Journal of Experimental Psychology: General

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CITATION

Stillman, P. E., Lu, Z.-L., & Fujita, K. (2019, July 1). Construal Level Shifts Integration and Segregation of the Brain Network. *Journal of Experimental Psychology: General*. Advance online publication. http://dx.doi.org/10.1037/xge0000637

BRIEF REPORT

Construal Level Shifts Integration and Segregation of the Brain Network

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The ability to expand and contract one's mental horizons allows people to regulate toward ends that are both distant and near. One challenge that people face when regulating toward distant relative to near ends is the lack of information about detailed specifics. In response, construal level theory (CLT) proposes that people engage in high-level construal—a representational process that highlights the essential properties of events that are invariant across potential instantiations. To tailor responses to more immediate events, however, CLT proposes that people engage in low-level construal—a representational process that highlights idiosyncratic specifics that distinguish events from one another. The present article uses network neuroscience to investigate the neurocognitive mechanisms for these representational processes. While undergoing fMRI, participants were instructed to think about the distant versus near future, and completed tasks that directly manipulated high-level versus low-level construal. Thinking about the distant future and engaging in high-level construal both promoted integration across the network (indexed by global efficiency). Thinking about the near future and engaging in low-level construal promoted segregation within the network (indexed by clustering coefficient). These are the first findings to document how the brain reconfigures to support the expansion versus contraction of one's mental horizons, and provides new insight into the neural mechanisms that help people regulate toward distant versus near ends.

Keywords: construal level theory, self-regulation, network neuroscience, integration, segregation

Supplemental materials: http://dx.doi.org/10.1037/xge0000637.supp

The ability to expand and contract one's mental horizons allows people to regulate toward ends that are both remote and immediate (Atance & O'Neill, 2001; Schacter & Addis, 2007; Suddendorf & Corballis, 2007). Planning, for example, requires people to expand their regulatory scope, using their expectations of what might happen in the distant future to guide decisions and actions in the here-and-now. Behavioral execution, by contrast, requires attunement to local cues and tailoring of action to suit present condi-

tions. This modulation of regulatory scope not only allows people to transcend direct experience and orient to more distant ends, but also to immerse and be responsive to events in one's immediate environment.

A central challenge to thinking about events that are psychologically distant—that is, those removed from direct experience—is the lack of reliable detailed specifics. Construal level theory (CLT; Liberman & Trope, 2008, 2014; Trope & Liberman, 2003, 2010) proposes that people address this challenge by construing distant objects and events in terms of the essential and invariant properties that are unlikely to change across instantiations—a representational process referred to as high-level construal. As objects become closer, CLT proposes that people construe events in terms of the detailed and idiosyncratic information that becomes increasingly available—a representational process referred to as low-level construal. This relationship between distance and construal is hypothesized to be overgeneralized—evident even when equivalent information is known about psychologically distant versus near events (Bar-Anan, Liberman, & Trope, 2006). In this way, high-level versus low-level construal are the psychological mechanisms by which people expand versus contract their regulatory scope.

Construal level theory proposes that key to high-level construal is cognitive abstraction—the treatment of distinct entities as interchangeable and substitutable (Liberman & Trope, 2008, 2014;

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Trope & Liberman, 2010). Understanding that fish, trees, and insects are all examples of "living things," for example, requires psychological processes that treat each entity as equivalent examples of a broader category. By promoting the identification of essential commonalities across multiple dimensions, abstraction facilitates the integration of disparate content that may not be directly comparable along any single dimension (Malkoc, Zauberman, & Ulu, 2005). By contrast, key to low-level construal is concretization. By highlighting the local and specific features that render an object distinct, low-level construal facilitates the generation of idiosyncratic representations that treat each entity as unique. Thus, CLT suggests that whereas high-level construal requires integration across disparate inputs and types of information to facilitate the identification of essential invariants, low-level construal requires specialization and segregation to facilitate the identification of detailed idiosyncrasies. No research to date, however, has provided direct neuro-cognitive evidence for the proposed role that integration and segregation play in supporting high-level versus low-level construal, and the concurrent expansion versus contraction of regulatory scope, respectively.

Network neuroscience—a branch of neuroscience that attempts to understand emergent cognitive phenomena by using graph theory tools to quantify the complex interactions across many brain regions (Barrett & Satpute, 2013; Bassett & Sporns, 2017; Bullmore & Sporns, 2009; Medaglia, Lynall, & Bassett, 2015; Sporns, 2010; see Figure 1)—has greatly expanded researchers' ability to examine integration versus segregation within the brain (Deco, Tononi, Boly, & Kringelbach, 2015; Shine & Poldrack, 2018; Sporns, 2013). By quantifying the connectivity strength between collections of regions, researchers can quantify the degree of integration (e.g., how readily information can traverse the network—a property indexed by global efficiency) or segregation (e.g., how densely interconnected nodes are with their neighbors, a property indexed by the clustering coefficient; see Figure 2).

The balance between integration and segregation, however, is dynamic, shifting across individuals and tasks. For instance, individuals with higher IQ exhibited evidence of greater integration (indexed via whole-brain global efficiency), particularly among frontal and parietal regions (van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009). This finding not only demonstrates the dynamic nature of these metrics at the whole-brain level, but further provides support for prior theories of intelligence that emphasize the importance of integration across the brain network (Jung & Haier, 2007). Subsequent research has similarly found that integration and segregation shift as a function of task (for a review, see Shine & Poldrack, 2018). For instance, Cohen and D'Esposito (2016) demonstrated integration and segregation vary as a function of task, with motor execution tasks promoting segregation, and working memory tasks promoting integration across the whole-brain network. These results suggest that the brain may dynamically reorganize to reflect the cognitive demands of the task at hand.

This dynamism suggests that, if integration and segregation are indeed central to high- and low-level construal (respectively), we would predict brain networks to reorganize to promote global efficiency or clustering coefficient when task demands induce high- versus low-level construal (respectively). Previous work provides some indirect support for this hypothesis. Segregation is promoted by, and predicts performance on, motor tasks (Bassett, Yang, Wymbs, & Grafton, 2015; Cohen & D'Esposito, 2016; Ma, Calhoun, Eichele, Du, & Adalı, 2012). Such tasks require tailoring one's actions to the specifics of the immediate environment and may thus be viewed as requiring low-level construal. Integration, in contrast, is enhanced during an N-back task (Cohen & D'Esposito, 2016), which requires integrating visual inputs with information not perceptually available, and may thus be viewed as requiring high-level construal. Finally, tasks that require traversing psychological distance via perspective taking (i.e., social distance; Parkinson, Liu, & Wheatley, 2014) similarly promote whole-brain integration (Shine et al., 2016). Together, these studies provide preliminary evidence that high-level construal promotes integration, whereas low-level construal promotes segregation.

To provide a direct test, we reanalyzed an existing dataset (Stillman, Lee, et al., 2017) in which participants completed two tasks while undergoing fMRI—one that directly manipulated construal level and one that manipulated expansive versus contractive regulatory scope via a temporal imagery manipulation (see Figure 3). We next constructed graphs that correspond to the functional connectivity patterns (assessed via time-series correlation) across 152 brain regions during different conditions of the two tasks (see Figure 4). Finally, we probed the integration and segregation of these networks (via global efficiency and clustering coefficient, respectively) to make inferences about the organizational properties of the brain under different levels of construal (Medaglia et al., 2015). We predicted that the brain network reconfigures to en-
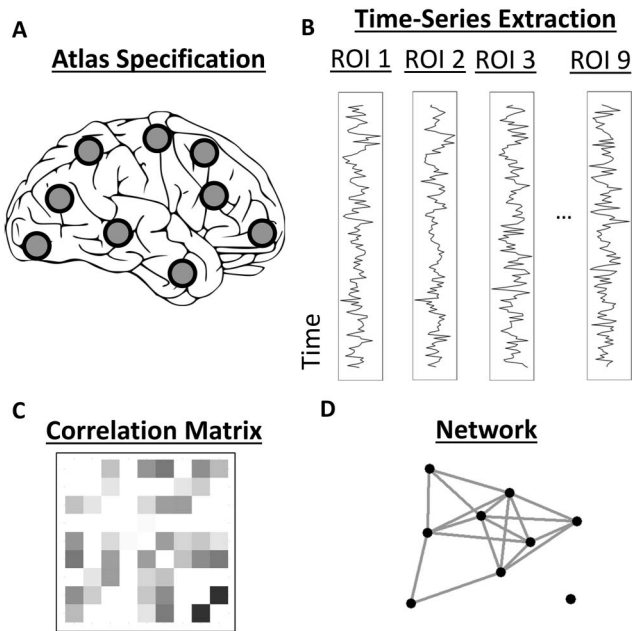
Figure 1. Flowchart of network construction using toy data. (A), the brain is divided up into a series of nodes (indicated by the 9 circles). (B), the time series for each node is extracted and (C) correlated with one another to produce an $n \times n$ correlation matrix, where n is equal to the number of nodes (9, in this case). In the matrix here, each point corresponds to the correlation between two regions, with darker colors corresponding to stronger correlations. Finally (D), these correlation matrices are then thresholded to produce a binary (on or off) connection, yielding a binary undirected network.
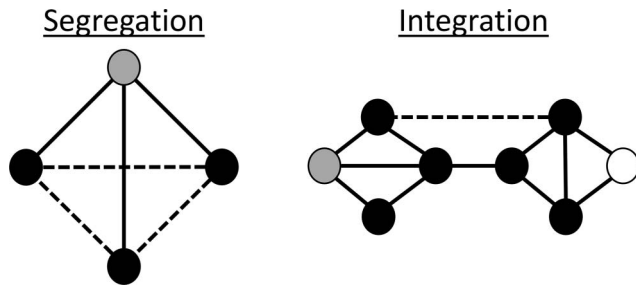
Figure 2. Depiction of segregation (left) and integration (right). Segregation, indexed via clustering coefficient (left), refers to the tendency for a node's neighbors to be connected with one another (i.e., closed triads). If the gray node is connected to all three black nodes (indicated by solid black lines), the clustering coefficient will increase with the addition of each dashed connection (i.e., the dashed connections changing from 0 to 1). Specifically, clustering coefficient is computed by taking the average proportion of closed triads (i.e., nodes whose neighbors are neighbors of each other vs. not) across all nodes. Integration, indexed via global efficiency (right), refers to the average distance between two nodes in a graph, and is quantified via the inverse of the average number of connections needed to bridge two nodes. For instance, the distance between the gray node and the white node is four, but if the dashed connection is included, the distance drops to three, thereby increasing global efficiency of that node pairing from ¼ to ⅓. Equations for each metric are provided in the online supplemental material.

hance integration versus segregation when people engage in high-level versus low-level construal, respectively. We should also expect similar modulation of the brain network when people respond to expansive versus contractive regulatory demands—functions that are supported by high-level versus low-level con-

strual—such as when imagining the distant versus near future (respectively).

Method

Participants

Thirty right-handed participants (21 female, ages 18–30) were paid $25 for participation (sample size derived from Spunt & Adolphs, 2014). All participants provided informed consent, and all protocols were approved by the Ohio State IRB.

Why–How Task

To manipulate construal level, we implemented the why–how localizer developed by Spunt and Adolphs (2014). Participants responded yes/no to image–question pairs that required participants to consider either the superordinate (high-level "why") goal that the action in the image served (e.g., "Is this person helping someone?") or the subordinate (low-level "how") means used to accomplish that action (e.g., "Is this person pushing a button?"). Each block (16 total) began with a question prompt for 2 s (e.g., "Is this person helping someone?"), and participants responded "yes" or "no" via a button box during the presentation of each of 8 images ("yes" was the correct answer for 5 questions). Images were displayed for 1.75 s, followed by a reminder of the question prompt for .35 s. Blocks concluded with 2 s of fixation. Each image was repeated twice so that the same image was presented for both "why" and "how" question prompts. We selected one randomized presen-
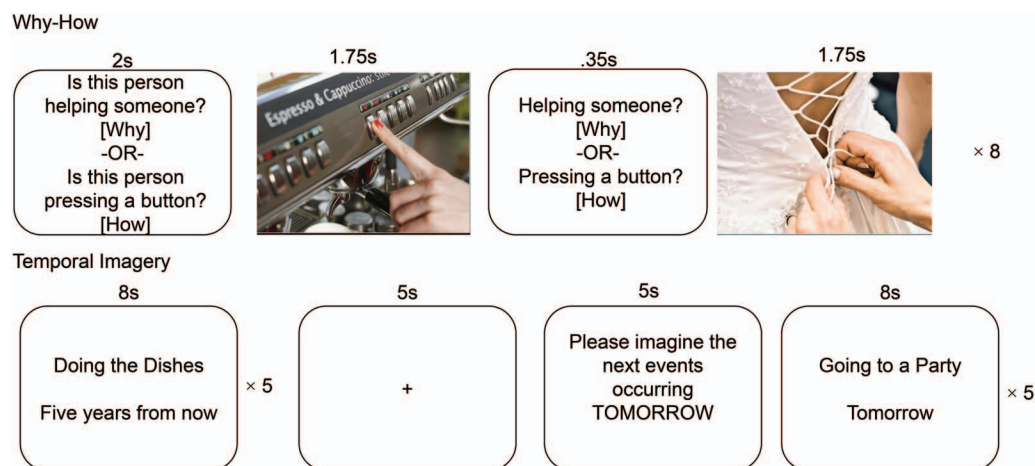
Figure 3. Schematic of the why–how task (top) and temporal imagery task (bottom). In the why–how task, participants identified whether the behavior depicted in a picture corresponded to one described by question prompts. Question prompts focused participants on the goals achieved by an action (high-level why) or means used to perform that action (low-level how). Each prompt was followed by 8 images, to which participants responded "yes" or "no." Question prompts reappeared between each image for .35 seconds. Participants saw 8 pictures per block, and there were 16 blocks in total. In the temporal imagery task, participants were asked to visualize themselves engaging in various actions either tomorrow (temporal proximity) or 5 years from now (temporal distance) in a block design. In each block (6 total), participants visualized 5 different actions for 8 seconds each. See the online article for the color version of this figure.
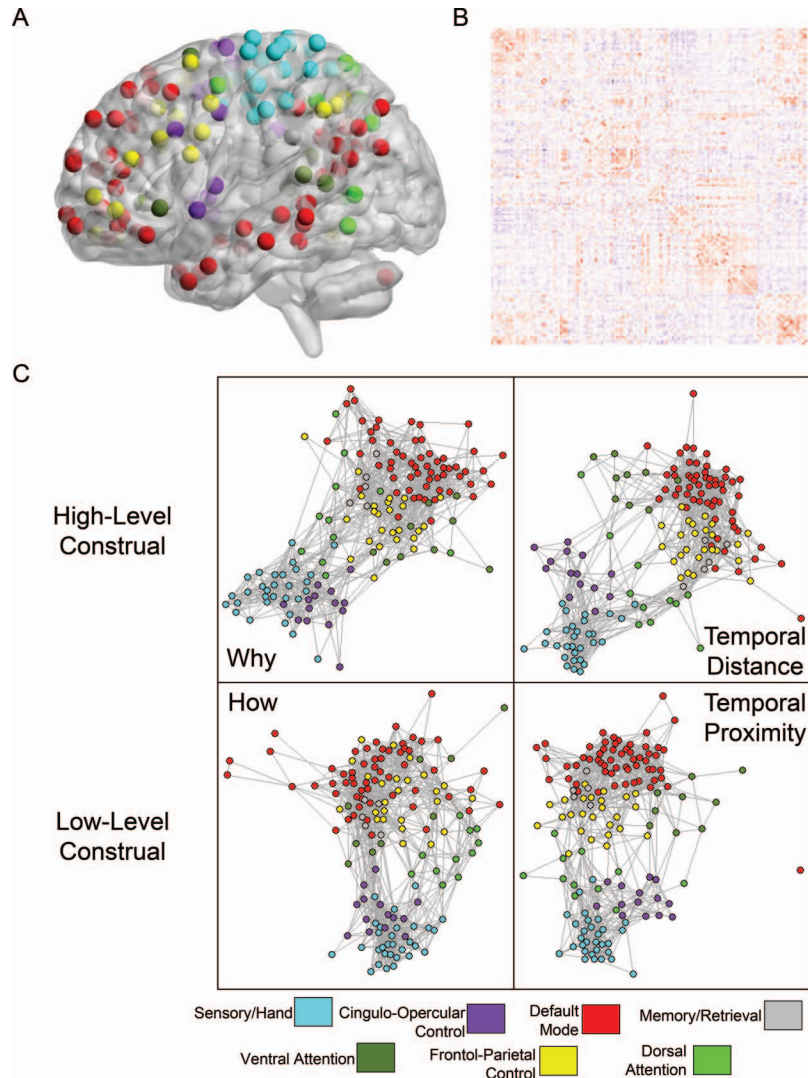
Figure 4. Overview of the present data. (A), we use a 152-node atlas described in Power and colleagues (Power et al., 2011), which further specifies subnetwork membership for each node, plotted here using BrainNet Viewer (Xia, Wang, & He, 2013). (B), the time series for each node is extracted across the blocks of interest (e.g., why blocks in the why–how task), and correlated with one another to produce a 152 × 152 correlation matrix. In the matrix here (depicting average correlation of the "why" blocks with other conditions given in Figure S1), each point corresponds to the correlation between two regions, with darker red corresponding to more positive correlations, and darker blue corresponding to more negative correlations. (C), these correlation matrices are then thresholded to produce a binary (on or off) connection, yielding a binary undirected network. The networks displayed here were derived by averaging together participants' correlation matrices for the condition of interest, then thresholding by setting the top 10% of connection strength to 1 and the remaining to 0. For reference, nodes are color-coded according to their subnetwork membership as suggested by the atlas. See the online article for the color version of this figure.

tation order for all participants optimized to maximize design efficiency (Spunt & Adolphs, 2014).

Temporal Imagery Task

Participants visualized actions (e.g., reading a book) either tomorrow (temporal proximity) or five years from now (temporal distance). As visualizing distant relative to proximal

events may be more difficult, we attempted to equate the accessibility and availability of distant versus near future thoughts by asking participants to imagine what their lives would look like in five years prior to entering the scanner, and before the start of the run. Participants then completed alternating blocks (6 total) in which they imagined near and distant future actions. Each block consisted of 5 trials, with each trial lasting 8 s. In between blocks was 5 s of fixation followed by
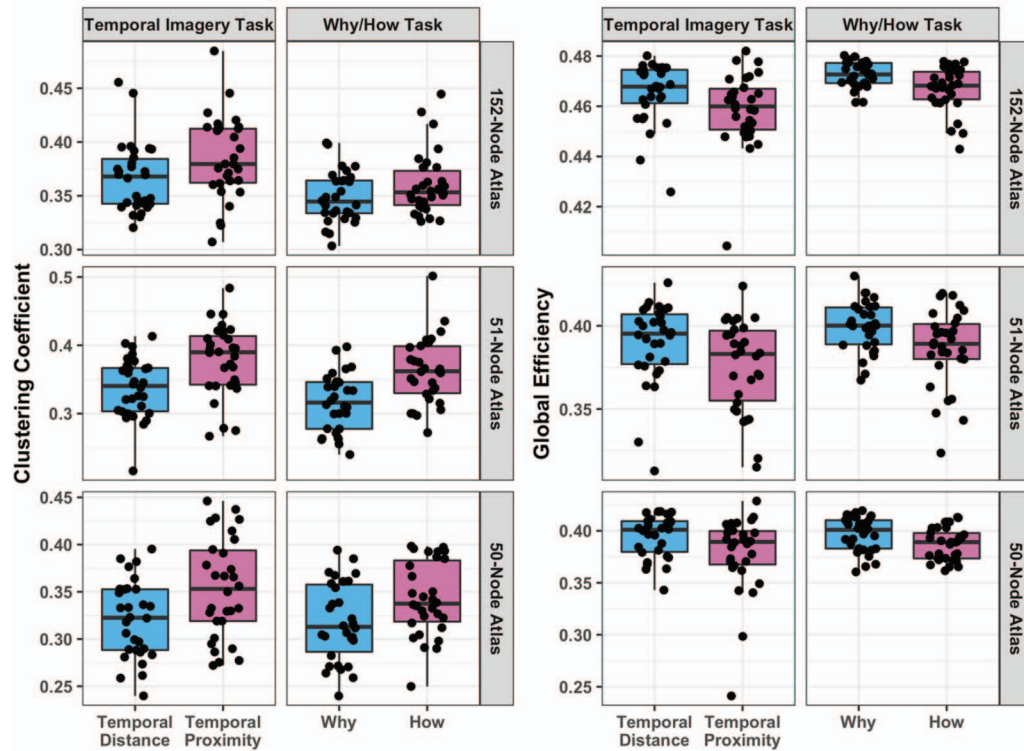
Figure 5. Box-plots for the segregation (clustering coefficient, left) and integration (global efficiency, right) for each task and each atlas using a 10% threshold. Each pairwise comparison is significant using *t* tests, with the exception of global efficiency in the temporal imagery task, which was marginally significant for the 152- and 51-node atlas (*p*s = .053 and .057, respectively). See the online article for the color version of this figure.

5 s of a prompt that read "please imagine the next events occurring TOMORROW [FIVE YEARS FROM NOW]." We randomized (between participants) the starting block, as well as whether the why/how or temporal imagery task was completed first.

Network Construction and Analysis

Acquisition and preprocessing. Full details of fMRI acquisition, preprocessing, and motion correction are given in the online supplemental material.

Connectivity matrices. We used a parcellation of the brain (Power et al., 2011) that divides the brain into 264 nodes. To address concerns that 264 nodes may represent too large a network for the number of time points that we recorded, we reduced the network to 152 nodes (see Figure 4) by retaining only nodes of subnetworks that we hypothesized would respond to our manipulations.[1] To further address concerns that this may still constitute too large a network, we took two random samples from these 152 nodes: one that sampled approximately one third of the nodes from each subnetwork in order to maintain the essential structure of the subnetwork (totaling 51 nodes), and one that retained 50 nodes at random (19 nodes of overlap, see Table S1 in the supplemental materials). Connectivity profiles across nodes were obtained via the CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). For each task and for each participant, we inputted into CONN (a)

the preprocessed data from the two functional runs (corresponding to the two different tasks), (b) the time series information for each block (onset, duration, and which condition the block belonged to), and (c) 6 motion parameters, 1 time series corresponding to each of white matter, cerebrospinal, and average gray-matter activity (Ciric et al., 2017; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012), to serve as covariates. We then convolved the time series for a specific condition (e.g., "why" blocks) with the canonical hemodynamic response function, extracting and concatenating the corresponding time points. Repeating this process with all conditions yielded a 4-D image for each participant for each condition (62 and 57 total time points for why/how and distance/proximity, respectively). Each time series was then aggregated using the three

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[1] For subnetwork identification, we use the labels given by Power and colleagues (2011). The retained subnetworks were the following: Default mode, Somatomotor (hand), Cingulo-opercular task control, Fronto-parietal task control, ventral attention, dorsal attention, memory/retrieval. The omitted subnetworks were the following: Visual, Auditory, Cerebellar, Somatomotor (mouth), Salience, Subcortical, and any node without a subnetwork label. We note this partitioning was determined a priori, and was the only partitioning approach tested. To demonstrate robustness, we report analyses using both the entire network, as well as a 91-node atlas based on the Harvard–Oxford anatomical atlas in the online supplemental material. Those results generally replicated those described here, although they were stronger (and more consistently significant) for the why–how task than the temporal imagery task.
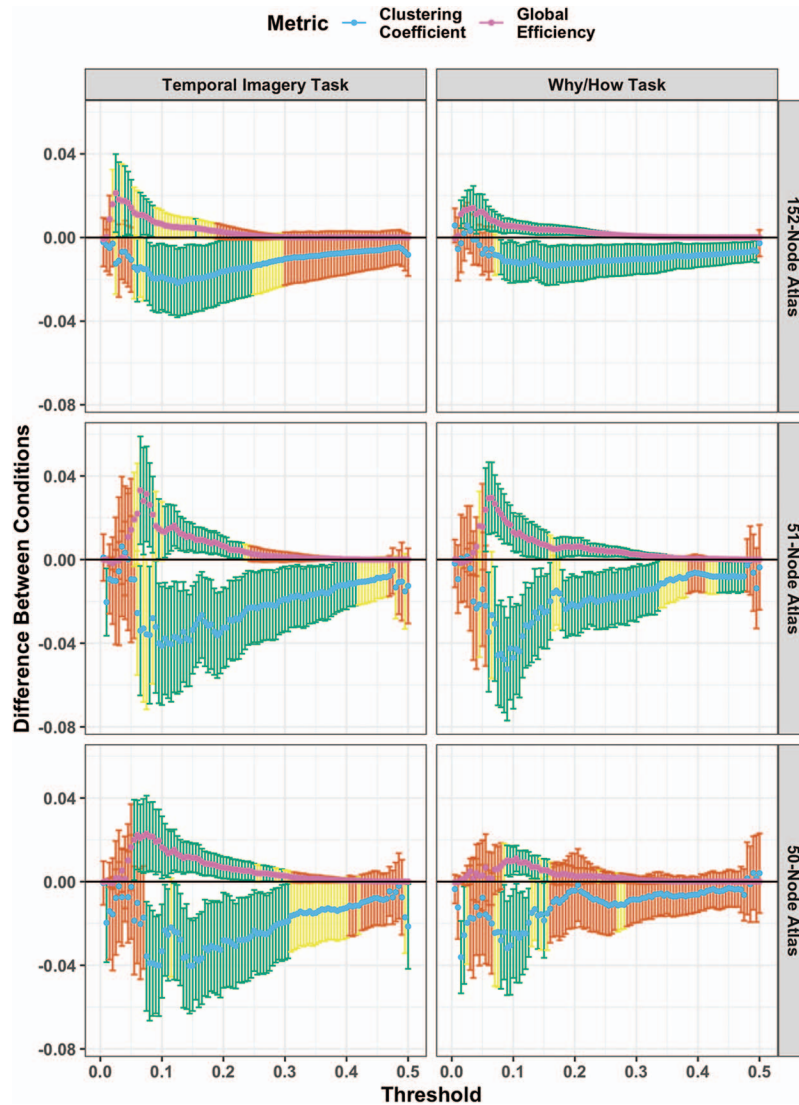
Figure 6. The mean difference between conditions for the clustering coefficient (blue points, below 0) and global efficiency (purple points, above 0) across different thresholds used to generate the binary network (e.g., a threshold of .1 corresponds to retaining the top 10% of edges between regions) for the why/how task (why minus how) and the temporal imagery task (temporal distance minus temporal proximity) for all three network specifications. Error bars correspond to 95% confidence intervals. Points with green error bars correspond to significant differences in the means, yellow error bars correspond to marginally significant differences, and red error bars correspond to nonsignificant differences. See the online article for the color version of this figure.

atlases (152-, 51-, and 50-node) described above, such that voxels within each of the regions were averaged together to create 152, 51, and 50 time series per condition per participant.

To gauge connectivity across these regions, we calculated (separately for each atlas) the correlation of each region with the others, controlling for motion, white-matter, cerebrospinal, and greyordinate regressors and weighted by the hemodynamic response function (HRF) convolved time series to account for the slowness of the BOLD signal. The resulting correlations were Fisher-transformed, yielding, for each atlas, four symmetrical weighted graphs for each participant, each corresponding to a condition of interest. We then thresholded these matrices, such that

the top 10% of connections from each matrix were set to 1 and the remaining were set to 0. Finally, to ensure our results are robust to different thresholds (Bassett, Nelson, Mueller, Camchong, & Lim, 2012), we reconstructed the networks using 100 different thresholds ranging from .5% to 50% in .5% increments.

Graph theory metrics and analysis. We then calculated, separately for each network constructed above, metrics for integration and segregation: global efficiency and clustering coefficient (equations given in the online supplemental material, as are consistent results using alternative metrics; for a more in-depth discussion, see Rubinov & Sporns, 2010). Global efficiency is quantified by first calculating the inverse of the shortest path

Table 1

Ranges of Thresholds for Which Each Metric Was Significant or Marginally Significant

Task	152-Node atlas		51-Node atlas		50-Node atlas	
	Clustering coefficient	Global efficiency	Clustering coefficient	Global efficiency	Clustering coefficient	Global efficiency
Why–how	7%–49.5%	1.5%–43.5%	6%–38%, 41.5%–47.5%	5.5%–35.5%	7%–15.5%	8.5%–16%
Temporal imagery	5.5%–29.5%	2%–18.5%	6%–46.5%	5.5%–24%	7.5%–40%	5.5%–31%

between two nodes for all node pairs, and then averaging across these values (Latora & Marchiori, 2001). Clustering coefficient is calculated by taking the average proportion of closed triads (i.e., nodes whose neighbors are neighbors of each other vs. not) across all nodes (Watts & Strogatz, 1998). We then subjected these scores to paired samples t tests to test differences between task conditions.

Results

Consistent with predictions, how relative to why trials were associated with significantly greater segregation, evidenced by increased clustering coefficient: 152-node atlas: $t(29) = 2.49$, $p = .02$, $d_z = .46$; 51-node atlas: $t(29) = 3.94$, $p < .001$, $d_z = .72$: 50-node atlas: $t(29) = 2.39$, $p = .02$, $d_z = .44$ (see Figure 5; Tables S2–S4). Why relative to how trials, in contrast, were associated with significantly greater integration, evidenced by increased global efficiency—152-node network: $t(29) = 3.54$, $p = .001$, $d_z = .65$; 51-node network: $t(29) = 2.95$, $p = .006$, $d_z = .54$; 50-node network: $t(29) = 3.11$, $p = .004$, $d_z = 57$. In parallel analyses in the temporal imagery task, temporal proximity relative to distance was associated with significantly greater clustering coefficient—152-node atlas: $t(29) = 2.41$, $p = .02$, $d_z = .44$; 51-node atlas: $t(29) = 2.98$, $p = .006$, $d_z = .54$; 50-node atlas: $t(29) = 3.04$, $p = .005$, $d_z = .56$ (Tables S5–S7). Temporal distance relative to proximity, in contrast, was associated with marginally greater global efficiency—152-node atlas: $t(29) = 2.01$, $p = .053$, $d_z = .37$; 51-node atlas: $t(29) = 1.98$, $p = .057$, $d_z = .36$; 50-node atlas: $t(29) = 2.26$, $p = .03$, $d_z = .41$.[2]

Our results further appear generally robust across thresholds, summarized in Figure 6, Table 1, and Tables S2–S7. The one exception to this is the 50-node network why/how data, which were only significant or marginally significant across both integration and segregation in the 8.5%–15.5% range, although it was directionally consistent outside of this range.

Discussion

Whether manipulated directly or evoked in response to expansive versus contractive regulatory demands, high-level construal promoted integrated network architecture (assessed via global efficiency), whereas low-level construal promoted segregated network architecture (assessed via clustering coefficient). These results suggest that changes in brain network connectivity may represent important neurocognitive mechanisms that support high- and low-level construal. Moreover, these findings document for the first time how the brain network dynamically reconfigures to promote integration versus

segregation in response to task demands that entail expanding versus contracting regulatory scope, respectively.

Two limitations are important to highlight. First, while our results appear robust to threshold and atlas specification, each network is constructed using a relatively small number of time points. This makes estimation of the 152-node atlas potentially rank-deficient, as we may not have adequate degrees of freedom. While we replicate the results with smaller networks, future research should verify whether these results hold using more time points. Second, it is possible that our results are due in part to greater difficulty of the high-level trials. However, within behavioral studies, difficulty is generally unrelated to construal level (e.g., high-level construal does not increase RTs; Stillman, Medvedev, & Ferguson, 2017), and while there are slight behavioral differences in why versus how trials (Spunt & Adolphs, 2014), these tend to be relatively minor. As such, we do not believe difficulty fully explains the present findings.

The present work adds to a growing body of research highlighting the importance of functional integration and segregation within the brain (Bullmore & Sporns, 2012; Collin, Sporns, Mandl, & van den Heuvel, 2014; Deco & Kringelbach, 2016; Dehaene, Charles, King, & Marti, 2014; Fries, 2005, 2015; Heitmann & Breakspear, 2018; Shine & Poldrack, 2018; Sporns, 2013). We build on an emerging body of work demonstrating that task demands can play a critical role in how the brain network dynamically reorganizes to facilitate integration or segregation, as well as demonstrates how network neuroscience techniques can test theories of segregation and integration.

The current results further lay the groundwork for an integrative theoretical framework that may both account for past work on the functions and dynamics of network organization, as well as generate novel predictions. For instance, past work has found that performance on cognitive tasks is sometimes supported by integration, and sometimes supported by segregation (Cole et al., 2013; Shine & Poldrack, 2018). The present results can organize some disparate task findings by suggesting that those tasks that require expansive scope should promote integration, whereas those that promote contractive scope should promote segregation. Finally, the CLT literature describes situational and motivational factors that shift construal level (e.g., mentalizing; Eyal & Epley,

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[2] As we also conducted analyses (reported in the online supplemental materials) on an additional metric of integration and segregation, we reran the above analyses using an alpha derived via a Bonferroni correction for two comparisons (i.e., alpha = .025). With the exception of the temporal imagery task influencing global efficiency (ps = .03, .053, and .057), all analyses were robust to this more stringent significance criteria.

2010; for a review, see Trope & Liberman, 2010), and each of these may correspond to shifts in integration versus segregation. We invite and encourage future research documenting how CLT may serve as a framework with which to explore and understand the antecedents and consequences of changes to the brain's functional architecture.

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