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Distributed alpha networks underlie individual differences in memory performance

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Abstract

Episodic memory, our ability to remember specific events, varies considerably across individuals. However, little is known about the neural basis of this variability. To address this issue, we investigated the role of distributed networks of oscillatory activity, as measured through electroencephalography (EEG). We observed that individual differences in alpha network structure reliably predict individual memory capacity. Specifically, individuals whose network profiles during encoding were most different from their resting state networks exhibited greatest subsequent memory performance, suggesting that optimal information processing requires substantial shifts in large-scale oscillatory organization. Furthermore, these results were not observed in circumscribed topographical regions or individual connections, indicating that distributed network approaches were more sensitive to functional processes than more conventional methods. These findings uncover a physiological correlate of individual differences in episodic memory and demonstrate the utility of multivariate EEG techniques to uncover brain-behavior correlates.

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Introduction

Episodic memory, our ability to remember events, locations, and associated contextual and emotional information, is one of the defining features of human cognition (Tulving 2002). Yet, the capacity to store and retrieve episodic details is highly variable across individuals (Loftus et al. 1992; Palombo et al. 2013). Magnetic resonance imaging (MRI) studies have demonstrated that this behavioral heterogeneity is rooted in neuroanatomical variation (Rudebeck et al. 2009; Poppenk and Moscovitch 2011), hemodynamic activity changes (Wig et al. 2008), and altered patterns of coordinated activity between key memory structures (Wang et al. 2010; Schedlbauer et al. 2014; King et al. 2015; Sheldon et al. 2016). However, MRI studies do not afford the temporal precision to examine the rapid fluctuations of neural activity that are fundamental to many aspects of cognition (Buzsaki 2004; Watrous et al. 2015).

Indeed, neural oscillations are strongly linked to episodic memory function. At the level of memories for single items, oscillatory power during both encoding (Sederberg et al. 2003; Guderian et al. 2009; Hanslmayr et al. 2009; Morton et al. 2013; Staudigl and Hanslmayr 2013) and retrieval (Düzel et al. 2003; Jacobs et al. 2006; Gruber et al. 2008; Khader and Rösler 2011) is related to memory accuracy. Moreover, successful remembering relies on the precise reinstatement of oscillatory encoding patterns, both in terms of topography and spectral composition (Manning et al. 2011; Jafarpour et al. 2014; Yaffe et al. 2014; Waldhauser et al. 2016). An additional determinant of successful memorization is the coordination of oscillatory activity between cortical regions (Weiss and Rappelsberger 2000; Fell et al. 2001; Summerfield and Mangels 2005a, 2005b; Burke et al. 2013; Watrous et al. 2013; Höhne et al. 2016). This approach has been extended to assess simultaneous electrophysiological interactions among large numbers of interconnected regions. This work has demonstrated the importance of global network structure for memory (Burke et al. 2013; Watrous et al. 2013) and suggests that large-scale approaches may be particularly sensitive to functional processes that are distributed across many brain regions rather than localized (Kriegeskorte 2008; Park and Friston 2013; Pessoa 2014; Petersen and Sporns 2015).

In contrast to this emerging understanding of what determines the fate of individual memories, little is known about the oscillatory basis of memory differences between individuals. Recent data suggest that differences in local alpha power during encoding predict memory capacity (Park et al. 2014; Jiang et al. 2015). Interestingly, alpha activity in the "offline" resting interval between training and testing is also correlated with memory performance (Brokaw et al. 2016), as is peak alpha frequency measured in the absence of any preceding task (Klimesch et al. 1990; Grandy et al. 2013). Together, these studies suggest that spontaneous oscillatory dynamics, particularly in the alpha range, may be a physiological marker of individual memory capacity. Typically, however, the relation between spontaneous activity and memory performance is assessed only once, obscuring whether intrinsic activity indexes momentary memory performance or a stable trait.

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In a companion paper (Cox et al. 2016), we offer an in depth characterization of the network structure of distributed oscillatory activity across and within individuals, as measured by electroencephalography (EEG). Briefly, we found that different individuals have distinct, stable, and identifiable network profiles, even though oscillatory organization demonstrated robust group-level correspondences for different frequency bands and oscillatory features. Moreover, we analyzed network structure during periods of memory encoding and during periods of rest, observing both overall differences and within-subject correspondences between these behavioral states. Crucially, we collected these data at two points in time, separated by ~6 months, allowing for independent replication of many of our findings.

In the current report, we use the same dataset to examine whether the individual oscillatory profiles described in (Cox et al. 2016) serve a functional role. Based on the aforementioned evidence that episodic memory networks are distributed widely across the brain (Burke et al. 2013; Watrous et al. 2013; King et al. 2015), and that oscillatory activity during encoding (Park et al. 2014; Jiang et al. 2015) and rest (Klimesch et al. 1990; Grandy et al. 2013; Brokaw et al. 2016) may be sensitive to aspects of memory performance, we here investigate whether large-scale oscillatory networks serve as a marker for memory processing. Note that our focus is on oscillatory profiles derived from continuous data, not stimulus-evoked responses. Given that several different frequency bands have been implicated in episodic memory performance (Düzel et al. 2010; Hanslmayr et al. 2012), and that distinct oscillatory metrics capture unique aspects of neuronal activity (Schyns et al. 2011; Burke et al. 2013; Arnulfo et al. 2015; Watrous et al. 2015; Bastos and Schoffelen 2016), we analyze networks across the theta (3-7 Hz), alpha (8-12 Hz), beta (13-30 Hz) and gamma (32-60 Hz) bands, separately for power, amplitude correlation, and phase synchrony profiles. While power indexes the extent of localized activity at a particular frequency, amplitude correlation and phase synchrony reflect the extent of coordinated activity between regions (Cohen 2014). More specifically, amplitude correlation indexes relatively slow co-fluctuations in signal amplitude, while phase synchrony captures cycle-by-cycle variations in phase alignment between neural regions; these metrics may thus have different sensitivity to functional processes (Watrous et al. 2015). Harnessing recordings from two separate visits, we are able to explore the large search space in data from one visit and to validate the reliability and stability of any observed relations in data from the second visit.

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Materials and Methods

A detailed overview of methods, including the task and network similarity analyses, can be found in our companion report (Cox et al. 2016). Here, we report analyses specific to the present study.

We performed several correlations between memory performance (immediate recall session A: average of $recall_{A1}$ and $recall_{A2}$; immediate recall session C: $recall_{C}$; retention

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from session A to B: average of $recall_{B1}/recall_{A1}$ and $recall_{B2}/recall_{A2}$) and network similarity, as indexed by Pearson correlation coefficients, for all network types, both within and between behavioral states. Because these correlation coefficients are not normally distributed, we first Fisher-z transformed them. We then correlated memory performance with (transformed) network similarity using the *robustfit* procedure in Matlab in order to de-weight the influence of outliers on the statistical relation (*bisquare* weighting option). Because this procedure does not return estimates of strength of correlation (such as Pearson's R), we additionally report R values as obtained by standard Pearson correlation analyses. In general, R values (for the memory-network similarity associations) corresponded well with the results from the robust regression, although in one particular instance an outlier resulted in a Pearson R of -0.01 although the robust regression indicated a significant negative relation.

Given the multiple comparison problem associated with the many correlations that we intended to run, we made use of the fact we had two separate sessions with memory scores available. We used Session A data to search for correlations between immediate recall and 36 network similarity variables (4 frequency bands, 3 oscillatory metrics, 3 behavioral states [rest-rest, task-task, encoding-rest]) in an exploratory manner ($P<0.05$, uncorrected). We then used Session C to determine whether these correlations could be confirmed ($P<0.05$) for encoding-rest and rest-rest correlations. For task-task network similarity, Session A and Session C task segments were of different kinds, with two encoding segments for Session A, and an encoding and control segment for Session C. Thus, encoding-encoding and encoding-control relation with memory could each be made in only one session. Similarly, control-rest was only available for Session C. Based on results implicating only alpha power and amplitude correlation networks, we then limited ourselves to these oscillatory features for Session C encoding-control and control-rest analyses. An analogous approach was used for the correlations between memory and topographical power and connectivity, where we similarly required effects to be present for both sessions. The relation between network similarity and memory retention was wholly exploratory, and was not corrected for multiple comparisons.

We observed that encoding-rest similarity of alpha networks was negatively correlated with memory performance, indicating that greater alpha network reorganization between these two states predict better memory performance. We asked whether subjects with similar memory performance showed similar shifts in network organization from encoding to rest. To determine this, we first calculated, on an individual subject basis, how much every connection (for amplitude correlation), or electrode (for power), contributed to that individual's encoding-rest similarity score. Using z-scored power estimates and connection strengths, we could calculate each element's contribution to network similarity as the product of that element's encoding and rest values. That is, the Pearson correlation is computationally equivalent to the sum of all z-scored products, with elements having similar z-scores in rest and encoding networks increasing the similarity index, and elements with less similar scores leading to a reduction of the correlation coefficient. In this manner, we extracted for each

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individual a "contribution pattern" for every unique pair of encoding-rest networks (14 pairs in total), indicating how much every electrode or connection boosted or impaired network similarity between encoding and rest. Averaging across network pairs, we then treated these contribution patterns as typical networks, and asked whether the network similarity of contribution patterns was more similar between individuals with similar memory scores than expected by chance. Specifically, we sorted participants by performance and averaged contribution-pattern similarity values between neighboring subjects. We then created a null distribution by randomizing subject order 1,000 times, thus destroying the memory-based ranking of the original observation, and recalculating the average similarity of adjacent contribution patterns at every iteration. Finally, we z-scored the original observation with respect to this null distribution, and calculated the associated P value.

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Results

For a detailed overview of experimental procedures, see (Cox et al. 2016). Briefly, 21 healthy volunteers completed the first visit of this study and 14 returned for a second visit, 3-8 months later. During the first visit, subjects underwent high-density EEG recording during several resting-state segments organized around the encoding and retrieval of two runs of visuospatial association in two sessions, separated by 2 h (Figure 1, Sessions A and B). Visit 2 (Session C) consisted of several additional resting-state segments surrounding another visuospatial memory task and a non-learning control task.

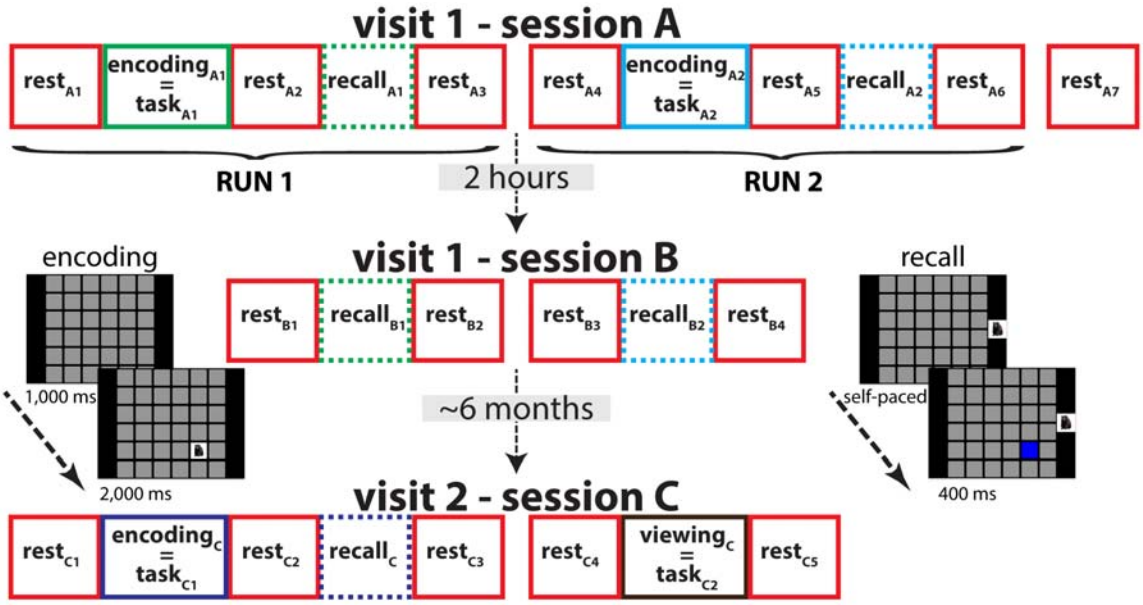

Figure 1. Protocol overview. Sessions A and B were separated by 2 hours, while Session C took place after approximately 6 months. In Session A, there were encoding and recall blocks interspersed with rest periods. In Session B, additional recall blocks were interspersed with rest. In Session C, subjects completed an additional memory task as well as a "viewing" control task

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with no memory component. EEG from rest and task blocks (solid lines) but not recall blocks (dashed) was analyzed. During encoding, 36 stimuli were presented, one at a time, each on a unique grid location. During retrieval, subjects were cued by presentation of a studied stimulus on the right of the screen, and instructed to select the corresponding location.

Memory performance

During Session A, subjects memorized picture locations for distinct semantic categories (animals and vehicles) in two separate blocks, with order counterbalanced, and retrieved them 5 minutes after their respective encoding block. Retrieval accuracy averaged across the two blocks was 52 ± 22 % (chance = 3%), although there was a practice effect, with better performance on the second block than on the first (59 ± 23% vs. 46 ± 24%; t(20)=-3.5, P=0.002). Scores between the two Session A blocks were highly correlated (R=0.74, P=0.0001), indicating similar improvement across subjects. In a 2x2 mixed ANOVA with between-subject factor ORDER (animal or vehicles first) and within-subject factor RUN (first/second), no significant main effect of ORDER or of ORDER/RUN interaction was found (both P>0.4), but there was a significant main effect of RUN (F(1,19)=12.0, P=0.003) corresponding to the practice effect noted above. Performance for the two semantic categories (independent of order) did not differ substantially either (t(20)=0.2, P=0.82), but was again highly correlated within subjects (R=0.62, P=0.003).

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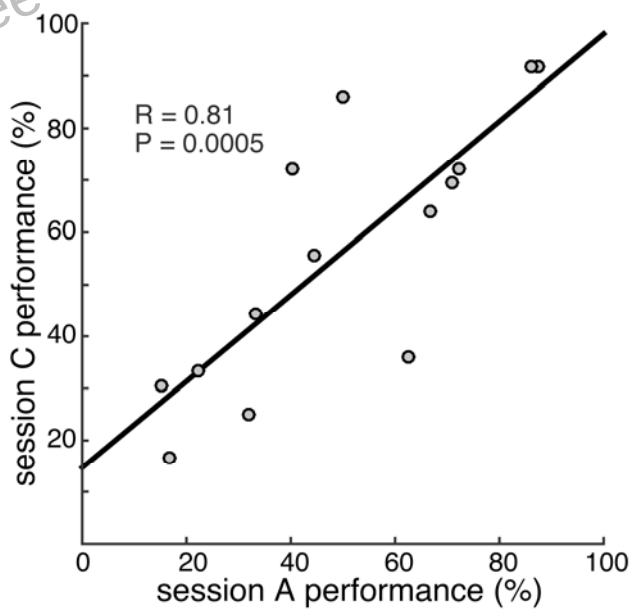

Figure 2. Trait-like memory performance. Memory performance was highly correlated across a 3-8 month period, indicating individual mnemonic efficacy is a robust trait. Session A performance averaged across the two runs. N=14.

At follow-up Session C several months later (see *Retention* for results concerning Session B of Visit 1), 14 returning subjects memorized and retrieved a third set of visuospatial associations. They also performed a non-learning control task where the

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same stimulus was repeatedly presented several times at each location. They were told to simply view these presentations and that there would not be any memory test. The order of the learning and control tasks was counterbalanced across subjects and did not affect performance (56.3 ± 23.1% vs. 56.3 ± 29.5 %; t(12)=0, P=1). Paired t-tests for these 14 subjects indicated that Session C performance was similar to average Session A scores (56 ± 25% vs. 50 ± 25%; t(13)=1.5, P=0.15), and that these scores were highly correlated within subjects across this 3-8 month period (R=0.81, P=0.0005; Figure 2). Together, these findings indicate that individual variation in episodic memory is a robust trait.

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Distributed oscillatory alpha networks predict memory

We analyzed the distributed pattern of oscillatory activity for every ~5 minute resting-state and task block. In four separate frequency bands (theta, alpha, beta, and gamma), we determined power at every electrode, and amplitude correlation and phase synchrony between each of 1548 non-adjacent pairs of electrodes (out of 1770 total pairs). This resulted in power vectors of length 60 and connectivity vectors of length 1548, reflecting the network configuration of oscillatory activity across the scalp. In what follows, we refer to these vectors simply as networks.

We calculated the degree of similarity between two networks as their Pearson correlation. We then averaged these correlation coefficients across network pairs of interest. Specifically, we determined network similarity among all rest segments, between the two task segments, and between all task-rest pairs. This yielded, for every individual, frequency band, and oscillatory metric, three network similarity scores: within-rest, within-task, and task-rest. We computed these scores separately for Sessions A and C. Note that, for Session A, task-rest similarity is equivalent to encoding-rest similarity, while for Session C only one of the two tasks concerned memory encoding. Hence, for Session C, we further determined encoding-rest, control-rest, and encoding-control similarity. Similarity scores were then Fisher transformed to render them more normally distributed.

We averaged every individual's Session A memory scores across the two retrieval blocks, and used a robust regression procedure to identify links between memory and network structure. Because robust correlation procedures do not return estimates of explained variance, we report R values stemming from the standard Pearson correlation in conjunction with P values from the robust fitting procedure. We used data from Session A to identify correlations between network similarity and memory performance that were significant at uncorrected $P < 0.05$. We then validated these exploratory findings using data from Session C as an independent test of these associations (see Table 1 for all significance values).

Using this approach, we found that neither within-rest network similarity, nor within-task network similarity were reliably related to immediate memory retrieval, suggesting

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that the stability of rest or task networks across multiple 5-minute periods is not meaningfully related to memory processes. However, during both sessions A and C, we observed significant associations between retrieval accuracy and the similarity *between* encoding and rest networks. Memory performance was best for subjects whose encoding network was most distinct from their rest network. Specifically, we found negative correlations between memory and network similarity based both on alpha amplitude correlation (Session A: R=-0.35, P=0.019; Session C: R=-0.66, P=0.004; Fig. 3AC) and on alpha power (Session A: R=-0.59, P=0.002; Session C: R=-0.67, P=0.014; Fig. 3BD).

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		ENCODING-REST		TASK-TASK		REST-REST	
oscillation metric	*frequency/session*	A	C	A encoding-encoding	C encoding-control	A	C
phase synchrony	theta	0.75	-	0.53	0.21	0.43	-
	alpha	0.13	-	0.40	0.08	0.71	-
	beta	0.78	-	0.39	0.07	0.30	-
	gamma	0.72	-	0.38	0.08	0.72	-
amplitude correlation	theta	0.76	-	0.70	0.26	0.68	-
	alpha	**0.019****	**0.004****	0.93	**0.03***	0.72	-
	beta	0.93	-	0.67	0.10	0.95	-
	gamma	0.17	-	0.28	0.23	0.41	-
power	theta	0.19	-	0.90	0.19	0.71	-
	alpha	**0.002****	**0.014****	0.40	**0.002***	**0.038***	0.62
	beta	0.64	-	0.75	0.13	**0.012***	0.90
	gamma	0.87	-	0.68	0.46	0.78	-

Table 1. Significance values for correlations between memory and network similarity. Bold values indicate P-values <0.05. For encoding-rest and rest-rest, Session C values are only given when P< 0.05 for Session A. For task-task, Sessions A and C consist of different behavioral states and values are provided for both sessions. * indicates significance in a single session, and ** indicates significance for both sessions.

We next asked, for subjects who completed both visits, whether encoding-rest difference assessed on one visit was predictive of memory performance in the other. Indeed, memory ability was negatively correlated with the similarity of rest and encoding networks across sessions in both directions for alpha power topographies (similarity$_C$ *vs.* memory$_A$: R=-0.67, P=0.019; similarity$_A$ *vs.* memory$_C$: R=-0.61, P=0.014), and in one direction for alpha amplitude correlation patterns (similarity$_C$ *vs.* memory$_A$: R=-0.70, P=0.01; but similarity$_A$ *vs.* memory$_C$: R=-0.26, P=0.39). Of note, we previously demonstrated that oscillatory network structure, while different from one individual to another, is highly stable across many months. Thus, these findings suggest that alpha encoding-rest similarity is a robust physiological marker of individual trait differences in memory performance, and not merely a reflection of patterns present during the encoding session.

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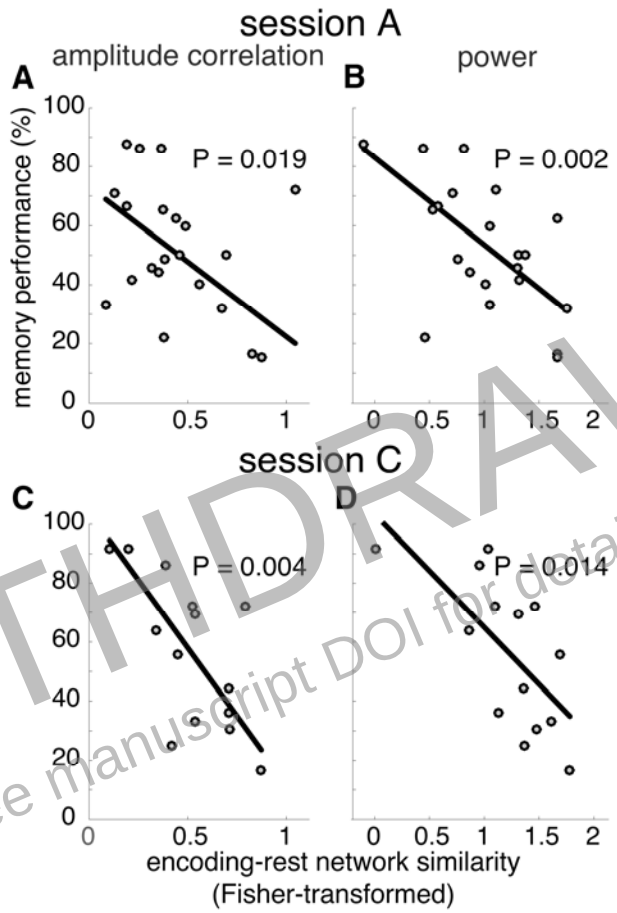

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Figure 3. Associations between memory and alpha network similarity based on amplitude correlation (left) and power networks (right). Reduced similarity of encoding and rest networks was associated with enhanced memory, during both Session A (AB) and Session C (CD). Note higher overall similarity scores for power networks compared to amplitude-based networks (different scales on x-axis). Network similarity is expressed as Fisher-transformed Pearson correlation coefficients.

Because power and amplitude networks were both correlated with memory, we wondered if they captured the same underlying physiological activity or if they predicted memory performance independently. We demonstrate in our related report that while network configurations based on different oscillatory metrics are significantly distinct, they still show high similarity (Pearson coefficients of approximately 0.5 in the alpha band). Consequently, encoding-rest similarity values were highly correlated between power and amplitude-connectivity networks (Session A: R=0.51, P=0.02; Session C: R=0.69, P=0.006). We entered Fisher-transformed encoding-rest similarity for power and amplitude-based connectivity as separate predictors into a multiple regression model predicting memory. For Session A, only amplitude networks were a significant predictor (P=0.02), but not power topographies (P=0.95). Accordingly, a stepwise approach revealed an improved fit of the model after removal of power networks as a predictor (P=0.005 vs. P= 0.02). For Session C, neither individual predictor

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was significant by itself (power: P=0.81, amplitude: P=0.15), but removal of power again improved the overall model (P=0.008 vs. P=0.01). We note, though, that when predictors are strongly correlated, parameter estimates may become unstable and caution should be taken when interpreting these results. Regardless, encoding-rest differences in power topographies and amplitude-based networks appear to be sensitive to overlapping components of the underlying physiological process, with distributed patterns of amplitude correlations more predictive of memory performance than power alone.

We next asked whether the association between memory and encoding-rest differences is driven by memory-specific processes occurring during encoding, or whether task-rest similarity predicts memory regardless of the cognitive task performed. To this end, we analyzed data from the control task in Session C. Interestingly, we found that Session C memory performance was also related to the network differences between the two Session C task blocks, encoding and control, for precisely the same alpha amplitude- and power-based networks (R=-0.55, P=0.03; R=-0.77, P=0.002). Importantly, we did not see corresponding relations with Session A memory for differences between the two Session A task networks that both corresponded to encoding blocks (R=0.01, P=0.93; R=-0.20, P=0.40). This suggests that better memory is associated with more distinct encoding and non-learning control networks, similar to the relation between memory and the dissimilarity of encoding and rest networks. In contrast, control-rest differences were only marginally associated with memory for amplitude correlation (R=-0.49, P=0.09), and just bordered on significance for power (R=-0.57, P=0.05).

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A schematic depiction of the similarity between different network types, and how these similarity scores in turn relate to memory, is presented in Figure 4. As we report in our companion article (Cox et al. 2016), network similarity was much greater between encoding and control networks (0.66 ± 0.18 and 0.90 ± 0.07 for amplitude- and power-based alpha networks, respectively), than between either of these task networks and rest networks (amplitude: 0.49 ± 0.17; power: 0.80 ± 0.23). These relations are visualized as thick and thin black arrows in Figure 4. Concerning memory, however, both greater encoding-rest network differences and greater encoding-control differences predicted memory performance (red arrows). Thus, the relation between network differences and memory is not a direct reflection of overall differences between network types, as the memory relation held both for pairs of highly similar encoding-control and much more dissimilar encoding-rest networks, but not for dissimilar control-rest networks.

It is important to note that because correlations with memory are derived from different combinations of the same network types, they are not independent. For example, individuals with greater encoding-rest similarity also had greater control-rest similarity (amplitude connectivity: R=0.85, $P=10^{-4}$; power: R=0.96, $P<10^{-7}$). Hence, it is unclear what the relative contribution of encoding, control, and rest networks is to behavioral performance. Moreover, while we observed a similar pattern of results for

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power and amplitude-based connectivity, and our previous analyses suggest power and connectivity networks index largely overlapping components of physiological activity, network similarity based on these metrics may still relate to memory performance in different manners. In particular, power, as a relatively coarse estimate of oscillatory activity, may be expected to be particularly sensitive to relatively gross network shifts, such as between encoding and rest, while connectivity may be better equipped to detect subtle network reorganizations when power topographies are highly similar (Chennu et al. 2016), as with encoding and control networks.

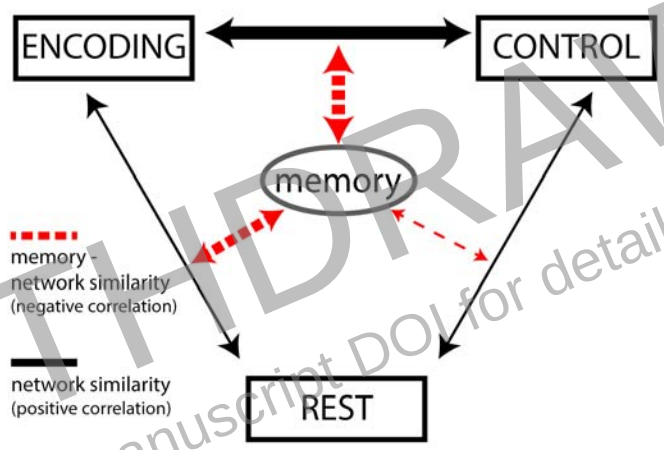

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Figure 4. Conceptual overview of alpha network similarity and relation with memory. Encoding and control networks (task networks) were highly similar (thick solid black arrow), while rest networks were much more distinct from encoding and control networks (thin solid black arrows). However, both encoding-rest network similarity and encoding-control network similarity were negatively correlated with memory (thick dashed red arrows), while control-rest network similarity showed a much weaker relation with memory (thin dashed red arrow).

To examine these notions in more depth, we entered all three Fisher-transformed similarity estimates (i.e., encoding-rest, encoding-control, and control-rest) as predictors into a multiple regression analysis, separately for the power and amplitude correlation metrics. For power, we saw that memory performance was still predicted significantly by encoding-rest similarity (P=0.04), less robustly by encoding-control similarity (P=0.07), and not at all by control-rest similarity (P=0.28). Indeed, a stepwise regression leading to removal of the control-rest predictor resulted in an improved fit of the model (P=0.009 vs. P=0.02). For amplitude correlation, encoding-control similarity still predicted memory performance (P=0.02), but encoding-rest similarity did not (P=0.18), nor did control-rest similarity (P=0.54). In line with these results, a stepwise regression retained only encoding-control as a predictor (model fit P=0.001 vs. P=0.008). Thus, amplitude correlation and power metrics emphasize different network combinations (encoding-rest vs. encoding-control) as driving the bivariate correlations reported above. These findings are in agreement with the idea that connectivity metrics are more sensitive than power to the relatively subtle changes in brain organization seen between highly similar encoding and control networks. However, due to the unavoidable

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correlated nature of the predictor variables firm conclusions should not be drawn from this apparent reversal. Nonetheless, for both oscillatory metrics, similarity involving the encoding network predicted memory, but control-rest similarity did not. In sum, then, these findings suggest that memory-specific processes during the encoding block underlie the observed associations between network structure and memory.

Localized alpha activity does not predict memory

Is there a systematic topographical basis to the relation between network structure and memory, specifically between alpha encoding-rest network similarity and memory? Figure 5 (left) visualizes Session A amplitude-based alpha patterns during rest and encoding for all electrode pairs in five individuals spanning the range of memory scores. Scatterplots demonstrate how rest and encoding patterns were less similar for subjects with better memory. Topographical connectivity plots showing the strongest connections (Fig. 5, middle and right) emphasize this difference in encoding-rest correspondence as a function of memory performance, and furthermore suggest that the precise connections differing from rest to encoding vary per subject. Similar between-subject variability in encoding-rest correspondence is obtained when focusing on the weakest or intermediate strength connections (not shown).

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To confirm this impression quantitatively, we first assessed, for each subject separately, how much each electrode or connection contributed to that individual's observed encoding-rest similarity (see *Materials and Methods*). We reasoned that if good memory performance relies on systematic encoding-rest changes in a particular set of electrodes or connections, participants with comparable memory scores should be expected to have more similar patterns of these contribution weights. We sorted participants by performance and determined the similarity of these "contribution patterns" between every pair of neighboring participants. We then averaged the obtained values across pairs and compared this estimate to the average similarity of neighboring subjects' contribution patterns after randomizing the subject order, thus destroying the memory-based ranking of the original observation. Yet, we found no consistent evidence for similar encoding-rest network shifts for individuals with comparable memory ability (amplitude correlation: Session A, P=0.83, Session C, P=0.88; power: Session A, P=0.15, Session C, P=0.69), suggesting that while larger network reorganizations from rest to encoding are associated with better memory, different brains reorganize themselves differently.

We performed several additional control analyses to elucidate whether specific electrodes or connections underlie the link between distributed oscillatory patterns and memory (Supplementary Text). While we observed several statistically significant effects in individual sessions, none of these findings replicated to the other session. As such, these findings cannot adequately account for the robust network similarity results seen across sessions.

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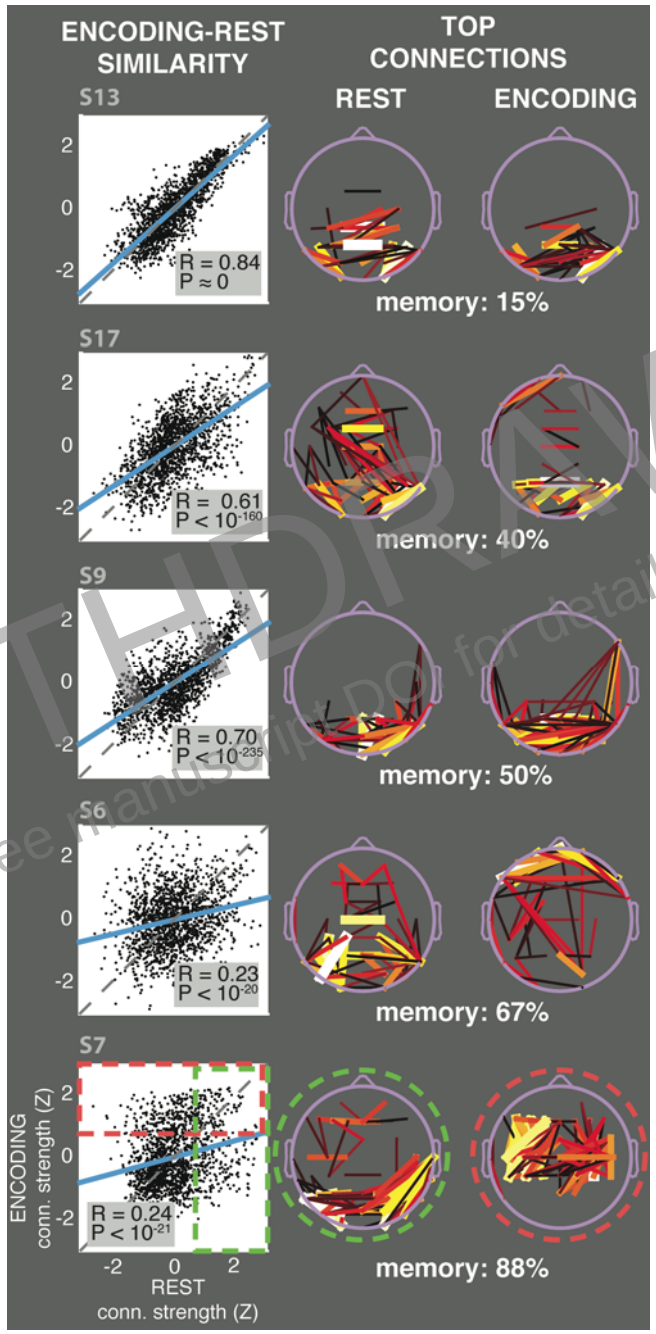

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Figure 5. Encoding-rest network similarity for high and low-performing individuals, based on alpha amplitude correlation patterns during Session A. Rows present five individuals, ordered from low memory performance (top) to high (bottom). Left column scatterplots show network similarity between encoding (averaged across two encoding blocks) and rest (averaged across 7 blocks). Axes reflect z-scored connection strengths. Individuals with better memory showed more distinct rest and encoding profiles. Middle and right columns show strongest connections (above mean + 1.5 standard deviation) for rest and encoding, with thicker yellow/white lines for stronger connections and thinner orange/brown lines for weaker connections. Dashed rectangles and circles in bottom panels indicate approximate correspondence between top connections in scatterplot and topographical plots. Topographically, no clear pattern was

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apparent cross-subject regarding which connections were most involved in encoding-rest network shifts.

Distributed alpha networks may track memory retention

Two hours after the end of Session A, in Session B, participants performed delayed retrieval tests for the material encoded in Session A. With respect to Session A immediate tests, absolute performance was reduced for both Session B delayed tests (block 1: 41 ± 24 %; t(20)=2.9, P=0.009; block 2: 55 ± 25 %; t(20)=1.9, P=0.08), resulting in cross-session retention rates of 85 ± 29% and 89 ± 26% that were similar for both tests (t(20)=-0.7, P=0.51). Interestingly, we found that memory retention across the 2 h interval was also negatively related to Session A encoding-rest network similarity. Specifically, this relationship held for amplitude-based networks in the alpha (R=-0.42, P=0.001) and beta bands (R=-0.01, P=0.013; small R value due to robust fitting procedure, see Methods). Thus, these findings suggest that larger network deviations from rest to encoding may foster even more long-term effects on memory. However, retention was significantly associated with initial memory performance (R=0.45, P=0.04), possibly explaining the link for the amplitude-based alpha networks. Indeed, this effect is removed when adding encoding performance as a covariate. Since follow-up Session C did not employ a delayed retrieval block, we could not independently replicate these Session A findings and they remain exploratory.

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Discussion

In this work, we took a novel approach to relate large-scale oscillatory patterns derived from continuous data to memory performance. We observed a robust relation between memory performance and the difference in the oscillatory patterns present during encoding and those present during rest or control task activity. In particular, these effects were apparent for alpha power topographies and the alpha amplitude correlation structure. Notably, these results could not be explained by localized differences in power or connectivity, indicating that distributed patterns may be more sensitive than circumscribed locations to functionally relevant activity (Kriegeskorte 2008; Park and Friston 2013; Pessoa 2014; Petersen and Sporns 2015).

Numerous studies have related alpha activity to episodic encoding and retrieval processes in general (Hanslmayr et al. 2009; Khader and Rösler 2011; Waldhauser et al. 2016), and to individual differences in memory capacity in particular (Park et al. 2014; Jiang et al. 2015). Using a network-based approach, we observed specific relationships between alpha activity and between-subject variability in memory performance. In particular, we saw that the more oscillatory alpha encoding patterns deviated from those present during rest, the better memory performance was. These effects likely reflect a trait-like relationship, as 1) this relation held across two study visits spaced months apart, 2) memory performance was strongly correlated across this interval, 3) the association was still apparent when relating network similarity on one visit with

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behavioral performance on the other, and 4) our previous results indicate individual subjects' network organization is highly stable across this period (Cox et al. 2016). Furthermore, these effects appear to be related to functional memory processes, as we found that network differences between encoding and a behavioral task with low memory demands also predicted memory, while differences between this behavioral task and rest did so poorly.

Considering the alpha band in more detail, several related accounts hold that alpha activity regulates attentional resources and information flow by suppressing task-irrelevant neural regions (Klimesch et al. 2007; Jensen and Mazaheri 2010; Sadaghiani and Kleinschmidt 2016). Following this theory, one interpretation of our results is that greater alpha network changes from non-memory periods (rest or control task) to encoding may reflect more optimally organized functional inhibition patterns that facilitate learning and/or subsequent retrieval. Thus, these patterns could reflect more or less adequate deployment of attentional resources, which are intimately associated with alpha activity (Klimesch 2012). Indeed, both resting states and the viewing control condition, besides lacking the associative memory component, were also less engaging than the encoding blocks. Further taking into consideration that the structure of rest networks themselves did not relate to memory, we speculate that superior memory capacity is achieved by those individuals whose encoding networks most successfully break the status quo of the non-engaged control task and resting state networks. It is important to note this phenomenon is independent of absolute power and connectivity levels, as these metrics did not consistently relate to behavioral performance.

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The aspects of memory captured in these measures appear to be different from those involved in offline memory reactivation (Staresina et al. 2013; Tambini and Davachi 2013; Brokaw et al. 2016), which specifically relate brain activity in the post-encoding period to subsequent performance. Our findings reflect much more global, trait-like aspects of memory, as encoding-rest differences on one day can predict memory performance six months earlier or later.

Of particular relevance, a recent functional MRI study examined the similarity of rest and task networks in a fashion conceptually similar to ours (Schultz and Cole 2016). Intriguingly, that report found superior behavioral performance for those individuals whose rest and task networks *most* resembled each other, which is the opposite of our findings. The opposite signs of the fMRI and EEG correlations reinforce the notion that these two recording modalities are sensitive to fundamentally different aspects of brain dynamics that, furthermore, may have inverse relationships with behavior.

The relation with memory we uncovered was apparent both when we considered encoding-rest differences in the cortical distribution of oscillatory alpha power, and when we assessed how patterns of coherent alpha amplitude fluctuation across the cortex differ between encoding and rest. Multiple regression analyses indicated that power and amplitude-based connectivity are not independent predictors of memory

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performance, and, while sensitive to distinct aspects of oscillatory dynamics, likely capture overlapping components of the underlying physiological process. At the same time, when we assessed which network combinations best predicted memory, we found encoding-rest similarity to be the best predictor for power, whereas encoding-control similarity was the best predictor for amplitude-based connectivity. While these findings should be interpreted with care due to the correlated nature of all networks, they are in line with the general notion that functional connectivity measures may be able to uncover more subtle changes in brain dynamics than power estimates. It is also important to note that power and amplitude correlations, for which a behavioral link was found, both constitute oscillatory attributes with a relatively coarse temporal resolution. In contrast, connectivity based on more fine-grained phase relations showed no relationship to memory. We suggest that while phase information is crucial for memory functioning when analyzed in close association with stimulus presentation (Klimesch et al. 2007; Staudigl and Hanslmayr 2013), when such phase synchrony patterns are measured across periods of minutes, as presented here, they do not meaningfully capture such memory processing.

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Interestingly, we were unable to consistently tie the observed relations between memory ability and distributed network structure to specific topographical regions or connections. Such relations have been described in the past for posterior alpha activity (Park et al. 2014; Jiang et al. 2015). However, our focus on blocks of continuous EEG activity collected over several minutes likely captures entirely different facets of electrophysiological activity than those obtained from brief activity time-locked to stimulus presentation as measured in these other studies. More fundamentally, as we describe in our companion paper (Cox et al. 2016), we found task-rest network similarity to be much higher within than between subjects (0.39 vs. 0.25 for alpha amplitude correlation; 0.70 vs. 0.52 for alpha power). Thus, extensive individual variation in oscillatory networks may explain why subject-specific encoding-rest pattern shifts did not result in consistently localized group effects. Rather than viewing this as a limitation, we propose multivariate network techniques may be more sensitive tools to isolate functional processes than conventional mass-univariate approaches, a conclusion shared by various other recent empirical and theoretical accounts (Kriegeskorte 2008; Palva et al. 2010; Park and Friston 2013; Van de Nieuwenhuijzen et al. 2013; Pessoa 2014; Gonzalez-Castillo et al. 2015; Honkanen et al. 2015; Kaneshiro et al. 2015; Petersen and Sporns 2015).

In conclusion, we uncovered a robust link between large-scale alpha EEG networks and episodic memory performance, with network parameters explaining up to half of the between-subject variance in memory performance. The trait-like nature of this relation underscores the fundamental importance of individual differences in oscillatory organization for cognition, although the origins both of this relation and its variation between individuals remains elusive. Combined with our findings of several statistically separable oscillatory networks embedded in EEG activity (Cox et al. 2016), these results indicate that a wealth of information can be extracted from network analyses, both to

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characterize neurophysiological dynamics in novel ways and to identify brain-behavior correlates that may further our understanding of human cognition.

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