

Similarity of Computations Across Domains Does Not Imply Shared Implementation: The Case of Language Comprehension

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Abstract

Understanding language requires applying cognitive operations (e.g., memory retrieval, prediction, structure building) that are relevant across many cognitive domains to specialized knowledge structures (e.g., a particular language's lexicon and syntax). Are these computations carried out by domain-general circuits or by circuits that store domain-specific representations? Recent work has characterized the roles in language comprehension of the language network, which is selective for high-level language processing, and the multiple-demand (MD) network, which has been implicated in executive functions and linked to fluid intelligence and thus is a prime candidate for implementing computations that support information processing across domains. The language network responds robustly to diverse aspects of comprehension, but the MD network shows no sensitivity to linguistic variables. We therefore argue that the MD network does not play a core role in language comprehension and that past findings suggesting the contrary are likely due to methodological artifacts. Although future studies may reveal some aspects of language comprehension that require the MD network, evidence to date suggests that those will not be related to core linguistic processes such as lexical access or composition. The finding that the circuits that store linguistic knowledge carry out computations on those representations aligns with general arguments against the separation of memory and computation in the mind and brain.

Keywords

language, domain specificity, executive functions, working memory, cognitive control, prediction

Incremental language comprehension likely relies on general cognitive operations such as retrieval of representations from memory, predictive processing, attentional selection, and hierarchical structure building (e.g., Gibson, 2000; Tanenhaus et al., 1995). For example, in any sentence containing a nonlocal dependency between words, the first dependent has to be retrieved from memory when the second dependent is encountered. These kinds of operations are also invoked in other domains of perception and cognition, including object recognition, numerical and spatial reasoning, music perception, social cognition, and task planning (e.g., Botvinick, 2007; Dehaene et al., 2003). The apparent similarity of these kinds of mental operations across domains has led to arguments that the brain contains domain-general circuits that carry out these operations and that language draws on these circuits (e.g., Fitch

& Martins, 2014; Koechlin & Jubault, 2006; Novick et al., 2005; Patel, 2003; Fig. 1a).

Indeed, a network of frontal and parietal brain regions—the *multiple-demand* (MD) system (also known as the executive- or cognitive-control network; Fig. 2b)—has been shown to respond during diverse cognitive tasks and to be linked to constructs such as working memory, inhibition, attention, prediction,

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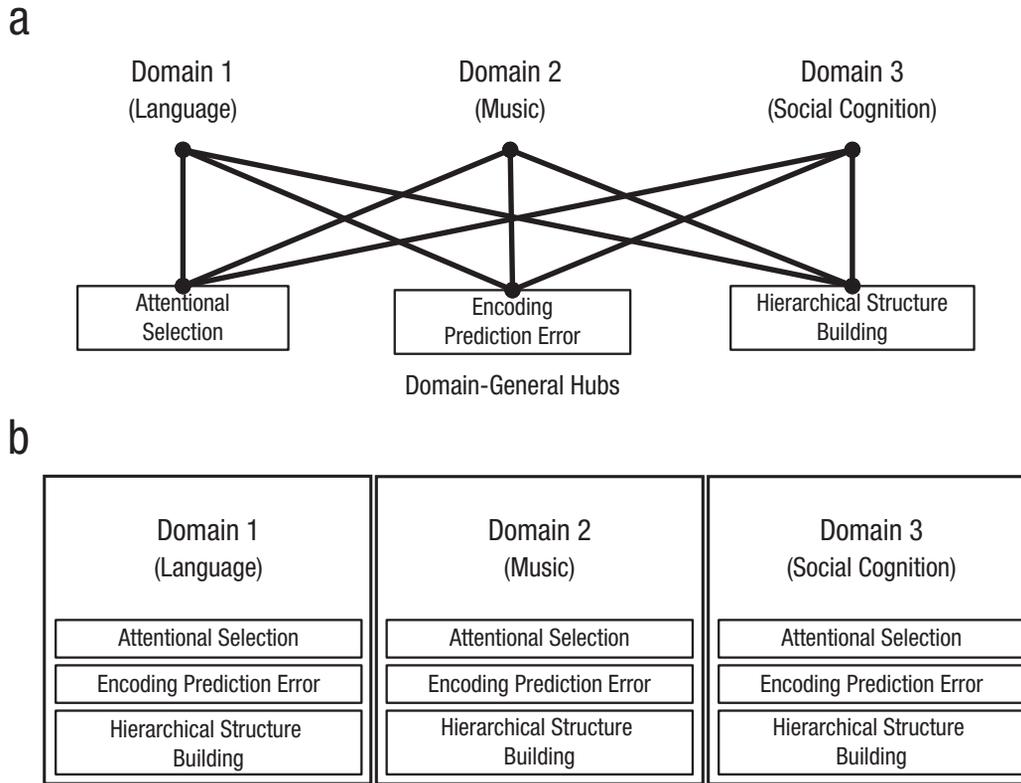


Fig. 1. Schematic illustrations of (a) an architecture in which computations that are used across domains are implemented in shared circuits and (b) an architecture in which such general computations are implemented locally within each relevant set of domain-specific circuits. The architecture in (a) assumes separation between memory circuits (which store domain-specific knowledge representations) and computation circuits (which support attention, prediction, structure building, and other operations across domains); in the architecture in (b), the circuits that store domain-specific knowledge representations also carry out computations on those representations (e.g., Dasgupta & Gershman, 2021; Hasson et al., 2015).

structure building, and fluid intelligence (e.g., Duncan et al., 2020). These findings make the MD network an ideal candidate for carrying out hypothesized domain-general operations. However, many domains—including language—rely on domain-specific knowledge representations stored in specialized brain areas and networks. For example, language recruits a network of frontal and temporal brain regions that respond in a highly selective manner during language comprehension (Fedorenko et al., 2011; Fig. 2a), and damage to these regions in adulthood leads to selectively linguistic deficits (e.g., Fedorenko & Varley, 2016).

During language comprehension, the MD network may work together with the language network, carrying out general operations on domain-specific knowledge representations. However, it is also possible that the language network locally implements general types of computations (e.g., retrieval of information from memory, predictive processing, and structure building; Caplan & Waters, 1999; R. L. Lewis, 1996; Martin et al., 1994). More generally, these kinds of computations,

although important for various domains, may not draw on shared circuits (e.g., Dasgupta & Gershman, 2021; Hasson et al., 2015; Fig. 1b), possibly as a way of minimizing wiring lengths (Chklovskii & Koulakov, 2004). In this view, the MD network may be a general fallback system for domains or tasks for which the brain lacks specialized circuitry.

In this article, we review a recent body of work in which various aspects of human sentence comprehension were investigated using functional MRI (fMRI) techniques that reliably distinguish the language network from the domain-general MD network (see Fedorenko & Blank, 2020, for review), so that their functional response properties could be probed independently. (This approach is complementary to—but more direct than—past work, which has used dual-task paradigms and examination of brain-damaged patients to probe the role of domain-general resources in language comprehension; e.g., Caplan & Waters, 1999; Martin et al., 1994.) The results have consistently shown (a) strong sensitivity in the language network, (b) little

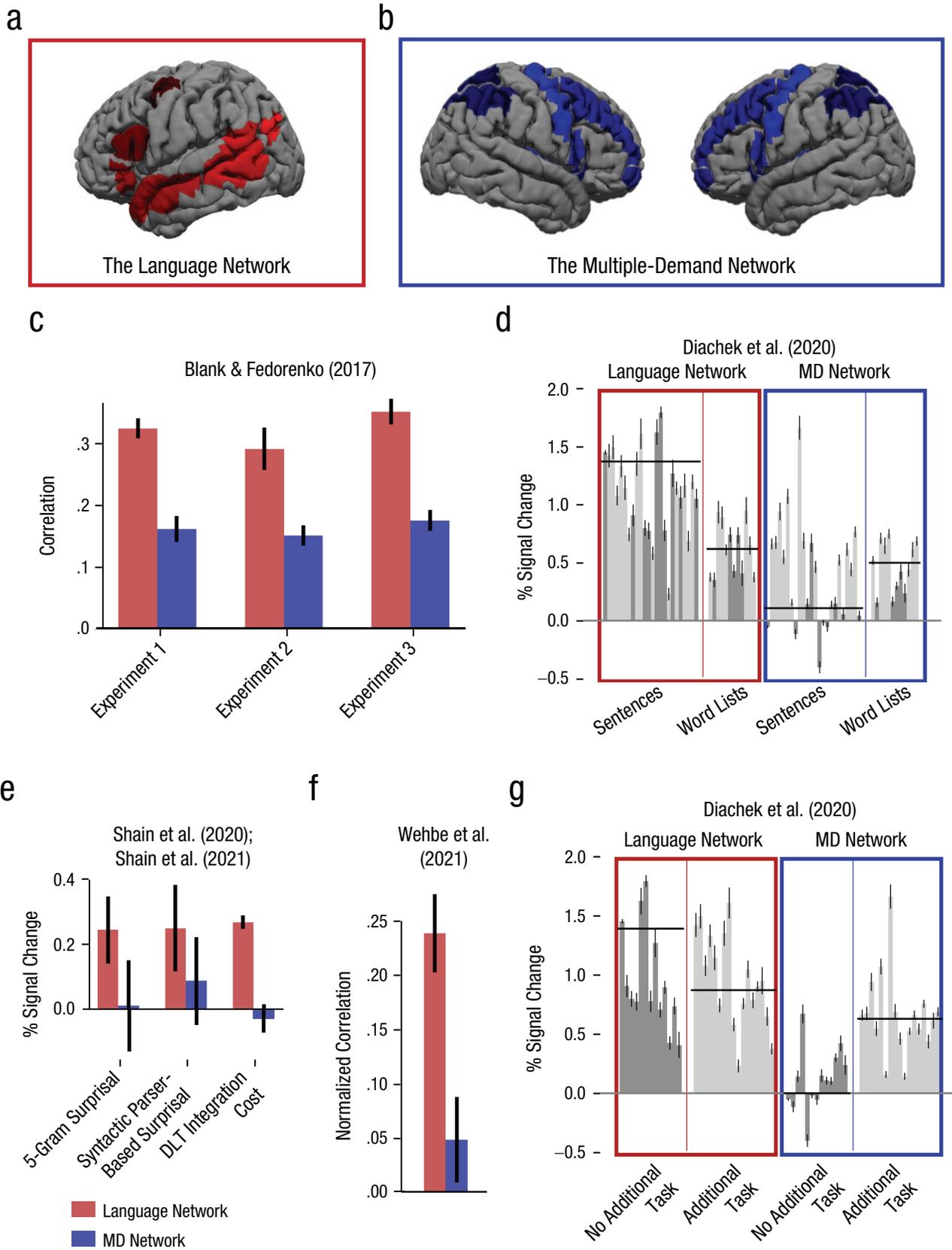


Fig. 2. (continued on next page)

Fig. 2. Location of the language and multiple-demand (MD) networks and evidence that putatively domain-general cognitive operations important for language processing are carried out locally within the language system, rather than the MD network. The brain images show the location of the (a) language and (b) MD networks as identified by group-level patterns of activation in response to sentences versus nonword lists (Fedorenko et al., 2011) and hard versus easy working memory tasks (Fedorenko et al., 2013), respectively. These locations were used to constrain the definition of functional regions of interest in each individual participant in all the studies whose results are presented in the graphs (c–g). The graphs summarize recent functional MRI findings showing that the language, but not the MD, network responds to diverse aspects of language comprehension. Results are averaged across the regions within each network, but the patterns also hold for each region individually. The graph in (c) shows the correlation in neural response across participants in each network during naturalistic story comprehension (Blank & Fedorenko, 2017). The correlation was stronger in the language network than in the MD network, which suggests that stimulus tracking was stronger in the language network. The graph in (d) shows the response of each network during processing of sentences and word lists (Diachek et al., 2020). The average response across participants and experiments, indicated by the horizontal lines, revealed that the language network was more strongly engaged for sentences than for word lists, but the opposite pattern held in the MD network. (Darker gray bars show results from passive reading and listening experiments, and lighter bars show results from experiments in which language processing was accompanied by a secondary task (e.g., a memory probe, comprehension, or sentence judgment task). The graph in (e) shows effects of 5-gram surprisal (Shain et al., 2020), syntactic parser-based surprisal (i.e., surprisal derived from a computational model of syntactic structure building; Shain et al., 2020), and integration cost (Shain et al., 2021) in each network during naturalistic story comprehension. Integration cost was operationalized as in the dependency locality theory (DLT; Gibson, 2000). The language, but not the MD, network was sensitive to all three measures. The graph in (f) shows the performance of reading times (a measure of comprehension difficulty) in self-paced reading and eye tracking during reading (quantified as the correlation between model predictions and observed responses in out-of-sample data) as predictors of activity in the two networks (Wehbe et al., 2021). The language, but not the MD, network was robustly sensitive to comprehension difficulty. The graph in (g) shows the response of each network during passive reading or listening and when language comprehension was accompanied by an additional task (Diachek et al., 2020). The language network responded robustly during language comprehension regardless of the presence or absence of an extraneous task, but the MD network responded only in the presence of an extraneous task. Horizontal lines correspond to averages across participants. Error bars indicate ± 1 SEM by participants in (c), (d), (f), and (g) and ± 1 SEM by functional region of interest in (e).

response in the MD network, and (c) significantly stronger responses in the language network than the MD network for every investigated component of natural-language comprehension, including word predictability, working memory retrieval, and generalized measures of language comprehension difficulty. Together, these findings support the existence of a self-sufficient specialized language system that carries out the bulk of language-related processing demands.

The MD Network Does Not Closely Track the Linguistic Signal

Activity in a brain region or network that supports linguistic computations should be modulated by the properties of the linguistic stimulus. One method for estimating the degree of stimulus-linked activity (or stimulus *tracking*), developed by Hasson and colleagues (e.g., Hasson et al., 2010), is based on the correlations across individuals during the processing of naturalistic stimuli. The logic is as follows: If a brain region or network processes features of a stimulus, different individuals should show similar patterns of increases and decreases in neural response in that region or network over time. Note that this method makes no assumptions about what features in the stimulus are important, so it provides a theory-neutral way to estimate the degree of stimulus-linked activity. In three experiments, Blank and Fedorenko (2017) investigated synchrony in neural

response across individuals during naturalistic language processing and found strongly stimulus-linked responses in the language network, as expected. Critically, however, the MD network exhibited substantially lower levels of stimulus-linked activity (Fig. 2c). To rule out the possibility that the MD network tracks linguistic stimuli closely but in a more variable way across individuals than the language system does, Blank and Fedorenko also examined within-participant correlations to multiple presentations of the same stimulus. Within-participant correlations in the MD network were lower than within-participant correlations in the language network and about as low as between-participants correlations in the MD network. This result indicates that the MD network's activity is less strongly modulated by changes in the linguistic signal than is the activity of the language network.

The MD Network Does Not Show a Core Functional Signature of Language Processing

Natural-language sentences exhibit rich patterns of syntactic (e.g., Chomsky, 1957) and semantic (e.g., Montague, 1973) structure that are not present in perceptually matched stimuli, such as lists of unconnected words or nonwords. Processing syntactic and semantic dependencies is widely thought to impose a computational burden (e.g., S. Lewis & Phillips, 2015), and thus an expected signature of language processing is an increased neural

response to sentences relative to control stimuli that lack structure. The language network robustly bears out this prediction (e.g., Fedorenko et al., 2011). In a recent large-scale study, Diachek et al. (2020) investigated whether the same is true of the MD network. Their sample consisted of fMRI responses from 481 participants, each of whom completed one or more of 30 language-comprehension experiments varying in linguistic materials. Some experiments included sentences, others included lists of unconnected words, and still others included both of these stimulus types. Results replicated past findings of stronger responses in the language network during the processing of sentences compared with word lists, but showed systematically greater MD engagement during the processing of word lists than during the processing of sentences, plausibly a reflection of the greater difficulty of encoding unstructured stimuli (Fig. 2d). This pattern is inconsistent with generalized MD involvement in sentence comprehension.

The MD Network Does Not Show Effects of Word Predictability

Effects of word predictability are robust in behavioral (e.g., Ehrlich & Rayner, 1981) and electrophysiological (e.g., Kutas & Hillyard, 1984) measures of human language processing, and it has been argued that frontal and parietal cortical areas—likely within the MD network—encode expectancies across domains (e.g., Corbetta & Shulman, 2002), including language (Strijkers et al., 2019). Thus, one possible role for the MD network in language processing is to encode incremental prediction error. With our colleagues, we (Shain et al., 2020) investigated this possibility by analyzing measures of word-by-word *surprisal* (e.g., Levy, 2008) in fMRI responses to naturalistic audio stories.¹ We examined effects of surprisal estimates based on both word sequences (5-gram surprisal models that predict the next word on the basis of the preceding four words) and syntactic structures (probabilistic context-free grammar models that predict the next word on the basis of an incomplete syntactic analysis of the unfolding sentence). These estimates of surprisal had significant (and separable) effects in the language network, but neither 5-gram surprisal nor syntactic parser-based surprisal had a significant effect in the MD network (Fig. 2e, first two sets of bars). Thus, whereas the results support the existence of a rich predictive architecture that exploits both word co-occurrences and syntactic patterns, this architecture appears to rely on a mechanism housed in language-specific cortical circuits, rather than on a domain-general predictive coding mechanism that may reside in the MD network.

The MD Network Does Not Show Effects of Syntactic Integration

Influential theories of human sentence comprehension posit a critical role for working memory retrieval in integrating words into an incomplete parse of the unfolding sentence (e.g., Gibson, 2000). Given that working memory is thought to be one of the core functions supported by the MD network (Duncan et al., 2020), one plausible role for this network in language comprehension is as a working memory resource for syntactic structure building. We (Shain et al., 2021) investigated this possibility by exploring the contribution of multiple theory-derived measures of working memory cost to explaining variance in the language and MD networks' responses to naturalistic linguistic stimuli. The language network showed a systematic and generalizable (to an unseen data portion) response to variants of *integration cost* as proposed by Gibson's (2000) dependency locality theory. Gibson posited that constructing syntactic dependencies incurs a retrieval cost proportional to the number of intervening elements that compete referentially with the retrieval target. This pattern did not hold in the MD network (Fig. 2e, third set of bars), where activity did not reliably increase with measures of integration cost (or other types of working memory demand explored in the study). Thus, whereas these results support a role for working memory retrieval in naturalistic language processing, they indicate that the working memory resources that support such computations reside in language-specific circuits, and that working memory resources housed in the MD network play little role.

The MD Network Does Not Show Effects of Comprehension Difficulty

The foregoing results challenge the hypothesis that the MD network plays a role in two of the core classes of computation posited by current theorizing in human sentence-processing research: prediction (e.g., Levy, 2008) and integration (e.g., Gibson, 2000). However, it is infeasible to enumerate and test the many other possible computations involved in human language processing—including those not covered by existing theory—in which MD may play a role. In another study (Wehbe et al., 2021), we bypassed this limitation by leveraging independent measures of reading times to predict fMRI responses to naturalistic stories. Reading times are widely regarded in psycholinguistics as reliable, theory-neutral proxies for language-comprehension difficulty and are commonly used as dependent variables to test hypotheses about the determinants of

comprehension difficulty (Rayner, 1998). Using this measure enabled us to test whether comprehension difficulty in general registers in the MD network, without precommitting to a particular theory of sentence processing. We found that activity in the language, but not the MD, network showed a strong effect of comprehension difficulty as measured by reading times (Fig. 2f). Thus, the MD network is unlikely to play a critical role in the computations that govern incremental (word-by-word) language-comprehension difficulty, regardless of how this difficulty is explained theoretically.

The MD Network Does Not Respond During Comprehension in the Absence of Extraneous Task Demands

This lack of evidence for the MD network's engagement during language processing appears to contradict many prior reports of activity in what appear to be MD regions during language processing (e.g., Novick et al., 2005). Critically, such results have almost always been obtained when word or sentence comprehension has been accompanied by an extraneous task, which may engage the MD network given its robust sensitivity to task demands (Duncan et al., 2020). Diachek et al. (2020) investigated this possibility by contrasting the MD network's engagement in language experiments that involved passive comprehension (visual or auditory) with its engagement in experiments that involved an additional task, such as responding to memory probes, answering comprehension questions, or judging semantic associations. Whereas the language network was equally engaged in the presence and the absence of an additional task, the MD network was engaged only in the presence of an additional task (Fig. 2g). In other words, passive language comprehension is sufficient to engage language-selective regions, but not MD regions, which suggests that MD engagement during language comprehension is primarily induced by nonlinguistic task demands (see Discussion).

Discussion

The evidence presented here challenges the hypothesis that domain-general executive resources support core computations of incremental language processing. The MD network (Duncan et al., 2020), where such resources are likely housed, does not closely track linguistic stimuli; responds more robustly to less language-like materials (e.g., more robustly to lists of unconnected words than to sentences); does not show evidence of engagement in predictive linguistic processing, retrieval of previously encountered linguistic elements from working

memory, or any other linguistic operation that leads to comprehension difficulty during language processing; and, unlike the core language network, is not engaged by passive comprehension, instead becoming engaged only in the presence of a secondary task (e.g., memory probe or sentence judgments, Figs. 2c–g). These findings greatly constrain the space of plausible language-related computations that the MD network might support and align with the architecture outlined in Figure 1b. In particular, it appears that the network that stores linguistic knowledge representations is also the network that performs all the relevant computations on these representations in the course of incremental comprehension, despite the fact that many of these computations may be similar to, or the same as, computations used in other domains.

Why have prior studies reached different conclusions about the reliance of language processing on domain-general resources? The answer is likely twofold. First, for many years, researchers have not clearly differentiated between the language-selective and the domain-general circuits that cohabit the left frontal lobe but are robustly and unambiguously distinct (see Fedorenko & Blank, 2020, for discussion). This failure to separate the two networks is due to a combination of (a) traditional group-averaging analyses, which blur nearby functionally distinct regions, especially in the association cortex, where the precise locations of such regions differ across individuals (e.g., Frost & Goebel, 2012), and (b) frequent reverse inference from coarse anatomical locations (i.e., concluding that a cognitive function was involved because anatomical brain areas previously associated with that function were active; e.g., Poldrack, 2006). Second, many prior studies have used paradigms in which word or sentence comprehension is accompanied by a secondary task and/or the linguistic materials used are highly artificial. Such paradigms may indeed recruit the MD network, which is robustly sensitive to task demands, but this recruitment does not speak to the role of this network in core linguistic operations such as lexical access, or syntactic or semantic structure building. For these reasons, we have focused our review on studies that (a) relied on well-validated functional localizers (Fedorenko et al., 2011) to identify the language and MD networks within each individual brain and (b) used naturalistic comprehension tasks (Hasson et al., 2018). Such studies converged on a clear answer: The domain-general MD network does not support core linguistic computations.

The fact that the language system appears to locally implement general computations such as memory retrieval, prediction, and structure building suggests that local computation may systematically accompany

functional specialization. This conjecture aligns with prior arguments for a tight integration between memory and computation at the neuronal level (Dasgupta & Gershman, 2021; Hasson et al., 2015). If a particular stimulus (be it a face, spatial layout, high-pitched sound, or linguistic input) is encountered with sufficient frequency to support specialization in particular circuits, then it may be advantageous for those circuits to carry out as much processing as possible in that domain, given that local computation may reduce processing latencies that would result from interactive communication with other systems (Chklovskii & Koulakov, 2004). Nevertheless, novel cognitive demands regularly arise, and it is infeasible to dedicate cortical “real estate” to each of them. A general-purpose cognitive system like the MD network is therefore indispensable to robust and flexible cognition (Duncan et al., 2020), including the critical ability to solve novel problems. Indeed, recent computational-modeling work has shown that an artificial neural network trained on multiple tasks will spontaneously develop functionally specialized subnetworks for different tasks; however, if new tasks are continually introduced, a subset of the network will remain flexible and not show a preference for any known task (Yang et al., 2019).

Although the studies summarized here rule out a large set of possibilities for the role of the MD network in language processing, more work is needed to evaluate the role of this network in language production, in more diverse linguistic phenomena (e.g., pragmatic inference, including during conversational exchanges), and in recovery from damage to the language network (e.g., Hartwigsen, 2018). Furthermore, the contributions of (possibly domain-general) subcortical and cerebellar circuits to language comprehension and cognitive processing require additional investigation; future work may show overlap between linguistic and nonlinguistic functions in such circuits.

Conclusion

Despite the apparent similarity between the mental operations required for language comprehension and those required by other cognitive domains, the evidence we have reviewed here challenges the hypothesis that domain-general executive circuits (housed within the MD network) play a core role in language comprehension. We conjecture that such circuits similarly do not play a core role in other domains that rely on domain-specific representations, and that the core contribution of the MD network to human cognition lies in supporting flexible behavior and the ability to solve new problems.

Recommended Reading

- Dasgupta, I., & Gershman, S. J. (2021). (See References). A review in which the authors argue that memory, in the form of *memorization* (storing computational outputs for future use), may be a ubiquitous component of neural information processing, rather than the domain of a designated resource.
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172–179. <https://doi.org/10.1016/j.tics.2010.01.004>. A review of evidence for the existence of a broad, domain-general frontoparietal multiple-demand brain system that supports executive functions and fluid intelligence.
- Fedorenko, E., & Blank, I. A. (2020). (See References). A review in which the authors argue that Broca’s area contains functionally distinct subregions that belong to the language and multiple-demand networks and that conflation of these subregions in much prior work has led to substantial confusion in the field.
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences*, 107(25), 11163–11170. <https://doi.org/10.1073/pnas.1005062107>. A review of evidence for functional specialization in the human brain, with emphasis on the visual system and discussion of general implications for cognitive architecture and research methods.

Transparency

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Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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Note

1. Given a probability model p , surprisal I is the negative log probability of a word w_i given its preceding context: $I(w_i) = -\log[p(w_i|w_0 \dots w_{i-1})]$.

References

- Blank, I. A., & Fedorenko, E. (2017). Domain-general brain regions do not track linguistic input as closely as language-selective regions. *Journal of Neuroscience*, *37*(41), 9999–10011. <https://doi.org/10.1523/JNEUROSCI.3642-16.2017>
- Botvinick, M. M. (2007). Multilevel structure in behaviour and in the brain: A model of Fuster's hierarchy. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1615–1626. <https://doi.org/10.1098/rstb.2007.2056>
- Caplan, D., & Waters, G. S. (1999). Verbal working memory and sentence comprehension. *Behavioral & Brain Sciences*, *22*(1), 77–94. <https://doi.org/10.1017/S0140525X99001788>
- Chklovskii, D. B., & Koulakov, A. A. (2004). Maps in the brain: What can we learn from them? *Annual Review of Neuroscience*, *27*, 369–392. <https://doi.org/10.1146/annurev.neuro.27.070203.144226>
- Chomsky, N. (1957). *Syntactic structures*. Mouton.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. <https://doi.org/10.1038/nrn755>
- Dasgupta, I., & Gershman, S. J. (2021). Memory as a computational resource. *Trends in Cognitive Sciences*, *25*(3), 240–251. <https://doi.org/10.1016/j.tics.2020.12.008>
- Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3–6), 487–506. <https://doi.org/10.1080/02643290244000239>
- Diachek, E., Blank, I., Siegelman, M., Affourtit, J., & Fedorenko, E. (2020). The domain-general multiple demand (MD) network does not support core aspects of language comprehension: A large-scale fMRI investigation. *Journal of Neuroscience*, *40*(23), 4536–4550. <https://doi.org/10.1523/JNEUROSCI.2036-19.2020>
- Duncan, J., Assem, M., & Shashidhara, S. (2020). Integrated intelligence from distributed brain activity. *Trends in Cognitive Sciences*, *24*(10), 838–852. <https://doi.org/10.1016/j.tics.2020.06.012>
- Ehrlich, S. F., & Rayner, K. (1981). Contextual effects on word perception and eye movements during reading. *Journal of Verbal Learning and Verbal Behavior*, *20*(6), 641–655. [https://doi.org/10.1016/S0022-5371\(81\)90220-6](https://doi.org/10.1016/S0022-5371(81)90220-6)
- Fedorenko, E., Behr, M. K., & Kanwisher, N. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences, USA*, *108*(39), 16428–16433. <https://doi.org/10.1073/pnas.1112937108>
- Fedorenko, E., & Blank, I. A. (2020). Broca's area is not a natural kind. *Trends in Cognitive Sciences*, *24*(4), 270–284. <https://doi.org/10.1016/j.tics.2020.01.001>
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences, USA*, *110*(41), 16616–16621. <https://doi.org/10.1073/pnas.1315235110>
- Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: Evidence from neuroimaging and neurological patients. *Annals of the New York Academy of Sciences*, *1369*(1), 132–153. <https://doi.org/10.1111/nyas.13046>
- Fitch, W. T., & Martins, M. D. (2014). Hierarchical processing in music, language, and action: Lashley revisited. *Annals of the New York Academy of Sciences*, *1316*(1), 87–104. <https://doi.org/10.1111/nyas.12406>
- Frost, M. A., & Goebel, R. (2012). Measuring structural-functional correspondence: Spatial variability of specialised brain regions after macro-anatomical alignment. *NeuroImage*, *59*(2), 1369–1381. <https://doi.org/10.1016/j.neuroimage.2011.08.035>
- Gibson, E. (2000). The dependency locality theory: A distance-based theory of linguistic complexity. In A. P. Marantz, Y. Miyashita, & W. O'Neil (Eds.), *Image, language, brain: Papers from the first Mind Articulation Project symposium* (pp. 95–126). MIT Press. <https://doi.org/10.7551/mitpress/3654.003.0008>
- Hartwigsen, G. (2018). Flexible redistribution in cognitive networks. *Trends in Cognitive Sciences*, *22*(8), 687–698. <https://doi.org/10.1016/j.tics.2018.05.008>
- Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory: Memory as an integral component of information processing. *Trends in Cognitive Sciences*, *19*(6), 304–313. <https://doi.org/10.1016/j.tics.2015.04.006>
- Hasson, U., Egidi, G., Marelli, M., & Willems, R. M. (2018). Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension. *Cognition*, *180*, 135–157. <https://doi.org/10.1016/j.cognition.2018.06.018>
- Hasson, U., Malach, R., & Heeger, D. J. (2010). Reliability of cortical activity during natural stimulation. *Trends in Cognitive Sciences*, *14*(1), 40–48. <https://doi.org/10.1016/j.tics.2009.10.011>
- Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron*, *50*(6), 963–974. <https://doi.org/10.1016/j.neuron.2006.05.017>
- Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, *307*(5947), 161–163. <https://doi.org/10.1038/307161a0>
- Levy, R. (2008). Expectation-based syntactic comprehension. *Cognition*, *106*(3), 1126–1177. <https://doi.org/10.1016/j.cognition.2007.05.006>
- Lewis, R. L. (1996). Interference in short-term memory: The magical number two (or three) in sentence processing. *Journal of Psycholinguistic Research*, *25*(1), 93–115.
- Lewis, S., & Phillips, C. (2015). Aligning grammatical theories and language processing models. *Journal of*

- Psycholinguistic Research*, 44(1), 27–46. <https://doi.org/10.1007/BF01708421>
- Martin, R. C., Shelton, J. R., & Yaffee, L. S. (1994). Language processing and working memory: Neuropsychological evidence for separate phonological and semantic capacities. *Journal of Memory and Language*, 33(1), 83–111. <https://doi.org/10.1006/jmla.1994.1005>
- Montague, R. (1973). The proper treatment of quantification in ordinary English. In K. J. J. Hintikka, J. M. E. Moravcsik, & P. Suppes (Eds.), *Approaches to natural language: Proceedings of the 1970 Stanford Workshop on Grammar and Semantics* (pp. 221–242). D. Reidel.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, & Behavioral Neuroscience*, 5(3), 263–281. <https://doi.org/10.3758/CABN.5.3.263>
- Patel, A. D. (2003). Language, music, syntax and the brain. *Nature Neuroscience*, 6(7), 674–681. <https://doi.org/10.1038/nn1082>
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, 10(2), 59–63. <https://doi.org/10.1016/j.tics.2005.12.004>
- Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, 124(3), 372–422. <https://doi.org/10.1037/0033-2909.124.3.372>
- Shain, C., Blank, I. A., Fedorenko, E., Gibson, E., & Schuler, W. (2021). *Robust effects of working memory demand during naturalistic language comprehension in language-selective cortex*. BioRxiv. <https://doi.org/10.1101/2021.09.18.460917>
- Shain, C., Blank, I. A., van Schijndel, M., Schuler, W., & Fedorenko, E. (2020). fMRI reveals language-specific predictive coding during naturalistic sentence comprehension. *Neuropsychologia*, 138(17), Article 107307. <https://doi.org/10.1016/j.neuropsychologia.2019.107307>
- Strijkers, K., Chanoine, V., Munding, D., Dubarry, A.-S., Trébuchon, A., Badier, J.-M., & Alario, F.-X. (2019). Grammatical class modulates the (left) inferior frontal gyrus within 100 milliseconds when syntactic context is predictive. *Scientific Reports*, 9(1), Article 4830. <https://doi.org/10.1038/s41598-019-41376-x>
- Tanenhaus, M. K., Spivey-Knowlton, M. J., Eberhard, K. M., & Sedivy, J. C. (1995). Integration of visual and linguistic information in spoken language comprehension. *Science*, 268(5217), 1632–1634. <https://doi.org/10.1126/science.7777863>
- Wehbe, L., Blank, I. A., Shain, C., Futrell, R., Levy, R., von der Malsburg, T., Smith, N., Gibson, E., & Fedorenko, E. (2021). Incremental language comprehension difficulty predicts activity in the language network but not the multiple demand network. *Cerebral Cortex*, 31(9), 4006–4023. <https://doi.org/10.1093/cercor/bhab065>
- Yang, G. R., Joglekar, M. R., Song, H. F., Newsome, W. T., & Wang, X.-J. (2019). Task representations in neural networks trained to perform many cognitive tasks. *Nature Neuroscience*, 22(2), 297–306. <https://doi.org/10.1038/s41593-018-0310-2>