifications*), participants saw 14 problems composed of abstract shapes and figures and selected the two of the five that differed from the other three. Figures and shapes differed in size, orientation, or content. The third subtest was (*Matrices*) participants were presented with 13 incomplete matrices containing four to nine boxes that had abstract figures and shapes as well as an empty box and six choices. Participants had to infer the relationships among the items in the matrix and choose an answer that correctly completed each matrix. In the final subtest (*Conditions*) participants saw 10 sets of abstract figures consisting of lines and a single dot along with five alternatives. The participants had to assess the relationship among the dot, figures, and lines and choose the alternative in which a dot could be placed according to the same relationship. A participant's score was the total number of items solved correctly across all four subtests.

Working Memory Span

Ospan

Participants solved a series of arithmetic problems while trying to remember a set of unrelated letters (F, H, J, K, L, N, P, Q, R, S, T, Y). Before beginning the real trials, participants performed three practice sections. The first practice was simple letter span. A letter appeared on the screen, and participants were required to recall the letters in the same order as they were presented. In all experimental conditions, letters remained on-screen for 1000 msec. At recall, participants saw a 4×3 matrix of letters. Recall consisted of clicking the box next to the appropriate letters (no verbal response was required) in correct order. The recall phase was untimed such that participants had as much time as needed to recall the letters. After recall, the computer provided feedback about the number of letters correctly recalled in current set. Next, participants performed the math portion of the task alone. Participants first saw an arithmetic problem, consisting of a sequence of operations (e.g., $(1 \times 2) + 1 = ?$). Participants were instructed to solve the problem as quickly as possible and then click the mouse to advance to the next screen. On the next screen, a digit (e.g., "3") was presented and the participant was required to click either a "True" or "False" box depending on their answer. After each problem, participants were given accuracy feedback. The math practice served to familiarize participants with the math portion of the task as well as to calculate how long it would take that person to solve the math operations. Thus, the math practice attempted to account for individual differences in the time required to solve math operations without an additional storage requirement. After the math alone section, the program calculated each individual's mean time required to solve the equations. This time (plus 2.5 *SD*s) was then used as a time limit for the math portion of the main session for that individual. Participants completed 15 math problems in this session. The final practice session had participants perform both the letter recall and math portions together, just as they would do in the real block of trials. Here participants first saw the math problem, and after they clicked the mouse button indicating that they had solved it, they saw the letter to be recalled. If a participant took more time to solve the problem than their average time plus 2.5 *SD*, the program automatically moved on and counted that trial as an error. Participants completed three practice trials each of set size 2. After participants completed all of the practice sessions, the program progressed to the real trials. The real trials consisted of three trials of each set size, with the set sizes ranging from 3 to 7. This made for a total of 75 letters and 75 math problems. Note that the order of set sizes was random for each participant. The storage score was the number of correct items recalled in the correct position. The processing score was the mean of the median time to correctly complete the processing component of the task (processing time). See Unsworth, Redick, Heitz, Broadway, and Engle (2009) and Unsworth, Heitz, Schrock, and Engle (2005) for more task details.

Symspan

In this task, participants were required to recall sequences of red squares within a matrix while performing a symmetry judgment task. In the storage alone practice session, participants saw sequences of red squares appearing in the matrix and at recall were required to click the correct locations in the matrix in the correct order. In the symmetry judgment task alone session, participants were shown an 8×8 matrix with some squares filled in black. Participants decided whether the design was symmetrical about its vertical axis. The pattern was symmetrical approximately half of the time. Participants performed 15 trials of the symmetry judgment task alone. The same timing parameters used in the Ospan were used. The final practice session combined the matrix recall with the symmetry judgment task. Here participants decided whether the current matrix was symmetrical and then were immediately presented with a 4×4 matrix with one of the cells filled in red for 650 msec. At recall, participants recalled the sequence of red square locations in the preceding displays, in the order they appeared by clicking on the cells of an empty matrix. There were three trials of each set size with list length ranging from 2 to 5. The same scoring procedure as Ospan was used. See Unsworth, Redick, et al. (2009) and Unsworth et al. (2005) for more task details.

Rspan

Participants were required to read sentences while trying to remember the same set of unrelated letters as Ospan. As with the Ospan, participants completed three practice sessions. The letter practice was identical to the Ospan task. In the processing-alone session, participants were required to read a sentence and determine whether the sentence made sense (e.g., "The prosecutor's dish was lost because it was not based on fact. ?"). Participants were given 15 sentences, roughly half of which made sense. As with the Ospan, the time to read the sentence and determine whether it made sense was recorded and used as an overall time limit on the real trials. The final practice session combined the letter span task with the sentence task just like the real trials. In the real trials, participants were required to read the sentence and to indicate whether it made sense or not. Half of the sentences made sense, whereas the other half did not. Nonsense sentences were made by simply changing one word (e.g., "dish" from "case") from an otherwise normal sentence.

There were 10–15 words in each sentence. After participants gave their response, they were presented with a letter for 1000 msec. At recall, letters from the current set were recalled in the correct order by clicking on the appropriate letters. There were three trials of each set size with list length ranging from 3 to 7. The same scoring procedure as Ospan was used. See Unsworth, Redick, et al. (2009) and Unsworth et al. (2005) for more task details.

EEG Recording

ERPs were recorded in the change detection tasks using our standard recording and analysis procedures, including rejection of trials contaminated by blinks or large (>1°) eye movements, movement artifacts, or amplifier saturation (Vogel & Machizawa, 2004). We recorded from 22 standard electrode sites spanning the scalp, including International 10/20 sites F3, F4, C3, C4, P3, P4, O1, O2, PO3, PO4, T5, T6, OL, and OR (midway between O1/2 and T5/6). Trials containing ocular artifacts, movement artifacts, or amplifier saturation were excluded from the averaged ERP waveforms.

Measuring the CDA

As is now standard procedure for measuring the CDA (Vogel et al., 2005; Vogel & Machizawa, 2004), ERPs recorded at posterior parietal, lateral occipital, and posterior temporal electrode sites (PO3, PO4, T5, T6, OL, and OR) were first binned as either contralateral side or ipsilateral side with respect to the memorized hemifield. Because each pair of electrode sites showed the CDA, we maximized the signal-to-noise ratio of our measurements by averaging the channels for each bin to make a single pair of the contralateral and the ipsilateral channels. The CDA amplitude was calculated as the difference between the mean amplitude for the contralateral and the ipsilateral activity in 300–1000 msec time window after the onset of the memory array for set size 6 as has been done previously (Fukuda, Woodman, & Vogel, in press).

RESULTS

Descriptive statistics are shown in Table 1. Most measures had generally acceptable values of reliability, and most of the measures were approximately normally distributed with values of skewness and kurtosis under the generally accepted values. Correlations among the laboratory tasks and the CDA measures, shown in Table 2, were weak to moderate in magnitude with measures of the same construct generally correlating stronger with one another than with measures of other constructs, indicating both convergent and discriminant validity within the data. Replicating prior work (i.e., Vogel & Machizawa, 2004), we found a robust relation between CDA and performance on the change detection measures with the CDA correlating with behavioral performance around .30. As can be seen in Figure 1, high working memory individuals (here based on the top quartile) had reliably larger CDAs on both change detection tasks compared with low working memory individuals (here based on the bottom quartile). Importantly, not only did the CDA on the task in which it was measured predict performance (i.e., the CDA on color change detection predicted color change detection performance), but the CDA predicted performance on nearly all of the visual working memory measures in the study. Thus, the CDA is a reliable and

Table 1. Descriptive Statistics and Reliability Estimates for All Measures

Measure	*M*	*SD*	*Skew*	*Kurtosis*	*Reliability*
Ospan	58.41	14.06	−1.61	3.24	.80
Symspan	30.26	8.11	−.87	0.56	.78
Rspan	55.54	14.30	−1.12	1.28	.83
Color	2.42	0.92	0.18	0.25	.70
Shape	1.95	1.48	0.11	−1.14	.46
Space	4.74	0.86	−1.39	2.29	.81
Orient	1.91	1.01	−0.09	−0.55	.76
Motion	1.73	1.07	0.08	−0.56	.74
ColorK	1.90	0.77	0.01	0.23	.77
ShapeK	1.58	0.94	0.24	−0.42	.81
Disengage	0.09	0.07	0.21	0.25	.22
Anti	0.63	0.14	0.11	−0.26	.71
48Drop	0.34	1.00	−0.16	−0.09	.22
Picsour	0.76	0.15	−1.18	2.11	.80
PA	0.50	0.25	0.08	−1.05	.85
DFR	0.57	0.14	0.36	−0.13	.73
Raven	10.41	2.94	−0.12	0.08	.74
NS	9.59	2.61	0.04	−0.63	.70
CF	34.07	4.56	−0.46	1.82	.70
Color CDA	−0.64	0.54	−0.02	0.16	–
Shape CDA	−0.66	0.57	−0.17	−0.18	–

Ospan = operation span; Rspan = reading span; Symspan = symmetry span; Color = color capacity task; Shape = shape capacity task; Space = space capacity task; Orient = orientation capacity task; Motion = motion capacity task; ColorK = *K* estimate from color change deterction task; ShapeK = *K* estimate from shape change detection task; Disengage = disengagement task; Anti = antisaccde; 48Drop = 48 drop change detection task; Picsour = picture source recognition task; PA = paired associates task; DFR = delayed free recall; Raven = Raven Advanced Progressive Matrices; NS = number series; CF = Cattel's culture fair test; Color CDA = contralateral delay activity for color change detection task; Shape CDA = contralateral delay activity for shape change detection task. Reliability estimates are from the full data set from Unsworth et al. (2014).

Table 2. Correlations among All Measures

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. Ospan	–																				
2. Symspan	.58	–																			
3. Rspan	.72	.52	–																		
4. Color	.33	.22	.35	–																	
5. Shape	.26	.29	.25	.45	–																
6. Space	.24	.28	.35	.49	.33	–															
7. Orient	.21	.30	.27	.48	.47	.40	–														
8. Motion	.15	.28	.20	.36	.49	.35	.70	–													
9. ColorK	.10	.14	.23	.36	.28	.23	.36	.35	–												
10. Shapek	.18	.34	.22	.31	.40	.21	.41	.37	.61	–											
11. Disengage	−.13	−.18	−.12	−.15	−.32	−.29	−.35	−.33	−.17	−.15	–										
12. Anti	.36	.36	.30	.30	.30	.28	.33	.31	.15	.32	−.30	–									
13. 48Drop	−.15	−.12	−.12	−.33	−.35	−.10	−.25	−.29	−.31	−.34	.28	−.21	–								
14. Picsour	.20	.23	.24	.32	.27	.23	.39	.40	.22	.26	−.14	.37	−.20	–							
15. PA	.33	.18	.41	.25	.20	.17	.23	.25	.15	.18	−.04	.28	−.10	.41	–						
16. DFR	.30	.18	.41	.27	.26	.23	.26	.22	.14	.11	−.18	.34	−.07	.30	.54	–					
17. Raven	.24	.31	.34	.33	.27	.23	.31	.36	.27	.30	−.16	.30	−.20	.36	.34	.32	–				
18. NS	.17	.28	.22	.23	.28	.21	.40	.41	.06	.22	−.20	.40	−.07	.31	.16	.23	.35	–			
19. CF	.33	.35	.37	.29	.26	.16	.39	.39	.21	.29	−.17	.45	−.18	.45	.43	.33	.41	.38	–		
20. Color CDA	−.11	−.10	−.23	−.25	−.12	−.15	−.24	−.22	−.33	−.33	.06	−.24	.16	−.25	−.23	−.14	−.28	−.15	−.25	–	
21. Shape CDA	−.05	−.15	−.17	−.15	−.08	−.16	−.21	−.20	−.26	−.34	.12	−.24	.14	−.27	−.16	−.06	−.29	−.20	−.28	.65	–

Ospan = operation span; Rspan = reading span; Symspan = symmetry span; Color = color capacity task; Shape = shape capacity task; Space = space capacity task; Orient = orientation capacity task; Motion = motion capacity task; ColorK = *K* estimate from color change detection task; ShapeK = *K* estimate from shape change detection task; Disengage = disengagement task; Anti = antisaccde; 48Drop = 48 drop change detection task; Picsour = picture source recognition task; PA = paired associates task; DFR = delayed free recall; Raven = Raven Advanced Progressive Matrices; NS = number series; CF = Cattel's culture fair test; Color CDA = contralateral delay activity for color change detection task; Shape CDA = contralateral delay activity for shape change detection task. Correlations >.15 are significant at $p < .05$ level.

valid measure of working memory delay activity that predicts behavioral estimates of visual working memory across a diverse array of working memory tasks.

Although the zero-order correlations provide some initial indications of relations between CDA and cognitive abilities, these correlations can be hampered by reliability issues and idiosyncratic task effects and thus do not provide the best estimate of the relation. Therefore, to better determine the structure of the data, we used confirmatory factor analysis. Confirmatory factor analysis is an analytic tool that examines the factor structure of the data by testing whether the data fit a hypothesized measurement model. Confirmatory factor analysis is used to create latent variables to examine underlying cognitive factors without the influence of idiosyncratic task effects. This method extracts the common variance shared across similar measures and provides truer estimates of potential relations. This approach allowed a more rigorous and detailed characterization of how delay activity is linked with broader cognitive abilities.

First, we specified a measurement model to determine if capacity, attention control, long-term memory, gF, and working memory span were related to one another and related to the CDA. Therefore, in this model, all of the capacity measures loaded onto a capacity factor, all of the attention control measures loaded onto an attention control factor, all of the long-term memory measures loaded onto a long-term memory factor, all of the gF measures loaded onto a gF factor, and the two CDA measures loaded on a CDA factor. The factors were all allowed to correlate with each other. Note that to improve model fit in all models, we allowed the error variances for the Color and Shape *K* measures to correlate.

The overall fit of the model was good ($\chi^2(173) = 283.33$, $p < .01$, RMSEA = .06, NNFI = .96, CFI = .96, AIC = 399.33).[1] Shown in Figure 2 is the resulting model.

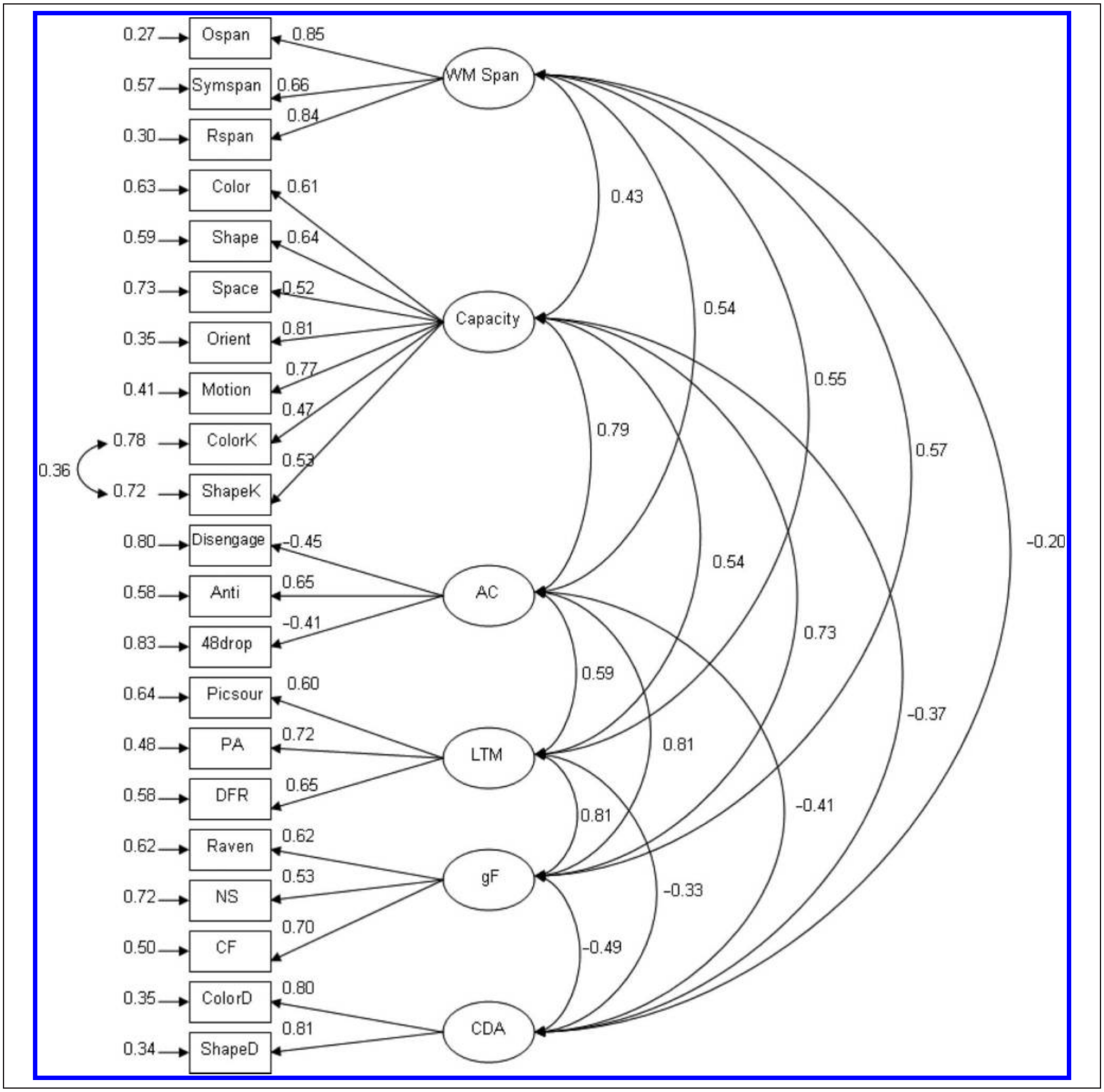


Figure 2. Model for working memory span (WM Span), capacity, attention control (AC), long-term memory (LTM), gF, and CDA. Paths connecting latent variables (circles) to each other represent the correlations between the constructs, the numbers from the latent variables to the manifest variables (squares) represent the loadings of each task onto the latent variable, and the numbers appearing next to each manifest variable represent error variance associated with each task. All loadings and paths are significant at the $p < .05$ level.

As can be seen, all measures loaded significantly on their construct of interest and all of the latent variables were moderately related to one another. Specifically, consistent with prior work with this data, all of the behavioral measures were moderately to strongly related at the latent level (Unsworth et al., 2014). Importantly, the two CDA measures loaded significantly and substantially on the CDA factor, and the CDA factor was related to the cognitive ability factors. That is, individual differences in the amplitude of the CDA during the delay period of a working memory task were significantly related to a number of cognitive ability factors. Specifically, as predicted, the CDA was related to both capacity and attention control, suggesting that behavioral estimates of working memory capacity and attention control were significantly related to delay activity indexed by the CDA. Furthermore, the CDA had a strong relation with gF and weaker relations with long-term memory and performance on working memory span tasks. Thus, neural activity during a working memory task where participants are required to maintain items over a delay was significantly related to a number of broader cognitive abilities.

Next, we utilized structural equation modeling to better examine these relations. In structural equation modeling, the latent variables created from the measurement model are used to better test structural relations (such as mediation models) among the latent variables. In the first structural equation model, we tested a model to determine if individual differences in the number of items that can be maintained would mediate the relation between the CDA and gF. That is, do individual differences in the capacity of working memory completely account for the relation between CDA and gF? To test this, we specified a model in which CDA predicted capacity, CDA predicted gF, and capacity predicted gF. If capacity accounts for the relation between CDA and gF, then we should see that CDA is related to capacity, capacity is related to gF, but CDA does not have a direct link to gF. If capacity does not fully mediate the relation between CDA and gF, then the direct path between CDA and gF should be significant. The fit of the model was good ($\chi^2(50) = 83.41$, $p < .01$, RMSEA = .06, NNFI = .96, CFI = .97, AIC = 139.41). As seen in Figure 3A, CDA predicted capacity, and capacity predicted gF, but the path from CDA to gF remained significant even after taking capacity into account. This suggests that capacity partially mediated the relation between CDA and gF (indirect effect = −.23, $p < .05$), but CDA still predicted gF after taking into account capacity. This suggests that potentially some other factor is needed to fully account for the relation between CDA and gF. Given prior research which has suggested that the CDA partially reflects attention control abilities (Drew & Vogel, 2008; Vogel, McCollough, & Machizawa, 2005; Vogel & Machizawa, 2004), it is likely that individual differences in both capacity and attention control account for variability in CDA and account for the relation between CDA and gF. To examine this, we specified another model in which CDA predicted capacity, attention control, and gF, and capacity and attention control both predicted gF. If the CDA reflects both capacity and attention control, then the CDA should be significantly related to both, and if individual differences in capacity and attention control jointly account for the relation between CDA and gF, then the relation between CDA and gF should not be significant with capacity and attention control in the model. The fit of the model was good ($\chi^2(84) = 180.44$, $p < .01$, RMSEA = .08, NNFI = .92, CFI = .93, AIC = 252.44). As shown in Figure 3B, CDA predicted both capacity and attention control suggesting that individual differences in both account for CDA. Importantly, once attention control was added into the model, CDA no longer accounted for unique variance in gF (indirect effect = −.41, $p < .05$). These results suggest that CDA reflects both capacity and attention control abilities, and both of these factors are needed to account for the relation between CDA and gF.

Next, we examined similar models with working memory span and long-term memory to determine if both capacity and attention control were needed to account for the relations with CDA. To examine the relation with working memory span, we specified a model where CDA predicted capacity, attention control, and working memory span, and capacity and attention control predicted working memory span. The fit of the model was acceptable ($\chi^2(84) = 207.57$, $p < .01$, RMSEA = .09, NNFI = .90, CFI = .92, AIC = 279.57). As seen in Figure 3C and similar to what was found with gF, once individual differences in

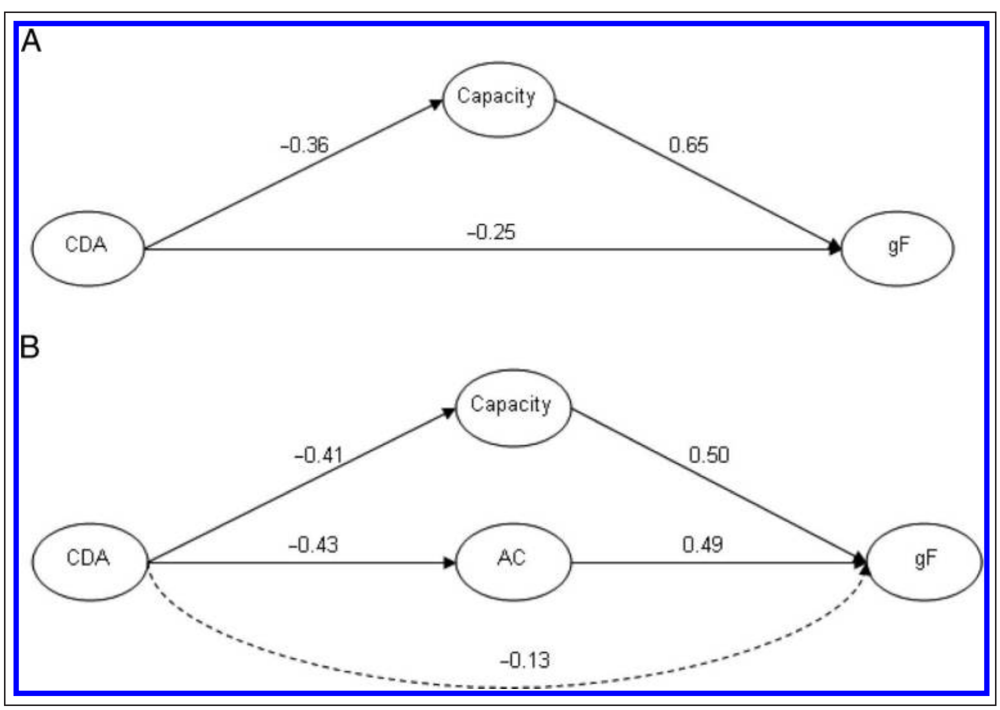
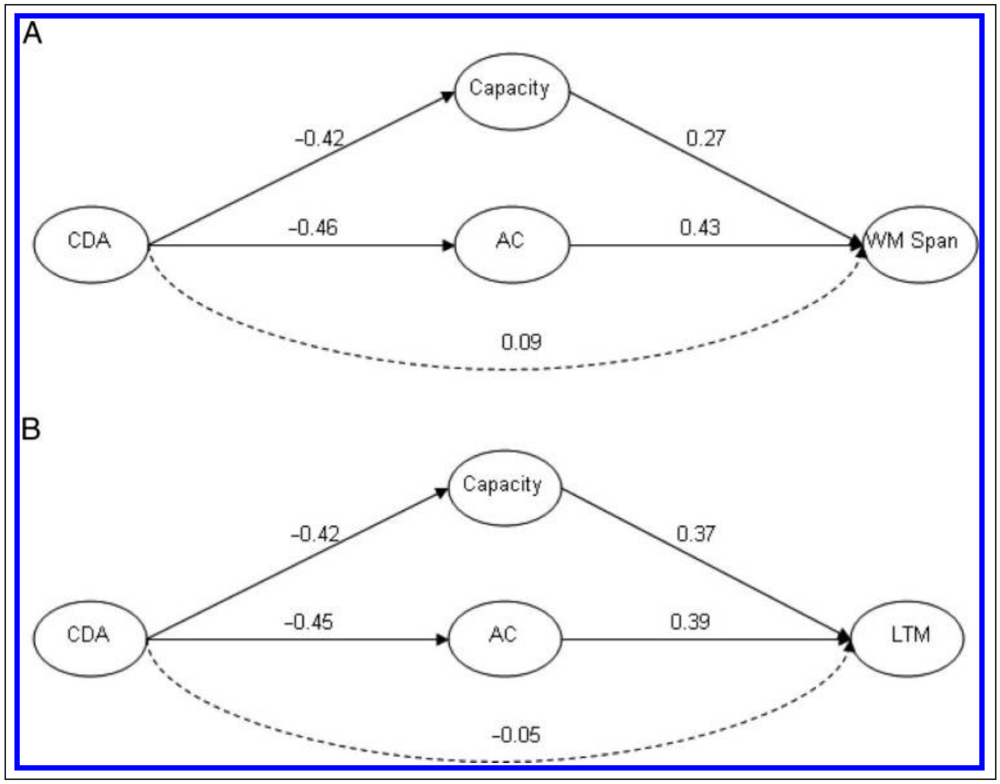


Figure 3. (A) Structural equation model for CDA, capacity, and gF. (B) Structural equation model for CDA, Capacity, attention control (AC), and gF. Single-headed arrows connecting latent variables (circles) to each other represent standardized path coefficients indicating the unique contribution of the latent variable. Solid lines are significant at the $p < .05$ level, and dotted lines are not significant at the $p < .05$ level.

Figure 4. (A) Structural equation model for CDA, capacity, attention control (AC), and working memory span (WM span). (B) Structural equation model for CDA, capacity, attention control (AC), and long-term memory (LTM). Single-headed arrows connecting latent variables (circles) to each other represent standardized path coefficients indicating the unique contribution of the latent variable. Solid lines are significant at the $p < .05$ level, and dotted lines are not significant at the $p < .05$ level.



both capacity and attention control were taken into account, CDA no longer predicted working memory span (indirect effect = $-.31$, $p < .05$). A similar result was found when examining long-term memory. The fit of the model was acceptable ($\chi^2(84) = 191.35$, $p < .01$, RMSEA = .09, NNFI = .90, CFI = .92, AIC = 263.35). As shown in Figure 3D, capacity and attention control jointly mediated the relation between CDA and long-term memory (indirect effect = $-.33$, $p < .05$). These results demonstrate that the CDA is related to individual differences in higher-order cognitive abilities, and this relation is due to variation in both the number of items that can be maintained (capacity) and the ability to control the contents of working memory (attention control; Figure 4).

DISCUSSION

Multiple studies have shown that neural activity during a working memory delay period can predict performance in the measured task, but none of this work has established whether this delay activity is also linked with individual differences in broader cognitive abilities. Here, we used a unique combination of electrophysiological recordings and latent variable techniques to demonstrate that delay activity is indeed directly linked with multiple distinct cognitive abilities and the broader construct of gF. The CDA is reliable and stable with measures of the CDA correlating and loading on a common CDA factor that explains variations in gF based on variations in attention control and working memory capacity. Although working memory tasks require a complex sequence of events for accurate performance (i.e., encoding processes, maintenance processes, and retrieval and decision processes), here we show that neural activity during the maintenance period alone is a powerful predictor of not only working memory but also intellectual abilities. Thus, the CDA was not simply tied to the idiosyncratic demands of the task during which it was recorded. Instead, this neural activity recorded during a working memory task in one session was a successful predictor of task performance in a broad array of contexts even when measured in a session over a week later. These findings suggest that the CDA reflects the operation of core cognitive processes that support a broad range of cognitive abilities.

The finding that CDA activity predicts broader cognitive abilities dovetails with existing literature and modern theory, but a robust demonstration with rigorous analytic techniques has been lacking. Our findings establish this link between neural activity and cognitive ability and bring a modest amount of unity between the behavioral and neural literatures on working memory and intelligence. Furthermore, using structural equation modeling techniques, it was shown that the relations between the CDA and cognitive abilities was because of both the number of items an individual can maintain (capacity) and the ability to control access to working memory (attention control). Thus, individual differences in capacity and attention control jointly account for the relation between working memory delay activity and cognitive abilities.

These results suggest a two-factor model of CDA activity in which one factor that gives rise to individual differences in the CDA is the overall capacity an individual has. Capacity refers to the ability to simultaneous apprehend multiple items in an active state to facilitate the processing of task-relevant information. Capacity is needed to ensure that multiple distinct items can be individuated and maintained in an active state and likely reflects functioning of parietal areas (in particular the intraparietal sulcus; Todd & Marois, 2005). The amplitude of the CDA is modulated, in part, by the number of items that an individual can distinctly represent and actively maintain over the delay (Anderson, Vogel, & Awh, 2013; Tsubomi, Fukuda, Watanabe, & Vogel, 2013; Drew, Horowitz, Wolfe, & Vogel, 2011, 2012; Drew, McCollough, & Vogel, 2006). The other factor that gives rise to the CDA is attention control. Attention control refers to the ability to protect items that are being actively being maintained in working memory, to effectively select target representations for active maintenance, and to filter out irrelevant distractors and prevent them from gaining access to working memory. Thus, attention control acts as a gatekeeper and protector of items being held in working memory and likely reflects functioning of frontal areas (Burgess et al., 2011; Voytek & Knight, 2010; McNab & Klingberg, 2008; Vogel & Machizawa, 2004). The CDA is modulated, in part, by the ability of an individual to select which items gain access to working memory and by the ability to allocate attention to items currently within working memory to protect them from internal and external distraction (Fukuda & Vogel, 2009; Drew & Vogel, 2008; Vogel et al., 2005). Thus, the CDA and individual differences in CDA amplitude reflect both the number of items that can be maintained in parietal areas and the ability to control the contents of working memory via frontal control processes. Individuals can differ in either the number of items that can be maintained, the ability to control attention, or both. That is, some individuals will have limits in overall capacity, which will lead to lower CDAs, whereas other individuals will have limits in attention control, which will also lead to lower CDAs. Importantly, these differences will also lead to individual differences in cognitive abilities such as gF. Combining psychometric and neuroscience methods provides a promising means to examine the cognitive and neural mechanisms that give rise to individual differences in working memory and cognitive abilities.

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Note

1. Model fits were assessed via the combination of several fit statistics. These include chi-square, root mean square error of approximation, standardized root mean square residual, the non-normed fit index (NNFI), and the comparative fit index (CFI). The chi-square statistic reflects whether there is a significant difference between the observed and reproduced covariance matrices. Therefore, nonsignificant values are desirable. However, with large sample sizes even slight deviations can result in a significant value. Also reported is the root mean square error of approximation (RMSEA), which reflects the average squared deviation between the observed and reproduced covariances. In addition, NNFI and CFI, which compare the fit of the specified model to a baseline null model, are reported. NNFI and CFI values greater than .90 and RMSEA values less than .10 are indicative of acceptable fit (Kline, 1998). Finally, the Akaike information criterion (AIC) examines the relative fit between models in which the model with the smallest AIC is preferred.

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