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REVIEW ARTICLE

Review of the Neural Correlates of Intelligence and Convergence on a Holistic Approach

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ABSTRACT: For over a century, scientists have sought to uncover the neurological correlates of intelligence. With recent advancements in neuroimaging technology, neuroscientists have been converging upon the neurological correlates of intelligence. This review compiles the most current and relevant evidence, from all perspectives, concerning the manifestation of intelligence in the brain. A network-based approach to intelligence was utilized during this review, relying on the flexible interactions between the intrinsic connectivity networks to explain intelligence. Indeed, the brain's most important intrinsic connectivity networks were the frontoparietal control network and the cingulo-opercular network, the brain's two control networks. The review begins with understanding the neural correlates of intelligence task processing and intelligence differences. Then, the final section of this review reveals the two most important threads connecting the various perspectives on intelligence: neural networks and neural flexibility. Through these threads, this review attempts to identify the neurological core of intelligence, opening the door for convergence upon a holistic approach to intelligence in the near future.

KEYWORDS: Behavioral and Social Sciences, Neuroscience; Intelligence; Perspectives; Networks; Flexibility.

Introduction

Intelligence, defined by the American Psychological Association as "the ability to derive information, learn from experience, adapt to the environment, and correctly utilize thought and information," has remained a topic of debate within the neuroscientific community. There have been many prominent theories that attempt to understand the neurological basis of intelligence, including the Neural Efficiency Hypothesis,[1] Parieto-Frontal Integration Theory (P-FIT),[2] and the Multiple-Demand (MD) Theory,[3] the Process Overlap Theory,[4] and The Network Neuroscience Theory of Intelligence.[5] This review attempts to cover the extensive evidence pertaining to intelligence to combine these various theories of intelligence into a more holistic view of intelligence in the brain. By no means will this review be able to cover every finding and every aspect of the neurological correlates of intelligence, but this review serves to highlight the most important aspects of the brain for intelligence.

Broadly, this review will analyze the neural correlates of intelligence through the connectivity of the major intrinsic connectivity networks (ICNs) within the brain. First, the review will examine the neural correlates of intelligence task processing through the functional and structural connectivity of the brain's ICNs. Next, the neural correlates of intelligence differences will be investigated, examining how the system outlined in the first section is augmented in higher-intelligent individuals. Last, the various intelligence models will be connected to produce a more holistic approach to the neural correlates of intelligence. Because this review doesn't attempt to propose a new theory of intelligence but rather identify the most important neural components for intelligence, this review will be more descriptive of intelligence than prescriptive.

Discussion

In 1904, Spearman recognized that a common factor, g, existed among the diverse cognitive abilities contributing to intelligence.[6] Jung & Haier in 2007 felt poised to answer the question regarding the neural correlates of intelligence (*g*). Similarly, I am poised to expand upon their model and others by combining the regional associations of intelligence with the connectivity dynamics associated with intelligence. This analysis will explain multiple questions related to the neural correlates of intelligence: what neural dynamics underlie the human ability to approach a task? How are the functional and structural dynamics of the ICNs manipulated to increase human intelligence capabilities? Finally, how do these findings bring together the theories of intelligence?

Intelligence Task Processing :

This section attempts to answer the first question: *what neural dynamics underlie the human ability to approach an intelligence task?* In 2007, Jung & Haier compiled an extensive review of studies that examined the regions involved in intelligence. Combining functional and structural associations, Jung & Haier implicated regions within the dorsolateral prefrontal cortex (DLPFC), superior parietal lobule, inferior parietal lobule, anterior cingulate cortex (ACC), temporal lobes, and occipital lobe.[2] Jung & Haier compile these regions into the Parieto-Frontal Integration Theory (P-FIT), which outlines six stages of intelligence processing. This stage of the review will be similar in that respect, with the following stages of intelligence processing: (1) Humans gather and process sensory information through auditory and visual means, triggering a task-positive neural state; (2) As basic perceptual processing is fed forward to the control regions, downstream control is initiated; (3) Rule generation begins, with the control regions

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flexibly recruiting downstream regions to obtain task-relevant information; (4) Once a rule is reached, this rule is applied through downstream working memory manipulation to find a solution; (5) The cingulo-opercular network (CON) sends this solution down towards the striatum which sends the motor response down to deeper subcortical structures; (6) Errors in intelligence processing are recognized by the CON and the frontoparietal control network (FPCN) facilitates the changes in downstream control necessary to correct the mistake.

It is important to note that the research devoted to task-processing dynamics associated with intelligence is relatively small. So, this section primarily consists of studies on cognitive control, which will be augmented by the few studies that discuss relevant task-processing features of intelligence. Since intelligence is a flexible means of implementing cognitive control, this approach is relevant, and I believe I can elucidate many important facets of intelligence that otherwise go unrecognized. Further, minute temporal dynamics are largely unknown for the neural processes in intelligence tasks. Using more recent scientific evidence, this section proposes a model for the processes our brain undergoes in attempting to solve intelligence tasks and suggests possible mechanisms that these networks use to achieve these functions. This model does not try to explain the temporal dynamics for intelligence tasks fully but instead organizes our current evidence of neural processing during intelligence tasks into a coherent temporal framework.

As individuals prepare for an intelligence task, the brain must be driven into a task-positive state from a resting state. Recent evidence has suggested that the dorsal posterior cingulate cortex (dPCC) is a perfect candidate for this function. With the PCC being the central hub of the default mode network (DMN), the dPPC has extensive connections to DMN nodes. Still, it is also widely connected with many other intrinsic connectivity networks, including the FPCN, CON, and dorsal attention network (DAN).[7-11] The widely integrative functional connectivity of the dPCC indicates greater functional relevance beyond the DMN, and recent evidence supports this claim. The dPCC is very active when individuals wait for an external cue to action, which involves high vigilance. However, activity falls when externally-directed attention on a specific task has been initiated.[10] From these results, Leech and colleagues conclude that the dPCC controls the balance between internally and externally directed control.[10] The mechanisms through which the dPCC enables the transition between attentional states is by influencing global metastability within the brain.[12] Metastability is a vague concept in the neuroscientific literature. However, this review utilizes Leech and Sharps' definition of metastability, where metastability reflects the variability of neural activity within the ICNs over time.[12] High metastability, reflecting highly variable neural activity, was associated with high PCC activity and enabled rapid transitions between neural states.[13] Therefore, the PCC likely tunes the brain's metastability, enabling the brain to enter a broadly focused state that enables highly flexible adjustments of neural connectivity to meet incoming demands.

Once the task begins, sensory stimuli flood our cortical sensory systems. Since the visual system is the most likely source of task-relevant information during intelligence tasks, this review will focus on its mechanisms specifically. The visual system hierarchy begins with specific feature processing in the striate and extrastriate cortex. The feedforward projections then divide along the ventral and dorsal pathways, encapsulating the visual system's 'what' and 'where' pathways, responsible for object recognition and the spatial location of an object, respectively.[14] With greater relevance later in the review, the temporal cortex is involved in object recognition processing, while the parietal cortex is responsible for the spatial location processing for visual stimuli. As the stimuli are fed forward, the attention networks likely become activated and begin the downstream control of visual regions. Indeed, evidence suggests that the ventral attention network (VAN) can redirect the DAN to unexpected or unattended stimuli,[15] providing a mechanism for attentional resources being directed towards new task-relevant stimuli. The initial attentional focus would aid in identifying the object and spatial location identification.

The right anterior insula (aINS) likely enables the switch between DMN and FPCN activity, initiating control signals and giving the FPCN access to salient external and internal information.[16] This evidence implicates the CON in utilizing the high metastability facilitated by the dPCC to transition global network activity into the specific task-relevant activation patterns necessary to meet task demands. The CON is responsible for task-set maintenance and control allocation,[29, 32-35] and the ability to direct global network activity to task-relevant states might be a mechanism the CON uses to achieve these functions.

Proper modulation of incoming information is necessary to prevent the control networks from reaching cognitive capacity. It provides the control networks with sufficient information to direct their neural control in behaviorally salient ways. The feedforward communication to the prefrontal cortex occurs through both corticocortical connections and subcortical modulatory pathways. Cocchi and colleagues demonstrated that the FPCN and CON could rapidly and flexibly obtain information processed by other specialized systems such as DMN, visual, and sensorimotor systems to achieve optimal goal-directed behavior.[17] In filtering unnecessary information, the subcortical systems direct the control systems in goal-oriented ways while reducing the control systems' cognitive load. The mesocortical dopamine system has been demonstrated to be one of the significant modulatory systems. It initiates and maintains motivation in the brain,[18] and prepares the prefrontal cortex (PFC) for incoming sensory information through dopaminergic pathways connecting the midbrain to the PFC.[19,20] Indeed, dopamine can excite or inhibit information transmission, filtering sensory information received by the PFC and enabling information to be encoded into the working memory.[21-23] Another region within the mesocortical dopamine system, the striatum, is also relevant for directing the control networks toward task goals. Importantly, it must be noted that the striatum plays a more fundamental role in neural function than what will be covered in this review, with neuroscientists only beginning to understand its functions. With respect to intelligence, the striatum generates a future

response strategy faster than the prefrontal cortex.[24] When approaching an intelligence-based cognitive task, the problem is usually novel, requiring a rapidly constructed strategy for task completion that could not have been planned previously. Thus, the striatum is crucial in biasing control networks towards behaviorally salient processing according to rapidly constructed plans for goal completion.

More broadly, the basal ganglia likely functions like a switchboard activating the control networks while deactivating the DMN.[25] This function is very similar to the function of the CON described above, and it is unclear how these two mechanisms relate to one another; however, the basal ganglia may prime the control regions for incoming information, for which the CON is responsible for more direct activation of the FPCN. As such, the basal ganglia likely capitalize on the metastability provided by the dPCC to coordinate a goal-oriented plan and activate the control networks to assert control. A recent review outlined the importance of the thalamus as a gated relay station for cortical and subcortical connections.[26] Specifically, the thalamus has modulatory mechanisms that regulate the relay of information from sensorimotor regions and the basal ganglia to the brain's frontal regions. Recent evidence also points to bilateral regions in the anterior thalamus as being a critical node of the CON,[27,28] and the anterior thalamus likely assists in the functions of the CON that will be discussed later.

With information being fed to the control networks, control must be implemented by the control networks to achieve task goals. Understanding the structural connections of CON regions is critical for understanding how the CON functions during intelligence tasks. The dorsal anterior cingulate cortext (dACC) has a much more isolated role, likely being responsible for determining the when, where, and how of control allocation;[29] meanwhile, the aINS has a much more integrated role, detecting salient features for additional processing and directing other brain networks.[16,30,31] Together, these two regions are important for task-set maintenance and control allocation.[29,32-35] Task-set maintenance requires the maintenance of task state network dynamics and determining the relevant information. Downstream, the CON likely achieves stable implementation of task sets in sensorimotor regions,[36] serving as a mechanism for deciding relevant externally derived information. Upstream, the CON mediates the antagonism between the DMN and the FPCN,[37,38] regulating the influence of internal cognition on task sets. The CON's ability to successfully mediate the activity and connectivity of the FPCN and DMN regulates the flow of internal information toward the FPCN. It maintains the control network dynamics necessary for the task set. Implicit in the CON's ability to maintain the task set upstream is its ability to regulate control allocation. Evidence suggests that both the aINS and dACC influence control signals in the DLPFC,[16,39,40] with task-based integration between dACC, DLPFC, and aINS being critical for guiding and supporting phasic control according to task goals.[17] The influence of the dACC and aINS likely serve different roles in influencing DLPFC control, routed in the dACC's ability to allocate control and the aINS' ability to provide working memory and attentional processes access to salient, bottom-up information.[16,29]

Intelligence tasks often require manipulating an individual's internal representation of external stimuli according to some externally-presented or internal-generated rule. When a rule is given in the task, the mechanisms for generating the rule are likely to be bypassed; however, most tasks require individuals to uncover the rule. Among the two control networks, the FPCN likely generates a rule[41,42] using behaviorally salient information that must be maintained. At the same time, external stimuli are manipulated within our working memory based on the rule.[41,43-45] To understand how the FPCN obtains the necessary information to generate a rule, we must understand the functional connectivity of the FPCN regions. Recent evidence suggests that the FPCN exerts control on a rostral-caudal axis of abstraction,[46-52] and this axis roughly aligns with its two distinct subnetworks.[53-56] The rostral-caudal axis of abstractness contains rostral regions that are responsible for temporal control, facilitating the maintenance of internal representation for future-oriented processing; intermediary zones that are responsible for contextual control, enabling the integration of internal and external representations according to prevailing context; and caudal regions that are responsible for sensorimotor control, asserting attention directed towards stimulus-action selection. Interestingly, the cerebellum has also been found to exhibit the same rostral-caudal axis of control during cognitively demanding tasks,[57] and has even been implicated in working memory manipulation.[58-60] However, research on the cerebellum's role in intelligence is still relatively small, with more research required to understand the cerebellum's precise functional role in intelligence. The two distinct subnetworks, roughly aligned along this rostral-caudal axis, are defined by their coactivation patterns with other neural networks: the FPCN A is strongly connected to the DMN, while the FPCN B is strongly connected to the DAN.[53-56] Nee found that FPCN A is most strongly implicated in temporal control and FPCN B is most strongly implicated in sensorimotor control, consistent with their connectivity profiles and alignment to the rostral-caudal axis. Contextual control requires the involvement of both networks, but FPCN B is more aligned with contextual control activation.[61] These results make sense, considering that FPCN A aligns more with the rostral regions, whereas FPCN B aligns more with the caudal regions. This network alignment also ties the internally-oriented rostral regions to DMN connectivity and the externally-directed caudal regions to the DAN. Additionally, the rostral and caudal extremes of this axis show greater segregation of connectivity representing their more specialized functions, tied to their specific network connectivity profiles, whereas the intermediary zone, responsible for contextual control, is the central integrative region of the FPCN.[61] These results indicate that the two subnetworks can operate in segregative or integrative fashions according to task demands, but the integrative functioning of the FPCN in contextual control is crucial for higher-level cognitive abilities.[61-64]

The cortical structure of the FPCN intimates a potential mechanism that the FPCN could use to generate a rule re

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quired for task completion. The FPCN potentially mediates the activation of DMN and DAN nodes and facilitates the transfer of internal and external information to control regions from the DAN and DMN nodes.[65] Hearne and colleagues suggest that transient, task-specific activations of DMN regions are critical for task performance under specific contexts. Further, the transient recruitment of DMN nodes is mediated by the rostrolateral prefrontal cortex (RLPFC) - also known as the anterior prefrontal cortex (aPFC) and Brodmann Area (BA) 10.[25] For example, one region of the DMN recruited by the control networks is the PCC.[38,66,67] However, opposite functional connectivity patterns between the dPCC and ventral posterior cingulate cortex (vPCC) occur as cognitive demands increase.[11] The differing functional connectivity patterns reflect the importance of the RLPFC to effectively mediate DMN nodes relevant for intelligence processing. Further, the function of the angular gyrus in comprehending event concepts and mentally manipulating representations is advantageous in some contexts,[68] but the increased functional connectivity of the AG as complexity increases also appears to interfere with task performance.[25] Therefore, not all DMN connections to the FPCN are advantageous. At the same time, some are advantageous only in specific contexts, and proper mediation of the DMN nodes' functional connectivity with the FPCN is necessary for task goals. With the caudal regions of the FPCN being more connected to the DAN,[55,61] these regions are responsible for collecting externally salient information for task goals. With the DAN being considered a task-positive network, its involvement in intelligence is more straightforward than the DMN, epitomized by a recent study that demonstrated DAN activity most strongly correlated with fluid intelligence.[69] The internal and external information collected by the FPCN requires assimilation, considering this information is collected mainly in the more segregated regions of the FPCN. The intermediary zones are a perfect place for such integration since it is known for top-down modulations that sharpen representations.[70,71] Assimilating and subsequently sharpening the distinct internal and external representations would serve as a perfect mechanism to generate a rule given the specific task demands. Preliminary evidence supports this proposition, with the mid-DLPFC being responsible for hypothesis generation during inductive reasoning.[42] More research should be done to support these results across a broader range of cognitive abilities. Further, the left DLPFC is likely critical for integrating FPCN and CON activity for optimal control,[17] suggesting that this region integrates relevant information from the CON on top of the collected externally and internally relevant information when generating a rule and asserting downstream control.

Recent evidence has elucidated the potential functions of DMN nodes in intelligence tasks beyond feeding internal information toward frontal DMN regions. Transient, task-dependent coupling between the dPCC, DMN, and FPCN nodes enables the integration of externally and internally directed thought.[11] The dPCC may be the centerpiece of this coupling due to its ability to coordinate the activity of ICNs to achieve effective control.[12] Integrating internally and externally directed thought in the DMN, specifically, could tribute to its function in idea generation,[72] suggesting an alternative route outside of the FPCN for aiding the generation of a hypothesis. Recent evidence by Dixon and colleagues indicates that DMN-DAN functional connectivity isn't always anticorrelated, expressing windows of positive correlation which the authors suggest represents information transfer between the networks;[73] so, the DMN has a mechanism for incorporating external information independent of FPCN connections. However, the PCC's role in the DMN's generation of ideas isn't entirely independent of the FPCN since the PCC can transition from a DMN node to an FPCN node during task states.[10,11,74] The task-dependent recruitment of the PCC and its involvement in integrating internally and externally-directed thought suggests that the PCC is a connector between internally-generated ideas and the FPCN, potentially aiding in the FPCN's generation of task rules. Indeed, Beaty and colleagues suggest that the FPCN evaluates the ideas generated by the DMN,[72] proposing a mechanism through which the FPCN and DMN could work together on certain tasks. The specific dynamics between the DLPFC and PCC in facilitating rule generation aren't entirely clear; the PCC's recruitment and relay of ideas may be reserved for more internally demanding intelligence tasks. It is important to note that there are no functional associations between DMN nodes and working memory manipulation, supporting evidence indicating that working memory processes are eternally oriented.[69] In contrast, the PCC and its involvement in intelligence tasks will be internally oriented.

The process of determining the rule for a given task likely falls under the step of rule inference since a few rules may be generated that require testing before the best rule for the task can be identified. The process of testing and weeding through hypotheses requires the process of conflict monitoring, something that will be described later. Santarnecchi and colleagues conclude that FPCN and DAN activity is geared towards generating a rule. As individuals transition to the rule application phase, frontal lobe activity decreases while occipital lobe activity increases.[69] Recent evidence attempting to model the function of the neocortex based on its columnar structure provides a possible explanation for these frontal lobe results. Hawkins and colleagues simulated the ability of the neocortex to recognize objects in our environment.[75] When scanning an object, initial sensory input constitutes common feature detection, causing dense activation. This dense activation reflects the uncertainty of failing to recognize an object rooted in the lack of information. However, as we scan the object, we accumulate features of the object until we reach enough features to adequately recognize an object, usually occurring when at least one sufficiently uncommon feature allows us to recognize the object. Broad inhibition within the output layer helps to maintain the sparsity of activation patterns,[76,77] likely representing the need to maintain a specific representation, spread this information, and inhibit other representations. With the significant homogeneity of the neocortex,[78] some neuroscientists have claimed that the entirety of the neocortex functions in the same way,[79] and the synaptic connections are what differ

entiate regional differences in observed functions. Considering these implications, the LPFC, implicated in generating and maintaining the rule governing a task, would undergo the same process for rule generation as posterior regions undergo for object recognition. The maintenance of a specific representation through inhibition would explain decreased frontal activation during rule application compared to rule inference; the uncertainty regarding the rule required for a task generates dense activation within the LPFC, causing continued recruiting of internal and external information until a rule is reached and activation is diminished to only a single representation.

With convergence on a rule, the way our brain manipulates behavior to achieve task goals must be explored. However, understanding this requires understanding the mechanisms with which the control networks exert control. Cole and colleagues posited the "flexible hub theory," asserting that the FPCN is composed of "brain regions that flexibly and rapidly shift their brain-wide functional connectivity patterns to implement cognitive control across a variety of tasks."[80] This hypothesis attempts to answer questions regarding the FPCNs importance in adaptive control tasks using two FPCN mechanisms: global variable connectivity and compositional coding. The FPCN has been found to have extensive global connectivity and the highest global variability connectivity,[81] meaning the vast cortical connections of the FPCN are highly susceptible to rapidly and flexibly changing during intelligence tasks. Further, global connectivity differences of the FPCN have been correlated with cognitive control abilities and intelligence,[82] demonstrating its importance in intelligence tasks. Compositional coding requires the reuse of task elements across task contexts,[83-85] and these functions have been found within the FPCN.[86] Indeed, compositional coding appears to be analogous to object compositionality explored by Hawkins and colleagues,[75] who posit that novel objects can be identified through the composition of already-learned objects that comprise the novel object. Using their example, let's say we see a coffee cup with a logo on it that we have not seen before. We can utilize our pre-existing knowledge to create a representation of this coffee cup by identifying its component parts, namely, the plain coffee cup and the logo. Using this model, compositional coding allows the FPCN to combine previously existing task elements to construct a rule, or combination of rules, required to complete a novel task. Therefore, compositional coding has massive implications for intelligence, potentially explaining how the FPCN enables unique and flexible control according to a generated rule to meet novel task goals. The Flexible Hub Theory also supports the cognitive epochs proposed for the MD system of the primate brain. Duncan explains that different cognitive epochs during task states are represented by overlapping neuronal populations within the frontal brain regions,[3] findings supported by other recent research.[87,88] The overlapping neuronal populations explain the mechanism underlying compositional coding, and the unique activity patterns demonstrate how novel and flexible downstream control can be achieved.

The vast cortical control of the FPCN mediates two critical functions required for cognitive tasks: working memory and attention. While the DLPFC is a critical frontal component in the FPCN and is essential for both working memory and attentional tasks,[89-91] Watanabe and Funahashi demonstrated that these two functions recruited the activation of largely overlapping prefrontal populations.[92,93] Two important conclusions can be made from these results. First, attention and working memory are two closely related cognitive processes mediated by the FPCN; second, working memory and attentional allocation must fight for resources within the FPCN. The dACC, a region of the CON, has been implicated in inhibitory control and suppressing irrelevant information,[94] which was recently found to be important in rule application.[69] It is possible that the CON takes on the most crucial role in attentional control during rule application, enabling more neural space for the working memory processes of the FPCN. Still, more research is required to support this claim.

To meet task demands, rule application requires that the internal representation of external stimuli is manipulated in an individual's working memory according to the rule maintained. The FPCN has been implicated in manipulating information according to goal-directed behavior.[95] This section discusses the mechanism employed by the FPCN and regulated by the CON to facilitate mental manipulation toward task completion. The LPFC coordinates the working memory manipulation required to meet task goals, while the visual and language processing regions are the template where representations are manipulated. With the mid-LPFC being the main integration center of the FPCN and the major region in contextual control, it is likely the most important frontal region in asserting the working memory manipulation; however, the rostral and caudal regions undoubtedly assist the mid-LPFC in its downstream control and exert downstream control on their own. The RLPFC is unique to humans and is critical for higher cognitive abilities in humans.[96] The RLPFC mediates the context-specific implementation of a rule and the maintenance of that rule.[17,61] These results suggest that the RLPFC does the "thinking" we associate with facilitating the timely implementation of a rule. The RLPFC is vital for higher relational thinking,[97,98] making it important for functions such as analogical reasoning, applying rules to novel features, and reasoning using compound rules.[99-103] These functions of the RLPFC epitomize the adaptability required of human intelligence networks, allowing humans to apply rules to novel features, a necessity for most intelligence tasks. The caudal regions of the LPFC likely coordinate with the DAN to enable the requisite eye movements and downstream enhancement required to focus on the salient stimuli from one moment to the next. However, more research needs to be done on the specific downstream function of the caudal LPFC. While contextual control activation patterns suggest the mid-LPFC actively coordinates both internal and external working memory faculties, it is also possible that these results reflect the overlapping of FPCN A and FPCN B nodes within the mid-LPFC, representing separate internal and external access within the region. Whether the internal and external control remains segregated or becomes integrated into the mid-DLP

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FC, this region is undoubtedly the most important region for downstream working memory control.

Being the other region within the FPCN, the PPC has also been found to have the same rostral-caudal axis for cognitive control abstraction as the LPFC,[104] and it is tightly linked to the LPFC in facilitating the maintenance and manipulation of information in subserving goal-directed behavior.[105] Further, recent evidence suggests that the superior parietal cortex (SPC) is important for working memory manipulation;[45] however, it is still being determined whether the SPC exerts downstream control to achieve this or if it is the interface where working memory is manipulated. More work will need to be done to understand which possibility is correct for SPC functioning. Still, it is also possible that the SPC both exerts downstream control on more basic processing regions and serves as an interface for working memory manipulation. In line with the evidence presented above, the rostral PPC regions appear to play less of a role in intelligence tasks, likely due to their connections with internally-oriented cognition, which is reduced during intelligence tasks in most contexts.

Within this section, most of the discussion has focused on the individual functions of the FPCN and CON networks; however, their interplay is important for understanding task dynamics. As previously discussed, Cocchi and colleagues found that phasic, task-specific control according to task goals depends on the task-based integration of the dACC, aINS, and DLPFC.[17] This evidence directly links the CON's role as a control allocator to the downstream control by the FPCN. Throughout the duration of the task, one way in which the CON manages the control allocated is through the dACC's likely role in evaluating response conflict, encompassing both attentional processes and error detection.[106] While both generating and implementing a rule, this CON function ensures that the cognitive process is consistent and in accordance with external information. Notably, the RLPFC is an important region for mediating the task-dependent integration of the CON and FPCN, with increased integration with both the dACC and DLPFC as task difficulty increases.[17] This integration likely reflects increased response conflict and, therefore, an increased need to adjust control, emphasizing that the importance of FPCN-CON connectivity only goes so far with too much integration worsening performance.[17] Despite the maladaptiveness of too much integration, the connectivity serves an important purpose, allowing the FPCN to update downstream control by cognitive systems and flexibly adapt throughout a task and correct mistakes, critical functions of intelligence.

Assem and colleagues attempted to refine and update the MD system of the primate brain,[3,107] finding a network consisting almost exclusively of FPCN and CON regions associated with intelligence. The willingness to classify the FPCN and CON as one network during intelligence tasks underscores the importance of their interconnectedness during a task state. This tight association reflects the significance of the CON in setting parameters for information recruitment, maintaining the task set, allocating control, and responding to conflict. The possibility of the FPCN updating the CON when switching task sets provides further avenues for FPCN and CON connectivity to be adaptive during task states. Further research should be dedicated to expanding our understanding of the connectivity dynamics of these two control regions during intelligence tasks.

A vital strategy for approaching intelligence tasks appears to be dividing cognitive tasks into simpler subcomponents. This strategy has been implicated in better task performance and has correlated with fluid intelligence.[108] For example, in number sequence tasks where an individual is required to guess the following number in the sequence based upon the rule for the sequence, let us say the rule is +2, then -5. Humans divide the problem into +2 and THEN -5: we don't do these operations simultaneously. The division of a task into task components reduces cognitive load, explaining its utility during intelligence tasks. Neurologically, the cognitive epochs previously discussed provide a viable mechanism for dividing a task into components. The CON has been considered a flexible integrator of task-based goals,[109-111] so the CON could signal slight adjustments of control within the FPCN during the transition between different cognitive epochs of a single task. It is also possible that the striatum plays a role in the shift between task components considering the association between the striatum and intelligence in humans and the association between the striatum and the capacity to set-shift in rats.[112-117] The CON's function in detecting conflict may provide an avenue for its ability to transition between task components, where previously relevant information is no longer relevant and previously irrelevant information is now relevant. Thus, the CON recognizes the need for a change in activity and facilitates the required modification for the next cognitive epoch.

Further, the transition between task components can be eased if we are aware of the rule governing the next component and, for example, holding the rule -5 in our mind while we apply the rule +2. The RLPFC is likely responsible for maintaining an alternative course of action,[118] potentially providing a neural storage system for the rule governing the next task component.

Once a solution to an intelligence task has been identified, the internal solution must be converted into a behavior. This review has widely established that the control systems connect with subcortical structures, enabling the onset of task control, transitions between task sets, and potential transitions between task components. The subcortical structures have also been found to mediate the connection between the cortical systems and motor outputs. Hearne and colleagues found that linking acquired representations with specific actions depends on striatal activity.[25] Further, Bonelli and Cummings reviewed multiple frontal-subcortical circuits relevant to behavior. For example, the ACC circuit appears important in enabling motivated behavior, while the DLPFC circuit allows information organization to facilitate a response.[119] Another important control region with connections to subcortical structures is the pre-supplementary motor area (preSMA). A few recent studies suggest that the pre-supplementary motor area (preSMA) is within the CON and has connections to both the FPCN and caudate.[120-123] The cortical and subcortical connections of

the preSMA are important for its possible functions in higher-level aspects of motor control, including updating motor plans and learning new motor sequences.[124] These results demonstrate that multiple cortical-subcortical pathways enable the proper motor response necessary for intelligence tasks. Furthermore, dynamic interactions between these various circuits likely enable the unique motor outputs necessary depending on the task context.

The final important function of the control systems in relation to intelligence tasks is the ability to recognize and adapt following errors. As discussed earlier, Cohen and colleagues characterized the ACC as functioning in evaluating response conflict, encompassing both attentional processes and error detection.[106] Therefore, the CON is likely responsible for recognizing these errors and adjusting the attentional control to minimize the conflict. This hypothesis is supported by more recent findings in a decision-making task that suggests the CON functions as a performance report measure.[125] These results indicate the ubiquity of this ACC function that is critical for adequately completing intelligence tasks. Interestingly, the same study identifies the right FPCN, but not the left, in bringing about behaviorally salient changes.[125] These results have not been replicated in studies testing intelligence, so this functional lateralization may not apply to intelligence tasks. However, the results suggest that the FPCN is critical for making the required changes to support goal-directed behavior. This finding is consistent with this review thus far.

Intelligence Differences:

To examine the neural correlates of intelligence, it is not enough to only discuss the underlying network mechanisms that facilitate intelligence task completion; instead, neural correlates of intelligence differences must also be analyzed. The neural correlates of intelligence differences have primarily been examined through functional and structural associations between brain regions and psychometric intelligence tests. This review section will attempt to contextualize these regional findings into their underlying networks. Further, intelligence differences have also been examined through the speed of processing metrics. Notably, there has been discussion as to whether more general or specific tract efficiency is more beneficial. Last, the recent work in network neuroscience has introduced a third perspective on the neural correlates of intelligence differences. Overall, this section attempts to answer this question: *How are the functional and structural dynamics of the ICNs manipulated to increase human intelligence capabilities?*

The Parieto-Frontal Integration Theory:

While the steps of processing proposed in the P-FIT were expanded upon in the previous section, this section addresses the structural and functional differences subserving intelligence differences. Recently, the P-FIT was updated, and these updates included the introduction of results from studies after the P-FIT was published, the pruning of studies only to include those that involved intelligence differences, and the division of the negative functional associations, positive functional associations, and positive structural associations with psychometric intelligence.[116] The regions that Basten and colleagues have implicated in intelligence include the frontopolar cortex (RLPFC), the lateral PFC, the ACC, the preSMA, the insula, the parietal cortex, the PPC/precuneus, the temporal cortex, the occipital cortex, the caudate nuclei, and the midbrain. Since Basten and colleagues' revisions are more recent and narrowed towards the focus of this section - intelligence differences - the regional associations with intelligence analyzed in this paper will originate from their revisions rather than from Jung and Haier. In light of the updates to task-processing stages proposed in this review, the regional associations proposed by Basten and colleagues will be analyzed by the ways in which they augment network functioning within their task-processing roles.

Beginning with the visual processing system, positive functional and structural associations with intelligence were found in both the 'what' and 'where' visual pathways. For the structural associations, Basten and colleagues used only voxel-based morphometry (VBM) studies measuring gray matter volume,[116] so this analysis will focus solely on the utility of differences in gray matter volumes. Recent evidence suggests that the positive structural associations increased these regions' feature and object recognition capabilities. In a recent study, capacity was defined as the number of objects a network can learn and recognize without confusion.[126] Their results indicated that increasing the number of neurons in either the input or output layers of a cortical column or increasing the number of cortical columns within the region, given the column sizes are fixed, can all increase neural capacity.[126] So, the greater gray matter volume within the visual system would likely enable more efficient and accurate identification of objects and relevant features. This structural advantage could reduce demand on higher cognitive regions by reducing unnecessary information being relayed to these regions through more efficient identification of salient stimuli. Positive functional associations with intelligence were found in both the temporal cortex's object identification regions and the parietal cortex's spatial attention regions. These activation correlates are unlikely to reflect initial processing stages; instead, they potentially reflect a more robust recruitment of these regions in maintaining salient information or utilizing these regions' representations for working memory manipulation. Along these lines, the positive structural associations in the temporal cortex could increase the capacity for working memory manipulation, easing the transition between object representations.

Looking at the DMN, there were regional associations in the PCC and precuneus with intelligence. To begin, the PCC experienced positive structural associations with intelligence. Applying the findings for neural capacity to the PCC, the greater gray matter volume in the PCC facilitates greater neural capacity for PCC functions, including generating global metastability for shifts in attentional focus and integrating information necessary for control from various brain regions. The efficiency of these processes would enable greater global network flexibility in shifting attentional state and integrating control processes. The precuneus is a DMN hub that increases connectivity with FPCN during a task,[127] and Basten and colleagues found both positive and negative functional associations with intelligence.[116] Along with the PCC, the precuneus

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is important for integrating information from systems segregated at rest.[11, 128-130] Furt her, the precuneus is implicated in a wide array of functions, with spatial functions and navigation being the two most relevant for intelligence tasks.[131,132] The positive and negative functional associations with intelligence could relate to the selective recruitment of this region depending on task context or fine-grained activation and inhibition of precuneus subregions. Both selective recruitment and fine-grained recruitment would reflect the control networks' flexibility of regional recruitment according to task goals and suggest that higher-intelligent individuals can better recruit the precuneus functions and information necessary for a given task.

Looking at the FPCN, all three types of associations were present. In the FPCN's frontal regions, both the RLPFC and the LPFC experienced positive structural associations with intelligence. Fewer features were required to identify an object as the number of cortical columns increased during the simulation run by Hawkins and colleagues,[126] and viewing these results from the perspective of the FPCN's frontal regions, the larger number of cortical columns may reflect more efficient identification of the rule in a task, requiring less external and internal information to reach the rule. Not only can a rule be identified through fewer features, but increased gray matter volume in the caudal and rostral regions also allows for the more precise input of information. This is rooted in the mechanism through which capacity increases: greater gray matter volume warrants activity profiles of representations to have fewer overlapping patterns. This means that the information sent to the frontal regions is also likely to be more precise in higher-intelligent individuals, further quickening rule identification. The greater efficiency of rule generation is highly cost-effective, spending fewer resources on generating the rule and more on the downstream control required to complete task goals. Beyond structural associations, both positive functional and negative functional associations exist between the LPFC and intelligence. There are multiple ways to interpret the functional associations of the LPFC and psychometric intelligence. The LPFC likely experiences both stable and dynamic activation throughout a task and across task components due to properties outlined in the Flexible Hub Theory and this review. These activation patterns would make functional associations hard to parse, and it is possible that some studies found positive associations while others found negative associations due to varying contexts. It is also possible that finer-grained regions within the LPFC were associated with positive and negative associations, respectively. Second, the neural efficiency hypothesis suggests that higher-intelligent individuals experience less cortical activation than average-intelligence individuals on the same task.[1] The idea behind these results is that these tasks would require less cognitive demand of the higher-intelligent individuals, warranting less activation. Recent evidence also suggests the opposite is the case, where higher-intelligent individuals experience greater cortical activation than average-intelligent individuals.[133] These results were contingent upon the task's complexity, suggesting that the average-intelligent individuals gave up, demonstrating less LPFC activation. In contrast, higher-intelligent individuals were engaged in the task since they had the capabilities to solve the problem. So, the positive and negative functional associations found could depend upon the difficulty of the tasks used in the studies Basten and colleagues analyzed.[116] Both the flexible hub explanation and the neural efficiency explanation are plausible, and it is also possible that both are true simultaneously; however, further research is necessary to understand the cause of the findings.

Beyond the frontal lobe, the FPCN also contains regions within the PPC. The positive functional associations within the PPC were present along the entirety of the rostral-caudal gradient.[116] It is possible that these results support the feedforward recruitment of internally and externally salient information in the frontal lobe during rule generation; however, it is also possible that these associations relate to the manipulation of representations in one's working memory during Rule Application. Recent evidence may support the second possibility. As problems become more challenging, lower-intelligent individuals struggle more with task solving, likely routed in their worse ability to divide problems into simpler components or plan a problem-solving strategy.[108,134] Thus, higher-intelligent individuals are more likely to reach the mental manipulation stage of task completion. These results are supported by the notion that Rule Inference is marked by a high amount of frontal activation. In contrast, Rule Application sees a reduction in that frontal activity as resources are devoted to posterior regions.[69] Since lower-intelligent individuals spend longer in Rule Inference than higher-intelligent individuals, the lower-intelligent individuals would have frontal-heavy activation profiles that would cause them to have less parietal activation than higher-intelligent individuals. Further, positive functional associations in object recognition or language regions could reflect the active manipulation of these areas according to task goals. Research should be done to understand the temporal dynamics of these associations further.

The results of Basten and colleagues in the LPFC and PPC could also indicate activation patterns within the DAN.[116] Some regions associated with intelligence in the LPFC and PPC could overlap with DAN regions, such as the frontal eye fields, ventral premotor area, and the superior parietal lobule. The associations within these regions are predominately positive functional associations and suggest that greater DAN activity is associated with intelligence. These results would indicate that higher-intelligent individuals have greater resources directed toward the attentional processing of sensory stimuli, a finding supported by associations between DAN activity and fluid intelligence.[69] However, it is likely that the positive functional associations in these regions are indicative of both FPCN and DAN activity, subserving the overall goal of task completion. While the DAN maintains attentional focus on the external stimuli, the FPCN can manipulate this information with the working memory to meet task goals.

The CON was associated with all three types of associations. Beginning with the dACC, both positive and negative functional associations were found with intelligence. The most likely explanation relates to the flexible nature of the CON,[109-

[111] causing flexible activation of the dACC that subserves its main functions in conflict resolution, control allocation, and task-set maintenance. Another explanation could be rooted in the adjacency of ACC regions implicated in the CON and salience network (SN) networks. The SN is involved in "representing and responding to homeostatically relevant internal or external stimuli and imbuing these stimuli with emotional weight."[135] Emotional interference has been proven to affect cognitive control negatively,[136] so the emotional functioning of the SN is counterproductive to the completion of intelligence tasks. In contrast, CON activity is advantageous considering its functions in conflict resolution and task-set maintenance. Therefore, dACC functional associations may reflect better inhibition of SN and better activation of CON.

The preSMA regions experienced all three associations with intelligence. These associations likely aid in this region's motor preparation and execution. Applying the cortical column mechanism previously discussed,[126] both the functional associations exhibited by the preSMA and the structural associations within the SMA likely reflect greater convergence onto one motor plan. Greater convergence in higher-intelligent individuals could be caused by better problem-solving abilities, reducing uncertainty about what action to take, or through the more distinct neural activity of specific motor plans. Finally, the aINS didn't experience any associations with intelligence. Considerating its integrative role in CON functions, the amount of aINS activity is likely less important than the quality of that activation. Controlling global dynamics in a behaviorally salient way requires unique and flexible activation patterns but not necessarily more or less activation.

Additionally, reduced activation within the posterior insula (pINS) was associated with intelligence. Some studies have implicated the pINS in the CON.[35,125] Regardless of the pINS' connectivity to the CON, its role in representing interoceptive information about the body's physiological status isn't necessarily relevant in intelligence tasks.[137] So, the negative functional associations with intelligence could be due to a reduction in resources dedicated to this function, preventing these regions from interfering with the control required for task goals. In the CON broadly, functional and structural differences within the dACC appear most advantageous for intelligence. This suggests that the core for improving CON function is enhancing its specific cognitive abilities more than its global influence on brain dynamics.

What most differentiated the results from the P-FIT and its revisions is the addition of the caudate and the midbrain.[2,116] Basten and colleagues suggest that the structural associations of these two regions relate to their involvement in the mesocortical dopamine system.[116] For the caudate, recent evidence suggests that increased gray matter volume is correlated with better delay discounting and decreased impulsivity.[138,139] These studies indicate that gray matter volume in the caudate is critical for maintaining long-term goals. Applying these results to intelligence tasks, increased gray matter volumes in the caudate may enable higher-intelligent individuals to maintain focus on task completion better. The structural associations of the midbrain are also likely to aid in maintaining long-term goals during task conditions. In their review, Ott and Nieder demonstrate how the dopaminergic connections from the midbrain to the PFC reflect the perception of behaviorally salient information by the PFC, and the dopamine released enables the encoding of this information into working memory.[140] Indeed, the midbrain aids in directing the PFC towards behaviorally salient stimuli, maintaining the long-term goals through the mediation of feedforward processes.

Modularity:

The past few years have seen a shift from examining intelligence concerning associations in regional gray matter volume and activation to instead examining associations of structural connectivity and modularity with intelligence. While this line of research is still a region-based approach, it lies within a network neuroscience perspective, epitomizing the recent shift to network neuroscience to tackle one of neuroscience's most significant challenges: uncovering the neural basis of intelligence. Thus, the structural connectivity and modularity of specific regions will be examined through their influence on the intrinsic networks they subserve and broader task dynamics discussed in the first section.

Recent research seeks to discover intelligence associations between node-specific measures of within- and between-module connectivity from cortical and subcortical regions previously implicated in intelligence.[141] Within the CON, Hilger and colleagues have found that intelligence was associated with lower within-module connectivity and higher between-model connectivity of the aINS. They reasoned that the aINS' connectivity pattern facilitated the processing of salient information between modules.[141] This conclusion is supported by the evidence proposed in the first section of the discussion. However, the global connectivity of the aINS does more. The aINS is also responsible for downstream task set maintenance and facilitating the proper allocation of control. Thus, the greater integrative capabilities of the aINS in higher-intelligent individuals not only enable the processing of salient information but it tries to maximize the efficiency and effectiveness of the attentional and working memory processes.

Interestingly, there were no associations found between the dACC and intelligence.[141] These results suggest that the connectivity of the dACC is relatively stable across intelligence levels and that variances in the connectivity of the dACC aren't as critical of a determinant for proper CON functioning as variances in the connectivity of the aINS. These results make sense, considering that the specialized functions of the dACC require a relatively isolated position in the brain. Still, the dACC also needs its between-module connections with the DLPFC and aINS to fulfill its functions. With respect to modularity differences, the ability of the CON to adjust global brain dynamics appears most critical to its role in task-set maintenance, control allocation, and conflict resolution. Interestingly, activation pattern differences suggest a mechanism for the enhancement of CON's specific functions, meanwhile modularity differences of the CON account for the enhancement of its global functions. Indeed, these results highlight the importance of multiple perspectives for

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studying the neural correlates of intelligence differences in generating a complete picture of neural enhancements in higher intelligent individuals.

Continuing the discussion on the control networks, many within- and between-network associations within the FPCN and intelligence are primarily centered within their frontal regions. For example, the anterior tip of the superior frontal gyrus, a region within the RLPFC, had both negative between-network and positive within-network modularity.[141] Hilger and colleagues understood this to represent the inhibition of distracting information from the DMN interfering with goal-directed behavior. The evidence suggested in this review would support this notion since interference by the DMN on the RLPFC has been proven to interfere with goal-directed behavior.[17] However, this review wouldn't support their suggestion that the RLPFC's influence in task contexts must be diminished. Instead, the RLPFC has been proven to play an integral role in the FPCN, supplying the higher-order abstract abilities required to complete tasks. So, the increased modular structure in higher-intelligent individuals may facilitate the RLPFC's specialized higher-order functions. Interestingly, the middle frontal gyrus (MFG) and inferior frontal gyrus (IFG) displayed positive within-module connectivity associations with intelligence. Both regions are a part of the LPFC, widely considered the central integrative hub of the FPCN, and a major connector hub,[82,111,142] so these results may initially appear contradictory to previous evidence, but they are not. There was no positive or negative association for these regions with between-module connectivity and intelligence, indicating that the integrative functions of the LPFC are relatively consistent regardless of intelligence level. According to recent network neuroscientific evidence, greater within-module connectivity produces more efficient processing,[143] potentially explaining the results within the LPFC. Greater efficiency supports critical functions of the LPFC by allowing greater capacity to generate task rules, meet working memory demands, and organize the downstream control required to complete task goals. Therefore, these results suggest that higher-intelligent individuals don't have an advantage in the integrative connectivity of the FPCN, instead showing benefits in the capacity for the higher-order thinking and control planning required to utilize their integrative functions most effectively.

Hilger and colleagues distinguished between two overlapping regions of the brain: the tempoparietal junction (TPJ) and the inferior parietal lobule (IPL). However, the results for both the TPJ and IPL were focused on the angular gyrus and supramarginal gyrus. These two regions are traditionally considered the IPL,[144] so this review will collectively refer to these regions as the IPL. During the initial processing stages, the IPL likely functions in language comprehension, processing language from simple sounds and phonemes to syntax and the meaning of information.[145] During rule application stages, the angular gyrus (AG) is likely responsible for comprehending event concepts and mentally manipulating representations. The supramarginal gyrus (SMG) is likely responsible for verbal working memory processes,[68,146] accessible by the FPCN during intelligence tasks. Hilger and colleagues found the IPL to have negative between-module connectivity and positive within-module connectivity associated with intelligence, and these associations were interpreted as reducing the IPL's influence during intelligence tasks, minimizing the interference of irrelevant processes on task goals.[141] It is unclear how much of a role the IPL plays in intelligence; but, considering that the IPL broadly overlaps with the FPCN,[54] has positive functional associations with intelligence,[116] and is responsible for functions important for specific intelligence tasks, it is unlikely that the functional connectivity variances serve an isolating role. So, the structural variances of the IPL may serve to aid in the specialized functioning of the IPL, enhancing functions that are advantageous for intelligence in specific contexts.

The last important finding involves the modularity of subcortical regions associated with intelligence; both the caudate and hippocampus had increased within-module connectivity associated with intelligence that Hilger and colleagues related to requiring a more independent position within their functional modules.[141] This conclusion is reasonably substantiated by the evidence presented throughout this review. To begin, the caudate has been implicated in imbuing the frontal control regions with the necessary motivation to complete task-relevant goals, facilitating both initiation and updates to these goals. So, greater within-module connectivity would increase the efficiency and effectiveness of the caudate's specialized function,[143] namely, generating the necessary goal-directed behavior. The results also indicate that the caudate has already established all the required between-module connections, regardless of intelligence level, required for its functions. This suggests that generating goal-directed signals within the caudate, more so than their propagation, is critical for explaining variation in intelligence. On the other hand, the within-module associations between the hippocampus and intelligence appear to follow the conclusion presented by Hilger and colleagues.[141] All major studies examining functional associations with intelligence find no functional associations between the hippocampus and intelligence.[2,3,107,116] Therefore, the hippocampus isn't significantly involved in intelligence, and its isolation from task-positive regions during a task, indicated by the increased within-module connectivity, would be advantageous during intelligence tasks.

The region-specific modularity correlates with intelligence are crucial for understanding how specific regions function within their broader network to facilitate critical task-relevant functions; meanwhile, general modularity correlates with intelligence and explores the underlying global mechanisms that drive the brain towards completing intelligence-based tasks. These general correlates have been studied in recent years.

A theme throughout the review has been the necessity of integration to facilitate high cognitive performance on intelligence tasks, with both the FPCN and CON having been demonstrated to have vast connections throughout the brain. Recent evidence has supported this position, finding that the

brain can flexibly shift between segregated (high modularity) and integrated (low modularity) states, with the integrated states being associated with high cognitive performance.[61-64] This push towards a more integrated topology is complementary to evidence that low rates of high-modularity states are associated with intelligence, better protecting higher intelligent individuals from network fragmentation that interferes with network communication required for task goals.[147] The topological patterns during task conditions allow for effective inter-regional communication by promoting integration and preventing fragmentation of specialized regions. These results underscore the need for long-range communication and the integration of vast cortical activation to meet task goals.

Hilger and colleagues also found that greater stability of network segregation over time was associated with intelligence and that the DAN was driving this network stability.[147] Their findings support results that implicated the DAN as having the most significant functional associations with fluid intelligence.[69] The DAN's association with fluid intelligence reflects greater attentional focus, which requires stable activation throughout the entirety of the task. Thus, the necessity for the DAN to maintain a stable attentional focus drives the stability of network segregation. Importantly, Santarnecchi and colleagues suggested that the weaker functional associations between FPCN and CON with intelligence reflected less important implications for these networks and intelligence than previously reported.[69] However, the lack of temporal stability for network integration suggests that the major connector hubs don't have temporally stable connections throughout task demands. In conjunction with the flexible hub theory and the CONs flexible connectivity,[80,109-111] these results suggest that control networks provide flexible connectivity required to meet the dynamic control demands throughout a given task. So, these networks are no less important for intelligence tasks than the DAN. Still, their integrative demands create flexible topological patterns during tasks that won't likely manifest in functional associations with intelligence. While both integrative and segregative patterns are important for intelligence, these patterns also provide a plausible avenue to connect previous intelligence studies, such as the study by Santarnecchi and colleagues,[69] to the evidence within network neuroscience.

The results connecting modularity with resting states and task states further the complexity of network dynamics facilitating intelligence. Unlike task conditions, intelligence lacks intrinsic associations with either segregation or integration at rest.[141,148-150] Despite discrepancies between the task and rest states, temporal stability of network organization from resting to task state is associated with intelligence, interpreted as requiring less network reconfiguration, and presumably cognitive effort, to switch from a resting state to a task state.[151] It is possible that higher-intelligent individuals possess a more effective resting state connectivity profile among the intrinsic connectivity networks that enables the minimal network reconfiguration required for intelligence tasks. Evidence supporting this claim comes from Hearne and colleagues, who found that greater connectivity between the FPCN and DMN during rest was associated with higher intelligence.[152] Higher-intelligent individuals have greater connectivity of intrinsic networks at rest, possibly explaining the greater stability from resting to task state. In contrast, lower intelligent individuals require greater network configuration when transitioning into a task state, requiring greater cognitive demand and creating a less efficient processing system. The results found by Hearne and colleagues may relate to the functioning of the PCC in facilitating the transition from resting to task states, where greater connectivity to the PCC by task-positive networks during rest eases the demand on transitioning between states. Notably, too much functional connectivity of intrinsic connectivity networks is suboptimal, impairing cognitive abilities as humans age and suggesting that higher-intelligent individuals likely obtain a near-optimal level of connectivity.[153]

Neural Efficiency:

Decades of research have examined how metrics of neural efficiency relate to intelligence differences. A pivotal trigger for this line of research was the Neural Efficiency Hypothesis, which proposed that higher intelligence was associated with less neural activation, interpreted as less neural effort.[1] In the more than three decades since this paper, many researchers have expanded upon these results by tying other variables to neural efficiency and intelligence, including speed of processing,[154] shorter characteristic path length and greater global efficiency,[155] and global white matter integrity.[156,157] However, a recent study has elucidated event-related potential (ERP) latencies as a highly reliable measure to explain variation in intelligence.

Schubert and colleagues examined whether higher intelligent individuals expressed global information processing correlations with intelligence or specific information processing correlates with intelligence using ERP latencies.[158] Their study indicated that the latter was true, finding that the latencies of later components explained 80% of the variance in general intelligence. Specifically, the P300 latencies showed the most significant association with the intelligence of all the ERP latencies. P300 is proposed to reflect the inhibition of extraneous processes to transmit information from frontal attention and working memory areas to temporal-parietal memory storage regions.[159] Since short-term/working memory has also been associated with more than half of the variance in general intelligence, and there has been an abundance of correlations between the speed of information-processing and short-term/working memory, Schubert and colleagues propose that the speed of higher-order processing aides working memory by facilitating faster inhibition of irrelevant information.[158] Further, they claim these processes serve intelligence by increasing the efficiency of selective attention and memory updating. Within the purview of this review, these results emphasize the importance of the allocation of resources on intelligence task completion. Funahashi details evidence that both attentional control and working memory capacity rely on overlapping neural populations within the LPFC, a pivotal FPCN region.[160] P300 appears to make the frontal cortex's downstream working

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memory and attentional control more efficient. Specifically, P300 appears to reflect the greatest efficiency on the attentional control aspects that can most effectively inhibit the influence of irrelevant information. This efficiency will open greater neural space for working memory, increasing its capacity and influence on downstream regions. These results underscore the importance of working memory capacity in intelligence tasks, explaining the importance of processing speed on this capacity.

The variances in ERP latencies found by Schubert and colleagues support the notion that higher-intelligent individuals have greater neural capacity caused by the increased efficiency of attentional processes. Along these lines, recent work has updated the Neural Efficiency Hypothesis by demonstrating that the pattern of neural effort reversed as task complexity increased, where higher-intelligent individuals showed increased activity in both FPCN and CON regions. In contrast, lower-intelligent individuals saw decreased activity in these regions.[133] These authors interpreted these results as increasing cognitive effort in higher-intelligent individuals as complexity increases, whereas lower-intelligent individuals cease to try after reaching their cognitive capacity.[133] Among many factors, the ERP latencies studied by Schubert and colleagues likely enable this cognitive capacity, reflecting the greater working memory capacity of higher intelligence individuals that allows them to take on cognitively complex tasks; meanwhile, the inefficiencies of these same processes causes lower intelligent individuals to reach capacity and give up on the task.

While the results previously discussed reflect neurological processes that amend the Neural Efficiency Hypothesis,[133,158] current research also suggests that a cognitive practice can influence our understanding of neural efficiency. During response selection, average-intelligent (A-IQ) individuals experience greater response conflict and greater working memory load, reflected in greater ACC and ventrolateral prefrontal cortex (VLPFC) activation, respectively, than higher-intelligent (H-IQ) individuals. Further, H-IQ individuals demonstrated greater activation during feedback evaluation, reflecting formulation of response strategies (caudate), motor planning (middle frontal gyrus), and task set reconfiguration (superior parietal cortex) than A-IQ individuals. These authors concluded that higher-intelligent individuals diverted greater cognitive resources toward planning the next response, reducing the activity required during response selection.[134] Devoting more resources to planning reflects a cognitive mechanism employed by higher-intelligent individuals to reduce neural demand and allow for greater efficiency during rule application. Notably, this is only possible when the rule for the upcoming task can be predicted; however, repeated efforts to encode task rules to memory could aid in rule generation for future, unpredicted tasks.

In this section of the review, it has been demonstrated that greater neural efficiency provides space for greater neural capacity, which is concentrated almost entirely in the frontal regions. For example, P300 makes inhibition of irrelevant processes more efficient,[158] opening up greater neural space for working memory in prefrontal neuronal populations; greater cognitive planning in H-IQ individuals enabled less prefrontal activation than found in A-IQ individuals,[134] reflecting more efficient processing of salient information and control; and this efficiency means that high-intelligent individuals had a greater capacity for increasingly complex tasks, allowing them to solve complex tasks that lower-intelligent individuals were unable to solve.[133] All of these results indicate that the most critical point is the transition from rule generation to rule application. This transition into rule application requires both the successful generation of a rule and the production of a response strategy based on the generated rule, with greater neural efficiency proven to aid both processes.

The Network Neuroscience Theory of Intelligence:

The Network Neuroscience Theory of Intelligence is the most comprehensive theory put forth in the network neuroscience field for the neural correlates of intelligence. While this review has discussed previous evidence related to network neuroscience - namely, variances in modularity - the Network Neuroscience Theory of Intelligence attempts to explain intelligence through network neuroscience rather than describe characteristics of intelligence.[5,141,147] The two central tenants of the Network Neuroscience Theory of Intelligence are that intelligence relies on the small-world model of cortical structure and that the capacity to transition between network states rapidly explains variances in intelligence.

The small-world structure of the cortex explains that the brain is comprised of densely interconnected modules that contain sparser, long-distant connections connecting modules from across the cortex. Barbey suggests that the densely interconnected modules enable specific cognitive operations; meanwhile, the long-range connections provide the integrative faculties to enable broad cognitive abilities, including intelligence.[5] Evidence presented throughout this review supports the importance of specialized cognitive abilities and their integrative recruitment. For example, the ACC's important role in conflict detection is crucial for the adaptive adjustments of control necessary for task completion.[106] The IPL's role in abstract and concrete language comprehension is vital for generating relevant information during rule generation and may be dynamically recruited during rule application depending on task demands.[145] In contrast, the LPFC and aINS have extensive global connectivity that warranted more integrative functions,[81,82,161-163] dynamically recruiting specialized functions such as those within the dACC and IPL. Indeed, the importance of the integrative and segregative functions of the cortex is exemplified by variances in regional modularity found to be advantageous for intelligence. Therefore, the small-world model of the brain relies on a balance among regions expressing more regular or random network structures. This variation of the small-world model creates the flexibility expressed during intelligence tasks, enabling integrative and segregative capabilities in the brain.

According to the Network Neuroscience Theory of Intelligence, general intelligence depends upon the dynamic reorganization of ICNs in service of system-wide

flexibility and adaptability.[5] The control networks provide the integrative template upon which task-specific connectivity is constructed from the dynamic recruitment of specific cognitive abilities. The control system's dynamic recruitment of specific cognitive abilities is rooted in the topological reorganization of the ICNs during intelligence tasks. For example, the FPCN can recruit specific DMN nodes according to task demands,[10,11,25,164] illustrating the accessibility of pre-existing knowledge and internal-oriented representations necessary for intelligence tasks. Further, the sensory regions recruited during task demands depend on the external stimuli present and the sensory manipulations upon one's internal representation necessary for task demands.

Beyond the reorganization of ICNs, intelligence difference relies on the capacity to flexibly transition between mental states.[5] Barbey suggests that the control systems enable these flexible transitions between network states since they exhibit greater degrees of variability that manifest in time-varying profiles of functional connectivity.[165,166] The control systems were explicitly tied to the capacity to reach difficult-to-reach states,[167] indicative of their vast long-range connections throughout the brain. Indeed, these weak, long-distant connections explained variance in general intelligence better than the strong, short connections.[168] So, the long-range connections of the control networks are crucial for general intelligence and enable the global shifts in network states. Within the context of this review, two network states critical for intelligence coincides with rule generation and rule application, where the brain strives to obtain a rule and manipulate working memory to achieve task goals. The initial feedforward processes that activate the control regions are likely direct, representing easy-to-reach states. From there, the control networks dynamically recruit brain regions upon the intelligence-general integrative template of connectivity. The convergence on a rule depends upon the proper recruitment of internally and externally sourced information, the specific downstream control characteristic of the different FPCN and CON subnetworks,[55,169] and the short-range interactions between the different subregions of the.[170,171] Indeed, rule generation relies on short- and long-range connections to traverse an indirect but necessary path to converge upon the rule. The frontal activity diminishes once the rule is reached, reflecting a more direct maintenance path. By its nature, this direct path represents an easing of the network state, and maintaining this pathway likely strengthens the connections as well, further easing the demand for its maintenance. Once again, the brain strives towards difficult-to-reach states, reflecting the long-range, downstream control by the frontal control regions to manipulate the working memory according to the rule acquired. At this stage, segregating the task into simpler subcomponents is advantageous and is correlated with intelligence.[108] Neurologically, these subcomponents manifest in cognitive epochs described by the MD Theory that activate respective neural ensembles,[3,43] flexibly asserting downstream control.[80] These neural mechanisms are designed to reduce demand, making it easier to reach a difficult-to-reach state. Each subcomponent may work the same way as rule convergence, where a subcomponent's completion coincides with slightly diminished activity, reflecting neural rewiring to create a more direct path and strengthening of the connection, which must be maintained during future components. However, the nature of this mechanism suggests that the greater numbers of components, indicative of increasingly complex tasks, reflect more and more indirect pathways to maintain our working memory. This mechanism could explain the benefits of dividing a task into subcomponents for higher intelligent individuals, where periodically easing the network state could allow higher-intelligence individuals to more effectively reach the difficult-to-reach state that enables the completion of task goals.

Beyond task components, the brain employs other mechanisms to ease transitions towards difficult-to-reach states required for intelligence tasks. The ERP latencies studied indicate that the best component in explaining variances in general intelligence is P300, which is implicated in more efficient inhibition of irrelevant information. This downstream control by the control networks contributes to its ability to reach difficult-to-reach states. As demonstrated in this review, more efficient downstream attentional control opens greater neural space for working memory, increasing working memory capacity. The DAN, responsible for attentional control, exhibits stable within-network functional connectivity and segregation during intelligence tasks.[147,172,173] These results indicate that the DAN cannot significantly contribute to the control network's ability to drive the brain into difficult-to-reach states because any significant changes in functional connectivity would not occur during task states. Despite the importance of the DAN's attentional control on intelligence,[69] the DAN's role appears to be rooted in creating more efficient attentional control to provide greater capacity for the control networks to drive the brain into difficult-to-reach states through their manipulation of working memory.

The significance of P300 doesn't stop at attentional efficiency; instead, Schubert and colleagues suggest that P300 also contributes to memory updating.[158] These results propose another insufficiently researched mechanism for easing transitions toward difficult-to-reach states: memory. Graham and colleagues found that planning during delay periods was associated with intelligence.[134] While intelligence tasks don't usually have delay periods, this planning indicates an effort to encode a rule to memory for future use. Encoding a rule to memory would be highly advantageous to intelligence tasks, allowing our control networks to converge more efficiently on a rule. While memory relies on easy-to-reach states, the memory must be applied to a novel task, requiring a difficult-to-reach state and giving memory room to contribute to intelligence.

A Holistic View?:

Thus far, this review has elucidated countless connections between the various theories of intelligence, augmenting our understanding of the neural correlates of intelligence. In addition, a few neural characteristics have been reoccurring threads, connecting these multiple theories and perspectives.

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Understanding these threads will augment our understanding of the neural correlates of intelligence, bringing us closer to a holistic view.

The first thread that was pervasive throughout all neuroscientific theories was neural networks. For both task processes and intelligence differences, global and regional neural dynamics were most effectively analyzed by tying these dynamics to their respective neural networks and explaining the significance of these results to intelligence. Analyzing the neural dynamics of the various neural networks proved crucial for tying the prominent theories together: The Network Neuroscience Theory of Intelligence,[5] the Process Overlap Theory,[4] the MD Theory,[3] and P-FIT all rely on neural networks to neurologically explain their theories.[2] The dynamic interplay between the brain networks was extensively discussed in the previous two sections and would be too extensive to outline here. However, the most important network findings discussed here, and prevalent throughout the various theories, is the importance of the control networks, specifically, how the control networks dynamically recruit other networks or network nodes to enable intelligence processing.

The control networks' ability to dynamically recruit other cortical networks and nodes requires understanding the second thread connecting the various theories of intelligence: flexibility. The control networks displayed flexibility in activation during task processes,[3,43,80,109-111] and displayed task-specific, time-varying functional connectivity.[43,165,166] Indeed, this review explains how these processes enable the domain-general integrative template upon which specific cognitive abilities are recruited for intelligence, providing up-to-date neural support for the Process Overlap Theory and explaining the mechanism that the P-FIT couldn't yet supply for the control network's ability to produce responses.[2,4] Further, this flexibility enables the brain to drive toward a difficult-to-reach state,[5] and higher-intelligent individuals can more efficiently drive the brain into these states. As previously discussed, P300,[158] planning,[134] and task components reflect three of the likely many ways that higher-intelligent individuals can more efficiently reach difficult-to-reach states.[108]

With the power to connect all perspectives of the neural correlates of intelligence, neural networks, and network flexibility could provide the foundation for a holistic perspective of intelligence. Indeed, recent papers are converging upon these two threads, most notably the Process Overlap Theory.[4] This pattern suggests that neuroscience is already converging upon the core of intelligence in the brain. These positive strides are very promising for the future of neuroscience.

Conclusion

With decades of research dedicated to identifying the neural correlates of intelligence, the neuroscientific community continues to refine its understanding of intelligence in the brain. This review has compiled the most up-to-date and relevant research on the neural correlates of intelligence task processing and intelligence differences. Notably, the evidence compiled in this review covered many different perspectives on intelligence, requiring analysis of the crossroads between these perspectives. The first two sections culminated in this review's final section, which covered the threads that most consistently connected the various perspectives of intelligence: neural networks and neural flexibility.

More important than this review's time-tested accuracy is the potential for further refinement of our understanding of intelligence due to the threads identified in this review. Indeed, this review opens exciting new possibilities for the future of intelligence research in neuroscience.

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