Title: The shifting architecture of cognition and brain function in older adulthood

Running head: Architecture of aging

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Abstract

Cognitive aging is often described in the context of loss or decline. Emerging research suggests that the story is more complex, with older adults showing both losses and gains in cognitive ability. With increasing age, declines in controlled, or fluid, cognition occurs in the context of gains in crystalized knowledge of oneself and the world. This inversion in cognitive capacities, from greater reliance on fluid abilities in young, to increasingly crystalized or semanticized cognition in older adulthood, has profound implications for cognitive and real-world functioning in later life. This shift in cognitive architecture parallels changes in the functional network architecture of the brain. Observations of greater functional connectivity between lateral prefrontal brain regions, implicated in cognitive control, and the default network, implicated in memory and semantic processing, led us to propose the Default Executive Coupling Hypothesis of Aging (DECHA). In this review we provide evidence that these changes in the functional architecture of the brain serve as a neural mechanism underlying the shifting cognitive architecture from younger to older adulthood. We incorporate findings spanning cognitive aging and cognitive neuroscience to present an integrative model of cognitive and brain aging, describing its antecedents, determinants, and implications for real-world functioning.

1. INTRODUCTION

Across society, from public policy to popular culture, cognitive aging has become synonymous with cognitive decline. This unfortunate heuristic is inaccurate in the context of a growing body of evidence showing that the full spectrum of cognitive aging encompasses both gains and losses (Park, Polk, Mikels, Taylor, & Marshuetz, 2001, Figure 1). In this review we characterize the evidence for a shift in the architecture of cognition across the lifespan, with a view to better characterizing the full spectrum of cognitive aging. Next we describe how the changing architecture of brain function provides a striking parallel to these cognitive changes. Finally, we propose a novel model of neurocognitive aging to better bridge our understanding of cognitive and brain aging, to generate predictions for both gains and losses, and finally to propose a putative neural mechanism connecting these trajectories of cognitive and brain aging.

Dual intelligences and the semanticization of cognition. An accurate portrayal of aging cognition must consider the dual nature of fluid and crystallized intellectual ability, and their respective trajectories, across the lifespan. Fluid intelligence indexes cognitive operations that require goal-directed, or controlled processing. We refer to these fluid abilities throughout the review as cognitive control processes, necessary for directing attentional resources to relevant aspects of the environment, inhibiting distractions, and flexibly allocating processing resources to sustain goal-directed behaviors (Carpenter, Just, & Shell, 1990; Cattell, 1971). Crystallized intelligence indexes the collective store of semantic knowledge about ourselves and the world that is accumulated over the life course (Cattell, 1971). We refer to these crystalized abilities here as semantics, encompassing a vast repertoire of prior knowledge including routines, habits, stereotypes, and schemas, as well as the thoughts and behaviors, repeatedly encountered over a lifetime (Jefferies, 2013; Ralph, Jefferies, Patterson, & Rogers, 2017).

These two facets of cognition, control processes and crystalized knowledge, age differently. Cognitive control abilities show marked and near linear declines with increasing age (Park et al., 2001; Verhaeghen & Cerella, 2002). In contrast, semantics continue to accumulate and are preserved well into later life (Park et al., 2001; Verhaeghen, 2003). While these dual trajectories have been thoroughly described as independent facets of cognitive aging, surprisingly little research has examined how they interact. This is rather remarkable given the striking inversion of cognitive abilities that occurs across the adult life course (Park et al., 2001, and see Figure 1). We refer to this shift as the *semanticization of cognition* in older adulthood, and the impacts can be seen across a diverse array of cognitive domains from memory (e.g. Umanath & Marsh, 2014), to socio-emotional functioning (e.g. Carstensen, Fung and Charles, 2003), as well as in multi-domain abilities such as decision-making and problem-solving, with implications for real world functioning and independence (e.g. Agarwal, Driscoll, Gabaix, & Laibson, 2009; Li, Baldassi, Johnson, and Weber, 2013). Yet how and why this shift occurs has not been fully explored.

Models of neurocognitive aging. At the level of the brain, two of the most commonly reported patterns of functional brain change in older adulthood include (i) greater recruitment of prefrontal cortical regions, implicated in cognitive control, and (ii) reduced suppression of the default network, an assembly of functionally-connected brain regions implicated in access to mnemonic representations of oneself and the world

(Andrews-Hanna, Smallwood, and Spreng, 2014). Increased recruitment of lateral prefrontal brain regions has been described as Hemispheric Asymmetry Reductions in Old Age (HAROLD, Cabreza, 2002) or a Posterior to Anterior Shift in Aging (PASA, Davis, Denis, Deselaar, Fleck, and Cabeza, 2007). These early influential models of neurocognitive aging emerged from an abundance of evidence showing that older adults display a consistent pattern of enhanced prefrontal recruitment, including greater bilateral activation, across many cognitive tasks. Enhanced recruitment is attributed to greater demands for cognitive control processes, necessary in the context of degraded signalling from earlier processing zones located in posterior brain regions (Li and Lindenberger, 2001; Li and Rieckmann, 2014; Payer, Marsheutz, Sutton, Hebrank, Welsh, and Park, 2006). Later, models emerged to suggest that this dedifferentiated pattern of enhanced prefrontal recruitment serves to support cognitive functioning in the context of structural and functional changes in later life. This pattern of functional brain adaptation has been captured in the Compensatory Recruitment of Neural Circuits Hypothesis (CRUNCH, Reuter-Lorenz and Cappell, 2008) or the Scaffolding Theory of Aging Cognition (STAC, Park and Reuter-Lorenz, 2009) models of neurocognitive aging.

Neurocognitive aging has been explored through the lens of large-scale functional brain networks (Damoiseaux, 2017). The default network, a collection of intrinsically-connected brain regions including the posterior cingulate cortex (PCC), medial PFC (MPFC), inferior parietal lobule as well as medial and lateral temporal lobes, has been particularly implicated (Hafkemeijer, van der Grond, and Rombouts, 2012). This network is typically activated during internally-directed cognitive processes that rely on access to stored mnemonic representations to guide goal-directed behaviors (Andrews-Hanna, et al. 2014). In contrast, default network brain regions are suppressed during performance of externally-directed tasks (Buckner, Andrews-Hanna and Schacter, 2008). Age-related changes in the default network include reduced suppression, as well as decreased within-network and increased between-network connectivity, that is poorly modulated by task context (e.g. Rieck, Rodrigue, Boylan and Kennedy, 2017; Spreng and Schacter, 2012 and see Damoiseaux, 2017, Hafkemeijer et al., 2012 for reviews).

Connecting cognitive and functional brain change: A new proposal. Considered together, these functional brain changes, involving regions implicated in cognitive control (lateral prefrontal cortex) and access to prior knowledge representations (default network), closely parallel the shift in cognitive architecture described earlier. There has been little research, however, to connect these patterns of cognitive and brain aging. Our work provided some of the first evidence that lateral prefrontal engagement and reduced default network suppression are functionally-coupled in older adulthood. This led us to propose the Default–Executive Coupling Hypothesis of Aging (DECHA, Turner and Spreng, 2015). This hypothesis predicts that as goal-directed cognition becomes less dependent on declining control resources, and increasingly influenced by prior knowledge (i.e. the semanticization of cognition), the default network is engaged, and becomes increasingly – and inflexibly – coupled with lateral prefrontal brain regions (Figure 2).

While broadly consistent with other neurocognitive aging theories in positing a role for increased prefrontal engagement, DECHA differs from these earlier compensatory accounts by highlighting the role of cognitive context in determining whether these brain changes are functionally adaptive or maladaptive. Put simply, if access to semantic knowledge is relevant to the current task, greater default–executive coupling should be adaptive (Adnan, Beaty, Silva, Spreng, and Turner, in press; Spreng, Dupre, Selarka, Garcia, Gojkovic, Mildner, and Turner, 2014). In contrast, if prior knowledge is irrelevant or distracting, this pattern should lead to poorer performance (Rieck, Rodrigue, Boylon, and Kennedy 2017; Turner and Spreng, 2015). The DECHA reflects a growing body of evidence showing that this coupling pattern is increased, and poorly modulated by task context, in older adulthood (Rieck et al., 2017; Spreng and Schacter, 2012). Here we suggest that DECHA opens a novel avenue for exploring these parallels in cognitive and brain aging. Critically, as a putative neural mechanism, reflecting both declining fluid abilities *and* increasing semantic knowledge (i.e. the semanticization of cognition), the DECHA is able to characterize the full spectrum of aging cognition, encompassing both gains and losses in adaptive, goal directed behavior in later life.

Objectives for the review. In the sections that follow, we expand upon the findings introduced here to provide a comprehensive review of the cognitive and functional brain changes that occur with age, how they promote the semanticization of cognition in later life, and how this shift in cognitive architecture parallels the shift in brain function described in the DECHA. We begin in Section 2 by describing the shifting architecture of cognition from younger to older adulthood and highlight the impacts, both negative and positive, on real world functioning. In Section 3 we directly interrogate our hypothesis that the semanticization of cognition is attributable to the interaction of increased semantics and declining control. We argue that this shifting architecture leads to an enduring shift in cognitive mode, from exploration and novelty seeking in young to greater exploitation of existing knowledge stores in later life. In Section 4 we turn to brain aging and provide a survey of the mounting evidence for enhanced recruitment of lateral prefrontal brain regions and reduced modulation of the default network across the adult lifespan, in addition to evidence for the functional coupling of these regions with advancing age. In the final section we bring together the evidence supporting our novel, cross-disciplinary theoretical framework, the DECHA, and argue that it represents an integrative neural mechanism underlying the shifting architecture of cognition in older adulthood.

2. THE SHIFTING COGNITIVE ARCHITECTURE OF AGING

In this section we review evidence for the semanticization of cognition in older adulthood and how this is manifest within specific domains, such as memory or social cognition, as well as in multi-domain abilities such as planning, problem-solving and decision-making. Our intention is not to provide a comprehensive survey of the impact of prior knowledge on cognitive functioning across the lifespan. Excellent reviews of this topic can be found elsewhere (e.g. Umanath & Marsh, 2014). Our goal is to provide an overview of the most pertinent research in this area as a basis for appreciating the parallels between cognitive and brain aging we draw later in the paper.

Cognitive aging and semantic knowledge gains. The semanticization of cognition has been characterized as an age-related transition towards reliance on prior knowledge, including semantics, conceptual-level knowledge, and schematic representations. This occurs in the context of declining access to detailed representations of the past (e.g.

episodic memories), as the unique and arbitrary associations that form the basis of these discrete representations decay over time (Craik & Bialystok, 2006). There have been numerous, often competing, models put forth to explain age-related cognitive decline. While a broader review of neurocognitive aging models is beyond the scope of this paper (see Anderson & Craik, 2017; Park and Reuter-Lorenz, 2009), age-related declines in inhibitory capacity (Hasher & Zacks, 1988), reduced speed of processing (Salthouse, 1996) are among the most often cited accounts. Evidence, however, is emerging to suggest that the accrual of semantic knowledge over the life course may be a superordinate factor, interacting with specific declines in control processes secondary to frontal brain changes (e.g. inhibition) or slowed speed of processing, to accelerate age-related cognitive changes. For example, a larger store of semantic representations, in the context of reduced inhibitory capacity, would be more frequently, and automatically or inadvertently, activated across a broader range of cognitive contexts (Hoffman, 2018). Similarly, an increased store of semantics would require longer searches through an expanded solution space, slowing processing speeds in later life (Blanco et al., 2016; Ramscar, Hendrix, Shaoul, Milin, & Baayen, 2014). Next we explore the impacts of the semanticization of cognition first with respect to domain-specific impact (verbal functioning, memory, associative learning, cognitive control), followed by multi-domain and more real-world implications (problem-solving, decision-making).

Domain-specific impacts. Beyond interactions with specific control processes, the impact of an age-related shift towards semanticized cognition have been investigated across multiple cognitive domains. With respect to verbal ability, older adults demonstrate superior performance on tasks assessing vocabulary size (Park et al., 2001; Verhaeghen, 2003). Older adult recognition for previously studied words is also better for those embedded within sentences than for those presented as stand-alone items. This has been attributed to linguistic expertise honed over a lifetime of reading (Matzen & Benjamin, 2013). Further, older, but not younger, adult vocabulary scores can significantly predict memory performance on a cued recall test (Hedden, Lautenschlager and Park, 2005).

In contrast, older adults have greater difficulty learning alternate versions of fairy tales, presumably because the over-learned, standard narratives proactively interfere with the encoding of the non-standard versions (Dalla Barba, Attali, & La Corte, 2010). A similar effect has been observed during the learning of misspelled words (MacKay, Abrams, & Pedroza, 1999) as well as incorrect mathematical solutions (Ruch, 1934). In each of these cases, prior knowledge disrupts learning and subsequent task performance.

However, the influence of prior knowledge may also provide protection from cognitive distortions. As reviewed in Umanath and Marsh (2014), an interesting example of this phenomenon involves the Moses Illusion in which participants are required to answer both factually correct and incorrect questions (e.g. How many animals of each species did Moses lead to the ark?). While older adults failed to notice factual errors at study (Noah is the protagonist of the ark narrative), they were less likely than young to provide the incorrect responses on subsequent test (e.g. Which biblical figure led pairs of animals to an ark?). The older adult advantage was observed even when older and younger participants were matched on prior knowledge (Umanath & Marsh, 2012).

This effect has also been observed in more ecologically valid contexts. Older adults are less likely than young to remember invalid versus valid prices for grocery items (Amer, Giovanello, Grady and Hasher, 2018; Castel, 2005). They are also less likely to exhibit susceptibility to the Illusory Truth phenomenon. This illusion describes the tendency of younger adults to perceive facts repeated more often as true. However, older adults are able to draw from their larger store of semantic knowledge to avoid this illusion, using prior knowledge to circumvent the learning of false information as a function of exposure (Brashier et al., 2017). In general, differences in memory performance between young and older adults are reduced or eliminated when to be remembered information is consistent with prior knowledge. In their review, Umanath and Marsh (2014) put it simply: "the more prior knowledge older adults can apply, the smaller the age difference in memory." (p. 214).

While the semanticization of cognition can protect older adults from encoding false or distorting information when it is incongruent with one's prior knowledge, this same process can also lead to memory distortions when prior knowledge is able to shape or influence encoding processes. An example of this is the phenomenon referred to as false memory formation. Here, reliance on prior knowledge leaves older adults more susceptible to the formation of imprecise or incorrect memories, or illusory associations, during encoding and retrieval of conceptually-linked word lists (Schacter, Koutstaal, & Norman, 1997). Using the Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959; Roediger & McDermott, 1995), participants studied word lists that share a common underlying theme, for example words associated with 'cold' (frost, snow, ice etc.). On a subsequent recognition test, older adults more frequently endorsed target-lures, words related to the theme, but were not on the original study list (e.g. frozen). The authors argued that these 'false memories' are generated as the result of richer associations for study items with a larger store of semantic representations in older versus younger adults. Consistent with this idea, in a separate experiment, Koutstaal and colleagues (2003) implemented a visual adaptation of the DRM paradigm in which participants studied a series of abstract images and were asked to identify the previously studied items from among a series of new images that included visually similar items on a later recognition probe. Unlike the previous results, older adults did not endorse more visually similar lures than the younger participants. However, in a separate condition, concrete labels were assigned to the images at study (e.g. watch, truck, lamp, bread). In this condition, older adults did endorse more target lures than the young, providing strong evidence that the formation of false memories was related to increased semantic associations as a result of the verbal labels assigned to the stimuli.

Semanticization of memory also observed during the recollection of personal past events or autobiographical recall. During the Autobiographical Interview, a structured interview to assess recollections of one's personal past (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002), older adults report proportionately more personal semantic information (e.g. I loved playing basketball in high school) than episodic details of their past (e.g. I shot the winning basket in the final game of the season in my junior year). As we describe later in the review, our work is beginning to show that the semanticization of personal past memories may be associated with changes in the network architecture of the brain in older adults (Spreng et al., 2018).

The influence of prior knowledge on cognition in older adulthood also extends to associative learning processes. It is well established that associative learning declines with age (Li, Naveh-Benjamin, & Lindenberger, 2005; Naveh-Benjamin, Craik, Guez, &

Kreuger, 2005). Typical research paradigms involve forming associations between two random word pairs (e.g. tree - bus; rose - sleep) over multiple learning trials. Associative learning is an active process drawing upon controlled cognitive abilities known to decline with age (Naveh-Benjamin et al., 2005). However, when prior knowledge can be accessed to support the learning of new associations, age-differences are significantly reduced (Amer and Hasher, 2014; Castel, 2005). This has also been investigated in the context of functional learning (Musielak, Giraudeau, Chasseigne, & Mullet, 2014). Functional learning is a form of associative memory that involves forming associations between item pairs (e.g. words) and a criterion item (e.g. a number). The critical adaptation from standard associative memory paradigms is that the word pairs and criterion variable are organized along a common superordinate dimension (e.g. size) that can be abstracted and used to support associative learning. As an example, 'tree – elephant' would be associated with a larger number while 'flower-insect' would be associated with a smaller number. In this form of associative learning, where access to prior knowledge can be used to support abstraction, age differences are practically eliminated, even in the oldest old (Musielak et al., 2014). Critically, functional learning has been argued to better reflect learning in the 'real world' where prior knowledge is frequently used to form new associative knowledge, in contrast to the learning of completely random associations common in most laboratory paradigms. As we saw above with the Moses and Truth Illusions, access to prior knowledge can also protect older adults from learning false associations in potentially manipulative situations such as misleading advertising (Brashier et al., 2017) or product pricing (Castel, 2005).

There is growing evidence that engaging one's semantic knowledge stores in later life can lead to better cognitive performance even on tasks typically associated with cognitive control abilities. For example, in a recent study, older adults showed equivalent learning to that of younger participants for a response set necessary for performance on a Stroop color-word test of inhibition. Critically, they were able to leverage this prior knowledge and transfer it across task conditions, resulting in equivalent performance between age groups on this classic test of cognitive control functioning (Cohen-Shikora, Diede, and Bugg, 2018).

Recent evidence from our laboratory has shown that, despite declines in fluid cognitive abilities, older adults perform similarly to younger adults on a cognitive control task assessing creative ability (Divergent Thinking Task: Adnan, Beaty, Silva, Spreng and Turner, in press). Interestingly, older, but not younger, performance on this task was associated with greater coupling of prefrontal and default network brain regions (see Section 5 below). This suggested to us that older adults may be relying on a relatively preserved store of semantic knowledge (associated with default network function) to support performance on this task in the context of declining control resources.

Even incidental engagement of prior knowledge can support controlled cognition in older adulthood. In an interesting demonstration of this phenomenon, older and younger adults were asked to perform two cognitive tasks in which they were required to ignore irrelevant information (words/non-words) that had been embedded in the task stimuli. Despite explicit instructions to ignore the distractor words, older, but not younger, adults showed conceptual-level encoding of the familiar (albeit distracting) word items, presumably supported by associations with prior semantic knowledge. Interestingly, the incidental encoding of the distractor items led to better performance for older than younger adults on a subsequent general knowledge test where the previously distracting items were now task relevant.

Multi-domain abilities and real-world implications. The studies described above provide evidence that engaging prior knowledge, even incidentally, can both hinder and support performance across multiple domains, from memory and associative learning to cognitive control tasks. The semanticization of cognition can also impact performance on more integrative, multi-domain, cognitive abilities such as problem solving. In a report of older and younger adults, participants were asked to select the most advantageous choice from among an array of options to maximize financial gains, and minimize losses, in a decision-making task (Blanco et al., 2016). Unknown to participants, the researchers imposed either a random trial architecture (i.e. previous knowledge could not predict future outcomes) or a structure such that previous response patterns could be used to make advantageous future choices. As predicted, older adults were slower in making decisions than the younger participants across both conditions. However, older adults made significantly better decisions in the predictive condition, where reliance on past knowledge was able to boost decision-making ability. Interestingly, they carried over this strategy, searching through previous knowledge stores, to the randomized trial blocks, resulting in poorer decisions for this condition. The authors concluded that a lifetime of reliance on prior knowledge, a typically adaptive strategy in real world contexts, led older adults to access their knowledge stores, even when it was maladaptive to do so (Blanco et al., 2016).

The contribution of previous experience and knowledge to cognitive functioning has also been observed during real-world problem-solving tasks. Older adults demonstrate relatively greater reliance on prior knowledge during open-ended social problem-solving tasks. In contrast, younger adults rely to a greater extent on controlled, episodic recollection and simulation processes. These studies suggest that an age-related shift towards semanticized cognition may have a direct impact on how older adults approach and ultimately solve problems in their everyday lives (Sheldon, McAndrews, & Moscovitch, 2011; Vandermorris, Sheldon, Winocur, & Moscovitch, 2013).

The semanticization of cognition in older adulthood has also been associated with altered reasoning and decision-making capacity. Fuzzy-trace theory (Reyna and Brainerd, 1995) posits that, with increasing age, these complex fluid intellectual capacities increasingly rely on more crystallized, or gist-based, cognitive processing. Reliance on these 'fuzzy', gist-based representations in older adulthood can be maladaptive, for example resulting in more false memories on the DRM paradigm as verbatim recollection declines (Brainerd and Reyna, 2015). However, gist-based processing, engaging lower order and thus more flexible mnemonic representations, is also associated with more intuitive decision-making as behavior becomes less constrained by fixed or verbatim depictions of past experience (Reyna, 2012). Consistent with the semanticization of cognition, gist-based memory is preserved relative to verbatim memory in older adulthood (Brainerd, Reyna, and Howe, 2009; Brainerd and Reyna 2015; Reyna and Brainerd, 2011). Thus, decision-making in real world contexts, which requires more flexible, or gist-based, processing to adaptively map past experience to current contexts may be an area of relative strength in later life.

Consistent with this idea, in one study older and younger adults performed a series of economic decision-making tasks (Li, Baldassi, Johnson, & Weber, 2013). The researchers assessed four aspects of decision-making including temporal discounting, financial and debt literacy and loss aversion. Somewhat surprisingly, older adults performed as well or better than the young on this real-world task. Critically, older adult performance was strongly correlated with their crystalized (but not fluid) cognitive abilities, an association not observed for the younger cohort. These findings led the authors to propose the *complementary cognitive capabilities hypothesis*. The complementary cognitive capabilities account argues that access to an expanding and stable repertoire of stored knowledge can support cognitive performance, and may even eliminate age-related cognitive decline, when prior knowledge is accessible, accurate, and adaptive for the current task context.

This shifting architecture of cognition across the lifespan, from cognitive control abilities to greater reliance on prior knowledge, has also been used to explain the 'economic decision-making sweet spot' in middle age (Agarwal et al., 2009; Samanez-Larkin, 2013). In this model of real world financial decision-making, late 40- and 50-year olds, falling roughly at the intersection of declining control and increasing semantics (Park et al., 2001; and see Figure 1), retain the capacity to flexibly adjust to shifting economic contingencies, while also drawing upon an accumulating repertoire of past experience, to support more adaptive financial borrowing strategies. This idea was directly tested in a study comparing the impact of fluid and crystalized cognitive abilities on financial credit scores (Li, Gao, Enkavi, Zaval, Elke, Weber, and Johnson, 2015). Domain specific crystalized knowledge (i.e. financial literacy) was able to offset the loss of fluid cognitive abilities and predicted higher credit scores in later life.

Moving beyond the financial domain, further support for the influence of prior knowledge on decision-making has been demonstrated as greater regard for inter-temporal choice (Lockenhoff, 2011). This simply refers to the amount of value discounting that occurs when deciding between an immediate versus a larger delayed reward. Younger adults show a steep discounting rate, exhibiting a strong preference for the immediate reward. In contrast, older adults show a much shallower rate of discounting, resulting in similar valuation of immediate and delayed rewards. This suggests that older adults are able to bring their lifetime of experience and knowledge about the benefits of postponed gratification to bear on their economic choices. Research from the emerging field of decision-neuroscience is beginning to elucidate the neural mechanisms underlying the influence of prior knowledge on decision-making processes in older adults (Samanez-Larkin & Knutsen, 2014; Samanez-Larkin & Knutson, 2015).

In this section we have reviewed evidence that the semanticization of cognition has a profound impact (both positive and negative) on cognitive and real world functioning in later life. Next we explore the determinants of this shift in cognitive architecture from younger to older adulthood. We examine whether these changes reflect an enduring shift in cognitive mode, and if increased reliance in later life on prior knowledge is an artifact of declining control abilities or a more deliberate shift in motivation towards favoring familiarity over novelty.

3. INCREASING SEMANTICS AND DECLINING CONTROL: A SHIFT IN COGNITIVE MODE IN OLDER ADULTHOOD?

In the previous section we described how the shifting architecture of cognition can both benefit and harm performance across multiple task contexts. Here we turn more directly to address the question of why such a change occurs. What are the central determinants of greater reliance on prior knowledge to guide thought and action in later life? We explore whether the accrual of semantic knowledge across the lifespan is alone sufficient to precipitate this shift, or is a decline in cognitive control necessary to promote the semanticization of cognition in later life. We then address whether the semanticization of cognition is an *in-situ*, or context-dependent, response or perhaps reflects a more durable shift in cognitive mode. Finally, we discuss Socioemotional Selectivity Theory, as an alternate account, suggesting that semanticized cognition in later life may not merely be a reaction to shifting cognitive resources, but rather an active strategy to promote affective well-being in the context of a foreshortened time horizon.

Increasing semantic knowledge. As should be clear from Section II, the shifting architecture of cognition in later life conveys both benefits and costs with respect to task performance across multiple cognitive domains. Investigating how and when prior knowledge is brought online to influence cognitive functioning may provide important insights into the shifting nature of cognitive and real-world functional abilities in later life. Crystalized, or semantic knowledge, is accessed more readily, drawing upon fewer attentional resources, than new learning which involves cognitive control to form novel associations between previously discrete percepts or between percepts and prior knowledge (Craik & Jennings, 1992). Through repeated exposure, re-encoding, and consolidation, activation of prior knowledge structures, based on stimulus familiarity, becomes less attention-demanding and increasingly automatic (Naveh-Benjamin et al., 2005). As a result, the accumulation of prior knowledge in the form of facts, habits, routines, schema and even stereotypes or prejudices exert greater control as familiarity increasingly drives cognition later life.

Increases in semantic knowledge across the lifespan suggests that intrusion of prior knowledge into ongoing thought and action will increase simply as a function of its availability. A larger store of more frequently encoded semantic knowledge increases the probability that it will be activated by specific percepts or thoughts occurring within a given task context. As older adults possess a larger store of semantic knowledge (Hoffman, 2018; Verhaeghen, 2003), it follows that knowledge representations will be activated across an ever larger range of perceptual and mental contexts. But is knowledge accumulation sufficient to explain the breadth of influence semantics exert on cognitive functioning in later life? Work suggests that declining control processes also play a critical role.

Declining cognitive control. Analogous to the separation of intellectual ability into fluid and crystalized capacities, the domain of semantic cognition has been similarly divided into semantic and control processes that facilitate access to a growing store of prior knowledge in later life (Hoffman, 2018; Jefferies, 2013; Lambon Ralph et al., 2017). In this model 'semantic control' is differentiated from domain-general cognitive control processes. Semantic control increases with age and enables older adults to strategically retrieve and monitor access to weaker semantic associations embedded within an expanding store of semantic knowledge. Put another way, semantic control processes, honed over time to strategically search this expanding database, are able to better leverage semantics to influence cognition (Hoffman, 2018). This idea is consistent with evidence, reviewed earlier, that older adults are able to draw more readily from prior knowledge to make better, albeit slower, decisions than young (Blanco et al., 2016).

However, gains in semantic control occur in the context of declining domain-general control processes, such as inhibitory processing (e.g. Hasher and Zacks, 1988). Reduced cognitive control can lead to poor filtering of irrelevant semantic associations and the leakage of prior knowledge into ongoing cognitive operations. Evidence for this 'leaky semantics' account is found in the false memory studies reviewed earlier (e.g. Koutstaal et al., 2003; Schacter, Koutstaal, Johnson, Gross, & Angell, 1997; Schacter, et al., 1997). In an ostensibly more adaptive context, the intrusion of semantics in the form of incidental encoding of familiar (but distracting) information, has been shown to improve performance on a subsequent task where previously distracting information had become relevant to current task goals (Amer and Hasher, 2014). Age-related declines in domain general cognitive control may, perhaps counter-intuitively, also lead to poorer engagement of prior knowledge. In an investigation of semantic fluency, older adults displayed more frequent switching between retrieval cues, leading to poorer performance on a semantic fluency task (Hills, Mata, Wilke, Samanez-Larkin, 2013). The authors interpreted this finding as evidence that declining inhibitory control in older adulthood resulted in an inability to suppress distracting retrieval cues, leading to increased and less efficient switching during semantic retrieval.

Together, these findings identify declining domain general control processes as an important determinant of the shift towards increasingly semanticized cognition in older adulthood. Specifically, there is mounting evidence that declining inhibitory capacity in older adulthood enables greater intrusion of prior knowledge into ongoing cognitive operations. This suggests that the semanticization of cognition is not solely determined by an accumulation of prior knowledge. Reduced cognitive control abilities also contribute to the growing influence of semantics on cognitive processing in later life.

A cognitive mode hypothesis. This two factor account of the semanticization of cognition in older adulthood, implicating a larger repertoire of semantics and declining control processes, parallels an emerging theory of goal-directed action which hypothesizes that human behavior is shaped by a constant tension between exploratory versus exploitative modes of functioning (Hills et al., 2015). Exploratory behaviors include a preference to seek novel associations, an orientation to learning, and a focus on the external environment over prior knowledge. Exploitative behaviors involve a preference to rely on previous knowledge and expectations, and a general aversion to novelty (Baror & Bar, 2016; Hills et al., 2015; Schwartenbeck, Fitzgerald, Dolan, & Friston, 2013).

Within the domain of human cognition, availability of cognitive control resources is an important factor in the shift from an exploratory to a more exploitative cognitive mode (Baror & Bar, 2016). In this study, younger adults were asked to generate free associations under conditions of high and low attentional load. Under low-load conditions, participants generated a greater number of novel, or exploratory, associations as compared to the high attentional load condition. As attentional resources were increasingly taxed, associations became more uniform, or exploitative, in nature. Further, subsequent priming of close associations was observed for high load conditions and for more remote associations under low attentional load. These results provide strong evidence that the availability of attentional resources determined whether participants approached the task from an exploratory or an exploitative cognitive mode (Baror & Bar, 2016). Lower cognitive control resources resulted in a shift towards exploitation of prior knowledge, and away from novelty seeking or the generation of new associations.

While these results have yet to be replicated in an older adult sample, the prediction for cognitive aging is clear. Declines in cognitive control, a hallmark of cognitive aging, should result in a shift from exploration to exploitation as a cognitive mode in older adulthood (see Figure 2). There is early, albeit indirect, support for this idea. Under conditions of high attention load older adults are more likely to produce 'false memories' on the DRM paradigm (Koutstaal et al., 2001), suggesting greater influence of prior knowledge on mnemonic performance. Similarly, the relative advantage for older adults on functional versus associative memory tasks has been attributed to the coupling of new and prior knowledge in working memory (Musielak et al., 2014). There is also evidence that age-related declines in episodic recall, associated with reduced control processes, results in an age-related shift towards exploiting prior knowledge as older adults increasingly draw upon semanticized recall to support memory functioning (Levine et al., 2002; Spaniol & Bayen, 2002). A shift in cognitive mode would also be consistent with our findings on creativity in aging discussed earlier (Adnan et al, in press). Older adults showed greater coupling of default to executive control brain regions, and this coupling was associated with *better* divergent thinking task performance across our sample of older adults. We interpreted this finding as older adults showing greater reliance on prior knowledge, or an exploitative cognitive mode, during creative cognition.

Semanticization of cognition and socioemotional selectivity. Evidence reviewed thus far suggests that a shift towards the semanticization of cognition, or an exploitative processing mode, occurs in response to a growing pool of semantic knowledge and reduced cognitive control in older adulthood. However, this shift may not merely be a reaction to the altered balance of knowledge and control, but rather an active, intentional process, precipitated by a shifting motivational hierarchy in later life. Socioemotional Selectivity Theory (SST, see Carstensen et al., 2003, for a review) suggests that the perception of a foreshortened time horizon shifts goal structures in older adulthood away from more expansive pursuits of new knowledge (i.e. an exploratory mode) and towards emotionally meaningful goals that provide more immediate personal satisfaction (i.e. an exploitative mode). According to SST, the shift from exploration to exploitation in later life reflects a parallel shift in motivational drives based on an increasing awareness of the finiteness of time. Perceived shorter time horizons motivate greater focus on more immediate and affectively salient goals.

Among the earliest evidence for SST was the discovery that the balance of one's social networks shifted towards increasingly close or intimate relationships in later life, with a relative decrease in the engagement of new or more casual acquaintances (Carstensen, 1992). These data suggest that the shift towards exploitation of prior experiences extends to the domain of social functioning, manifest in this context as a greater focus on more intimate social relationships. Critically, this socioemotional explanation for an age-related shift towards an exploitative cognitive mode is consistent with our DECHA model (discussed in detail in Section 5). A core node of the default network, the medial prefrontal cortex, and its connectivity to lateral prefrontal brain regions implicated in cognitive control, has been associated with many aspects of social cognition (Amodio and Frith, 2006; Forbes and Grafman, 2010). Critically, our work has also shown that this medial to lateral prefrontal cortex connectivity pattern is greater in older versus younger adults during both task (Turner and Spreng, 2015) and rest (Spreng et al., 2018), consistent with the DECHA.

In this section, we have demonstrated that ongoing accrual of semantic knowledge and experience across the adult lifespan, in the context of declining control resources, leads to the increasing semanticization of cognition and a shift in cognitive mode, from exploration to exploitation in later life. However, the neural basis of the shifting architecture of cognition has yet to be fully explored. In the following section we shift the focus of our review to the aging brain, highlighting the patterns of functional brain changes that we believe closely parallel the shift in cognitive architecture described in these opening sections. In the final section of the review we integrate these brain changes into a single model, the DECHA, a candidate neural mechanism bridging lifespan changes in cognitive and brain aging.

4. THE SHIFTING ARCHITECTURE OF BRAIN FUNCTION IN AGING

In the prior section, we discussed how the accrual of knowledge and experience across the adult lifespan, along with declining control resources, leads to the increasing semanticization of cognition with advancing age. We now turn to an examination of the shifting architecture of the brain that may underlie this co-occurring shift in cognitive architecture. We review structural and functional brain changes broadly, before focusing on changes specific to lateral prefrontal cortex and default network modulation with advancing age.

Structural brain changes. The human brain undergoes significant structural and functional changes across the adult lifespan (Spreng & Turner, in press). Global changes in grey matter, white matter, and ventricular volumes are a hallmark of normal brain aging. Lateral prefrontal cortices, implicated in cognitive control, appear particularly vulnerable to age-related structural change (Raz et al., 2005). Changes to the brain's white matter, axonal projections supporting communication among spatially distributed regions, or networks, are also a prominent feature of brain aging and are a strong predictor of age-related cognitive decline (Piguet et al., 2009; Snowdon, 1997; Yarchoan et al., 2012). Among large scale brain networks, structural changes to the default network have been commonly reported (Andrews-Hanna et al., 2014). Structural covariance studies have demonstrated network-level changes in typical aging and reduced integrity of this network is considered a neural network biomarker of the transition from typical to pathological aging (Spreng and Turner, 2013).

Functional brain changes. While the relationship between structural and functional brain changes remains an area of active debate and inquiry, both the STAC (Park and Reuter-Lorenz, 2009) and the CRUNCH (Reuter-Lorenz and Cappell, 2008) theories of neurocognitive aging suggest that these structural brain changes promote the formation or new, or the uncovering of latent, functional activity patterns to compensate for, or mitigate the impact of, deteriorating brain structures. Among the most commonly reported brain changes are greater recruitment and poor modulation of neural activity, primarily in prefrontal brain regions, in response to changing task demands (Cabeza, 2002; Grady, 2012). More globally, aging is associated with a pattern of functional brain change commonly referred to as neural dedifferentiation, or an inability to recruit specialized neural circuits associated with discreet processing operations (Park et al., 2001). Whether this dedifferentiation reflects a compensatory or maladaptive process remains a point of some debate (Grady, 2012; Spreng & Turner, in press; Turner & D'Esposito, 2010).

As we noted in the Introduction, functional brain changes are increasingly investigated through the lens of brain networks, or functionally connected assemblies of spatially distributed brain regions. Paralleling local changes, brain networks also become increasingly dedifferentiated in older adulthood. Network level changes are marked by reduced within-network and increased between-network connections (e.g. Chan et al., 2014; Geerligs, Renken, Saliasi, Maurits, & Lorist, 2015). These network interactions are also poorly modulated by task demands (Damoiseaux, 2017). To highlight the parallels between cognitive and functional brain aging, here we focus in more detail on two of the most commonly reported patterns of age-related functional brain change: Increased recruitment of lateral prefrontal brain regions, and reduced suppression of the default network.

Lateral prefrontal cortex activation. One of the earliest and most persistent patterns of age-related functional brain change observed during goal-directed tasks is enhanced bilateral recruitment of lateral prefrontal cortices (HAROLD, Cabeza, 2002). Lateral prefrontal cortices, and connections with posterior and subcortical brain regions, are critical for implementing cognitive control processes (Duncan, 2010; Shallice & Burgess, 1996; Stokes et al., 2013; Stuss & Levine, 2002). As cognitive control decline is a central feature of cognitive aging (Verhaeghen & Cerella, 2002), increased engagement of prefrontal cortices may reflect greater control demands in older versus younger adults.

This idea, most directly captured in the CRUNCH (Reuter-Lorenz & Cappell, 2008), posits that, with age, structural and functional brain changes result in noisier, lower-fidelity, and poorly-gated inputs for cognitive processing operations (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Li & Rieckmann, 2014; Schmitz, Dixon, Anderson, & De Rosa, 2014). These degraded inputs necessitate greater cognitive control, mediated by lateral prefrontal brain regions, to extract goal relevant signals from this noisier cognitive landscape (Park & Reuter-Lorenz, 2009). However, enhanced prefrontal recruitment may also be maladaptive, reflecting a loss of functional specialization (or dedifferentiation) secondary to structural brain changes (Park et al., 2001). In this interpretation, aging is associated with the degradation of specialized neural circuits, resulting in more diffuse and less efficient neural processing. While the cognitive implications continue to be debated, both compensation and dedifferentiation accounts converge in their prediction of age-related increases in lateral prefrontal brain activity during task performance.

Default network suppression. With the advent of whole-brain, functional neuroimaging methods more than two decades ago, changes in large-scale functional brain networks are rapidly becoming a hallmark of functional brain aging (Damoiseaux, 2017; Grady, 2012). As we noted earlier, the default network is an assembly of functionally-connected brain regions including the posterior cingulate cortex, medial prefrontal cortex, inferior parietal lobule as well as the medial and lateral temporal lobes (Buckner, 2004). This network was first identified for its reliable suppression across a range of externally-directed tasks in young (Raichle, MacLeod, Snyder, Powers, Gusnard, and Shulman, 2001) and older (Buckner, Andrews-Hanna, & Schacter, 2008) adults. Although its functions continue to be debated (Spreng, 2012), the default network is activated during internally-directed cognitive processes, including access to stored knowledge representations and experiences (Andrews-Hanna, Smallwood, & Spreng, 2014). Critically, this network has been implicated in associative and elaborative processing (Bar, Aminoff, Mason, & Fenske, 2007), linking perceptual information with internal representational knowledge structures to support cognitive processing (Spreng et al., 2014).

The default network is vulnerable to age-related changes. Activity within this network, typically suppressed during externally-directed cognitive tasks in young, is less deactivated in older adults (Lustig & Buckner, 2004). Functional connectivity within the default network also declines with age (Andrews-Hanna et al., 2007). Work suggests that reductions in connectivity within the default network predicts greater connectivity with frontoparietal control regions (Grady, Sarraf, Saverino, & Campbell, 2016). Critically, this pattern of between network connectivity appears to be poorly modulated by task context, with greater cross-talk observed at lower levels of task demand and across task contexts for older versus younger adults (Spreng and Schacter, 2012; Turner & Spreng, 2015). Poor modulation of network interactivity based on task context represents a fundamental alteration in the network architecture of the brain. As we argue in the next section, greater, and less flexible, coupling of default and prefrontal brain regions (i.e. DECHA), may provide a key neural conduit promoting the semanticization of cognition in later life.

Here we have focused on alterations in cortical structure and function to provide the necessary foundation for the introduction of our DECHA proposal in the following section. However, brain aging encompasses a much wider array of changes, including alterations in the structure and function of sub-cortical structures and neurotransmitter systems. While a more comprehensive review of these changes is beyond the scope of the review, one particular theoretical account of dopamine signaling, Novelty-related Motivation of Anticipation and exploration by Dopamine (NOMAD, Duzel, Bunzeck, Guitart-Masip, and Duzel, 2010), is of particular relevance to our model of semanticized cognition, or the emergence of an exploitative cognitive mode in later life. In the NOMAD account, reduced dopamine signaling within striatal-hippocampal circuitry is associated with age-related reductions in exploratory or novelty-seeking behaviors. This suggests that as striatal dopamine functioning declines with age, there is reduced dopaminergic tone within striatal-hippocampal circuits necessary to motivate cognitive processes associated with exploration, including episodic simulation, prospection, and planning for future events. Thus, a prominent feature of brain aging, reductions in the structure and function of the hippocampus (Bucker, 2004), mediated in part by deficient dopaminergic signaling, may be a neural mechanism underlying the shift towards a more exploitative cognitive mode in older versus younger adults. Interestingly, the hippocampus and medial temporal lobe formation, comprises one subsystem of the default network (Andrews-Hanna, Reidler, Sepulcre, Poulin, and Buckner, 2008). While speculative, loss of dopaminergic signaling to the hippocampus may alter the functional integrity of the default network more broadly, thereby precipitating greater coupling with frontal control networks – and promote a more exploitative cognitive mode. Indeed, this pattern of default-frontal coupling in response to declines in the functional integrity of the default network has been observed (Grady et al., 2016).

In the final section of the review we further explore the neural mechanisms associated with the semanticization of cognition, and a more exploitative mode of cognitive processing. Specifically, we argue that the DECHA provides a critical mechanism, linking the broad patterns of cognitive and brain aging discussed thus far in the review.

5. THE DEFAULT – EXECUTIVE COUPLING HYPOTHESIS: A UNIFIED ACCOUNT OF COGNITIVE AND BRAIN AGING

While age-related changes to lateral prefrontal and default network brain regions are both hallmarks of neurocognitive aging (Grady, 2012, Section 4), there has been scant consideration of whether or how these patterns intersect until recently. We demonstrated that lateral prefrontal engagement and reduced default network suppression co-occur, and are functionally-coupled, in older adulthood, leading us to propose the Default–Executive Coupling Hypothesis of Aging (DECHA; Turner and Spreng, 2015). We hypothesize that these functional brain changes parallel the shift in cognitive mode, from declining control processes, reflected in poorly modulated lateral prefrontal cortex activation, to greater reliance on prior knowledge, reflected in reduced default network suppression during goal directed tasks. We suggest that functional coupling of these two activity patterns provides a neural conduit promoting the semanticization of cognition (See Figure 2).

DECHA as dedifferentiation? Network dedifferentiation, resulting in greater cross-talk between brain networks, is a common feature of functional brain aging and has been generally associated with age-related cognitive decline (Chan et al., 2014; Geerligs et al., 2015). In this context, DECHA, as a specific exemplar of network dedifferentiation, should be associated with poorer cognitive performance in older versus younger adults. Indeed, we observed this in our study of the Tower of London planning task (Turner & Spreng, 2015). Moreover, greater default–executive coupling has been associated with lower fluid intellectual functioning during both task (Rieck et al., 2017) and rest (Spreng et al., 2018). However, a study examining age-related changes in functional connectivity among three networks specifically implicated in goal directed cognition, including default and cognitive control networks, suggests a more complex picture (Grady et al., 2016). Functional connectivity within and between networks was examined during performance of three tasks (associative memory, selective working memory and trait judgment). Between network connectivity of the cognitive control network (including core nodes in lateral prefrontal cortex) increased with age and this pattern was associated with better performance on the associative memory and trait judgment tasks in older, but not younger, adults. Interestingly, associations were not observed for the selective working memory task which, unlike the associative memory and trait judgment tasks, did not rely on mnemonic processing or activation of stored knowledge representations. Thus, consistent with the DECHA, increased connectivity between frontal and default network brain regions can lead to better cognitive performance. But, as we saw earlier, this benefit depends on the congruence between task goals and prior knowledge.

Context matters. An important early test of this 'context matters' principle was reported by Spreng and Schacter (2012). Here younger and older adults performed the Tower of London planning task, described above, and an analogous autobiographical future planning task. The two tasks were closely matched for sensorimotor demands and both involved a planning domain manipulation. Unlike the Tower of London task, the autobiographical planning task required participants to access personally-meaningful information to generate future plans. Both older and younger adults showed coupling of default and frontoparietal control networks during the autobiographical planning task, consistent with the idea that default–executive coupling can support cognition when prior knowledge is congruent with task goals. During the Tower of London task, the functional connectivity patterns for younger and older participants diverged. While younger adults showed greater coupling between frontoparietal control and visual attention regions, consistent with performing an externally directed visual task, older adults failed to decouple lateral prefrontal and default network brain regions. In short, they failed to modulate functional connectivity between default and executive control regions based on task context. This study provided the first direct evidence of task-based affiliation between default and executive control regions during a goal-directed task where access to prior knowledge was task relevant (i.e. autobiographical planning). Further, for young adults, network affiliations shifted between the two planning tasks based on the relevance of prior knowledge whereas older adults failed to flexibly shift network connectivity based on task context. This suggests that default–executive coupling may be less flexible in older adulthood. But how do these network-level findings relate to the age-related shift in cognitive modes discussed in Section 3? As we saw earlier, when planning was impersonal during the Tower of London task, young adults decoupled default and frontal brain regions; older adults maintained default–executive coupling and performed more poorly on the task. Goal relevance of prior knowledge and age are therefore key determinants of whether DECHA reflects an adaptive or maladaptive process.

When tasks require processing of stimuli devoid of personal meaning and unconnected to prior knowledge, DECHA predicts that positive coupling between default and executive control regions will lead to poorer performance in older adults. There is growing evidence for this idea. In a lifespan study of brain activity during performance on a spatial reasoning task, greater activation of lateral prefrontal cortex and greater deactivation of the default network in response to increasing task demand were correlated. Further, this association between positive and negative modulation in activity predicted poorer task performance as well as lower fluid reasoning ability outside of the scanner across the lifespan (Rieck et al., 2017). These findings are consistent with a large literature showing that reduced suppression of the default network and increased coupling with lateral prefrontal cortices is associated with poorer performance on externally-directed cognitive tasks (Damoiseaux, 2017; Grady, 2012; Keller et al., 2015; Persson, Lustig, Nelson, & Reuter-Lorenz, 2007; Spreng, Stevens, Viviano, & Schacter, 2016; Turner & Spreng, 2015).

Few studies to date have investigated how default–executive coupling influences cognitive performance when access to prior knowledge is consistent with task goals. It has long been assumed that default network activity must be suppressed to facilitate performance on all cognitive control tasks. However, studies have challenged this idea. Using a social working memory paradigm Meyer and colleagues (2012) asked participants to hold in mind personality traits of known others. They observed robust activation of core default network regions typically implicated in social cognitive tasks. Critically, this default network activity co-occurred with activation of lateral prefrontal cortices implicated in working memory processes. While the authors did not report functional connectivity analyses, this study provided early evidence that the default network is not uniformly suppressed during cognitive control tasks. Rather, default and lateral prefrontal brain regions can be simultaneously engaged when cognitive control operations require access to stored knowledge representations (e.g. Baird, Smallwood, Gorgolewski and Margulies, 2013; Konishi, McLaren, Engen and Smallwood, 2015; Spreng et al., 2010; Spreng et al., 2014; Spreng, Gerlach, Turner and Schacter, 2015).

DECHA as an enduring shift in functional brain aging. So far, we have shown that the behavioral impact of default–executive coupling, as a putative mechanism underlying the semanticization of cognition in later life, depends on the congruence between prior knowledge and task goals. The studies reviewed thus far relied on different tasks to demonstrate this point. However, a critical prediction of the DECHA is that greater default–executive coupling should be associated with *a shift* in cognitive processing toward greater reliance on semantics in older adulthood. Demonstrating such a relative shift in the influence of prior knowledge across the lifespan requires measuring the relative contributions of cognitive control and semantics within a single task. To test this prediction we investigated autobiographical memory performance and functional network architecture in younger and older adults (Spreng et al., 2018). We used the Autobiographical Interview (Levine et al., 2002) which enabled us to generate separate estimates of episodic and semantic recollection. Deriving these two measures from a single task allowed us to contrast the level of controlled retrieval, necessary for episodic recall, with the level of semanticized knowledge generated during remembrances of personal past events. Default–executive coupling was assessed with resting fMRI. We reasoned that if the shifting architecture of cognition occurs across the adult lifespan, then this shift should be most robustly reflected in these intrinsic network connectivity patterns, also shaped throughout the life course (Spreng et al., 2016). We first observed that default–executive coupling at rest was negatively associated with a measure of fluid IQ. This was consistent with our argument that default to executive coupling is not adaptive where prior knowledge is incongruent with task goals. The second, and more critical finding with respect to DECHA, was that greater default–executive coupling was associated with more semanticized autobiographical retrieval for older, but not younger, adults (even when controlling for fluid cognition). These results provide support for the idea that greater default–executive coupling is associated with the semanticization of cognition in later life (Spreng et al., 2018). Further work is necessary to test this hypothesis in additional cognitive domains where age-related shifts towards semanticized cognition have been reported (see Section 2).

Determinants of default–executive coupling. To further explicate the DECHA as mechanism to predict age-related cognitive changes we need to better understand the determinants of default–executive coupling and how variations in this pattern of network interactivity are associated with the semanticization of cognition. We have identified two factors: congruence with prior knowledge and the availability of control resources. As we reviewed in Section II, familiarity drives the semanticization of cognition. At the level of the brain, default network brain regions are activated simply by perceiving familiar stimuli (Bar et al., 2007; Leveroni et al., 2000; Spreng et al., 2014). Engagement of the default network by known stimuli, in the absence of explicit task demands, is consistent with a knowledge-based account of the semanticization of cognition in later life. Age-related increases in the accumulation and fluency of stored representations (Craik & Jennings, 1992) would result in greater default network activation and influence of prior knowledge on cognitive functioning in older versus younger adults. As we have seen, this can be both adaptive, as in the Moses and Truth Illusion experiments, or maladaptive, as in the false memory studies. However, activation of prior knowledge is a necessary but not sufficient determinant of default–executive coupling. Goal-directed tasks additionally require activated knowledge representations to enter the focus of attention to influence future thought and action. As access to the focus of attention is modulated by cognitive control processes, the availability of control resources is a second determinant of semanticized cognition in later life.

The interdependence of prior knowledge and control processes during ongoing cognitive operations was convincingly demonstrated in the investigation of exploratory and exploitative modes of cognitive processing described earlier (Baror & Bar, 2016, Section 3). In that study, cognitive control was supplanted by access to prior knowledge to support task performance. Similarly, as control resources decline with age, prior knowledge representations would be expected to move to the fore and exert greater influence over cognitive operations. We argue that greater, and less flexible, default–executive coupling in older adults serves as a putative neural mechanism associated with greater semanticization of cognition (Figure 2).

In a review of brain activity during semantic processing tasks, Binder and colleagues (2009) identified a robust pattern of default and lateral prefrontal activation in young adults. A recent review contrasting brain activity between younger and older adults identified age-differences in lateral prefrontal brain cortex but not in the default network (Hoffman & Morcom, 2018). As we have seen throughout the review, accessing prior knowledge conveys larger performance benefits for tasks that more closely mirror real-world functions, when past patterns of thought and action can be accessed to support current or planned behavior. However, there are two important differences between real-world and laboratory-based tasks. As we discussed earlier, laboratory stimuli are typically devoid of personal relevance, rendering knowledge of one's past behavior at best irrelevant and at worst, distracting. Additionally, laboratory-based tasks are highly constrained. Task rules and the current stimulus array, by necessity, guide behavior. Here again, knowledge of past behavior is unnecessary or potentially maladaptive. Thus the failure to observe robust, age-related changes in the default network during standard laboratory-based tasks of semantic cognition is perhaps unsurprising. As we have shown in Section II, engaging prior knowledge is more beneficial during less constrained, more real-world task contexts such as economic decision-making, problem-solving, or future planning. Critically, older adults display this tendency more than their younger counterparts, whether or not they are instructed to do so (Blanco et al., 2016; Musielak et al., 2014). Under these task conditions, mimicking unconstrained, real-world contexts, increased activation, and coupling of the default network with lateral prefrontal regions may not reflect maladaptive dedifferentiation, but rather a change in cognitive mode secondary to declining control resources with age (c.f. Baror & Bar, 2016). Constraints imposed by the task, precluding engagement or leveraging of this exploitative cognitive mode, may be another important determinant of default–executive coupling in later life. Unconstrained or everyday tasks leave greater scope to search and engage prior knowledge. Under DECHA, this would in turn lead to greater default network activity and increased coupling with lateral prefrontal brain regions to grant these representations privileged, or at least priority, access to the focus of attention.

We have now identified three putative determinants promoting the semanticization of cognition in older adulthood: congruence between items in the focus of attention and prior knowledge (i.e. familiarity), availability of cognitive control resources, and the nature of the task, either promoting or precluding an exploitative cognitive mode. Importantly, each of these implicate either default or lateral prefrontal brain regions, or their interaction. Default network activity is modulated by stimulus familiarity, while lateral prefrontal brain regions mediate cognitive control processes and are most reliably engaged during unconstrained tasks. While our work exploring DECHA as a neural network mechanism of cognitive aging is ongoing, we predict that a change in any of these factors (increased stimulus familiarity, decreased cognitive control, unconstrained task environment) would result in greater default–executive coupling and the semanticization of cognition in older adulthood.

DECHA: A novel account of neurocognitive aging. It is important to re-emphasize here that default–executive coupling, as reflected in the DECHA, does not predict task performance *per se*. Rather, it is the context-dependent engagement and flexible coupling of lateral prefrontal and default brain regions that may best predict adaptive, goal-directed behavior in older adulthood. We suggest that it is the context-dependency of the DECHA that distinguishes it from other leading neurocognitive aging theories such as HAROLD (Cabeza, 2002), PASA (Davis et al., 2008) or the CRUNCH (Reuter-Lorenz and Cappell, 2008) and STAC (Park and Reurter-Lorenz, 2009) reviewed in the Introduction. By incorporating both dimensions of the shifting architecture of cognition within a single framework, the DECHA is able to generate predictions of both cognitive gains and losses in later life. Further, we argue that considering both cognitive control demands and the relevance of prior knowledge is particularly important for predicting older adult capacity in real world settings, where access to prior knowledge and experience may convey greater benefit than in typical laboratory-based contexts.

Finally, as reviewed above, results from our lab and others suggest that these age-related network changes are measurable at rest, in the absence of explicit task demands (Ng et al., 2016; Spreng et al., 2018). We have previously suggested that functional connectivity patterns such as default–executive coupling, entrained over the lifespan may alter the intrinsic network architecture of the brain (Stevens & Spreng, 2014). These intrinsic network changes, shaped over years or decades, provide important insights into similarly protracted but durable shifts in cognitive abilities, We suggest that evidence for greater coupling between the default network and executive control regions is fully consistent with an ontogenetic shift towards increasingly semanticized cognition and an exploitative cognitive mode in later life. However, within-subject studies, contrasting task and resting-state network organization across age cohorts, will be necessary to address whether poor task-driven modulation of default–executive coupling is an emergent property of a more enduring age-related shift in the intrinsic network architecture of the brain.

In this final section of the review we have argued that DECHA provides not simply a descriptive but a mechanistic account of neurocognitive aging. By incorporating changes in brain regions associated with both cognitive control processes (lateral prefrontal cortex) and semantic cognition (default network), the DECHA may help to predict the dual trajectories of cognitive aging and further our understanding of how these cognitive and neural changes intersect to promote the shift from cognitive exploration to cognitive exploitation in later life.

6. CONCLUSION

Psychological and neuroscience studies of cognitive aging are disproving the fallacy that cognitive aging equals cognitive decline. The true story of cognitive aging is one of both gains as well as losses. With age comes an expanding repertoire of knowledge and life experience that can help navigate the routines – and the surprises – of daily life. Of course, repeating the past does not necessarily portend an optimal future. When and how past knowledge is accessed to guide goal-directed behavior can influence how successfully older adults are able to reason, problem-solve, and plan in their everyday lives. Indeed, this idea of engaging prior knowledge to guide real-world behavior closely resembles definitions of wisdom, where adaptive thought and action requires access to tacit knowledge about oneself, others, and situational contexts (Sternberg, 1998). Better access to a richer store of tacit knowledge, or the fundamental pragmatics of life (Baltes & Staudinger, 2000), is considered to be the basis of practical intelligence and a precondition for wise thinking. Interestingly, accessing these stores of prior knowledge, including representations of oneself, the thoughts and intentions of others, and how they interact *in situ*, all engage default network brain regions (Andrews-Hanna et al., 2014). While speculative, this raises the intriguing possibility that increased default–executive coupling may serve as a neural conduit allowing prior knowledge to enter the focus of attention and facilitate wise thinking in later life.

We have drawn upon findings from cognitive psychology and cognitive neuroscience to develop a comprehensive account of neurocognitive aging. Integrating parallel shifts in the architectures of cognition and brain function, the DECHA encompasses the full spectrum of aging cognition, generating predictions for both gains and losses, and their interactions, across the lifespan. However, in contrast to the rich literature identifying the shift in cognitive architecture from young, to middle, to older age (e.g. Park et al., 2001, Figure 1), few studies have directly examined lifespan changes in functional brain network interactions (but see Rieck et al., 2017; Chan et al., 2014). Future research is necessary to map interactions among functional brain networks and how they change across the full adult life course. A significant challenge going forward will be to identify a set of determining conditions for default–executive coupling, and the semanticization of cognition, from younger to older adulthood. This will require novel paradigms to experimentally manipulate the engagement of prior knowledge in order to determine a putative ‘set-point’, marking the shift from exploratory to exploitative processing and investigating how this baseline changes across the lifespan. This would provide the necessary behavioral markers to further test the DECHA and explore its utility as neural mechanism to predict individual differences in the trajectory of cognitive and real world functional capacities across the adult lifespan.

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FIGURES

Figure 1.

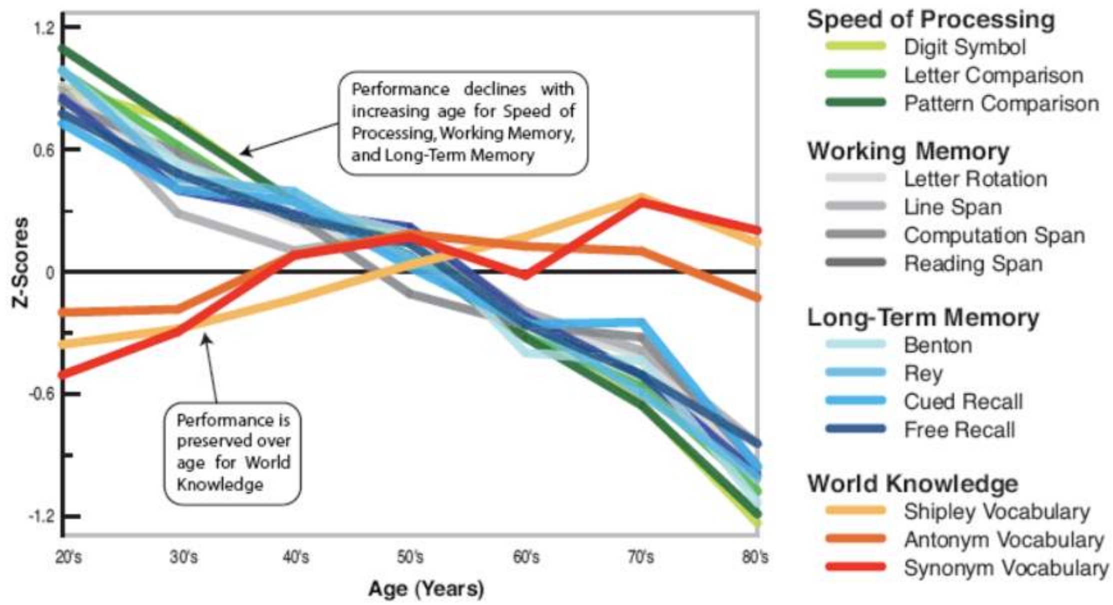

Figure 1. The shifting architecture of cognition across the adult lifespan. Cool colors represent age-related changes on tasks that have greater reliance on cognitive control and speeded processing. Warm colors represent age related changes on tasks that have a greater reliance on semantics or prior knowledge representations. As can be seen clearly in these data, the architecture of cognition undergoes a striking shift across the adult lifespan, a process we refer to here as the semanticization of cognition. Reproduced from Park, et al., 2001 with permission.

Figure 2

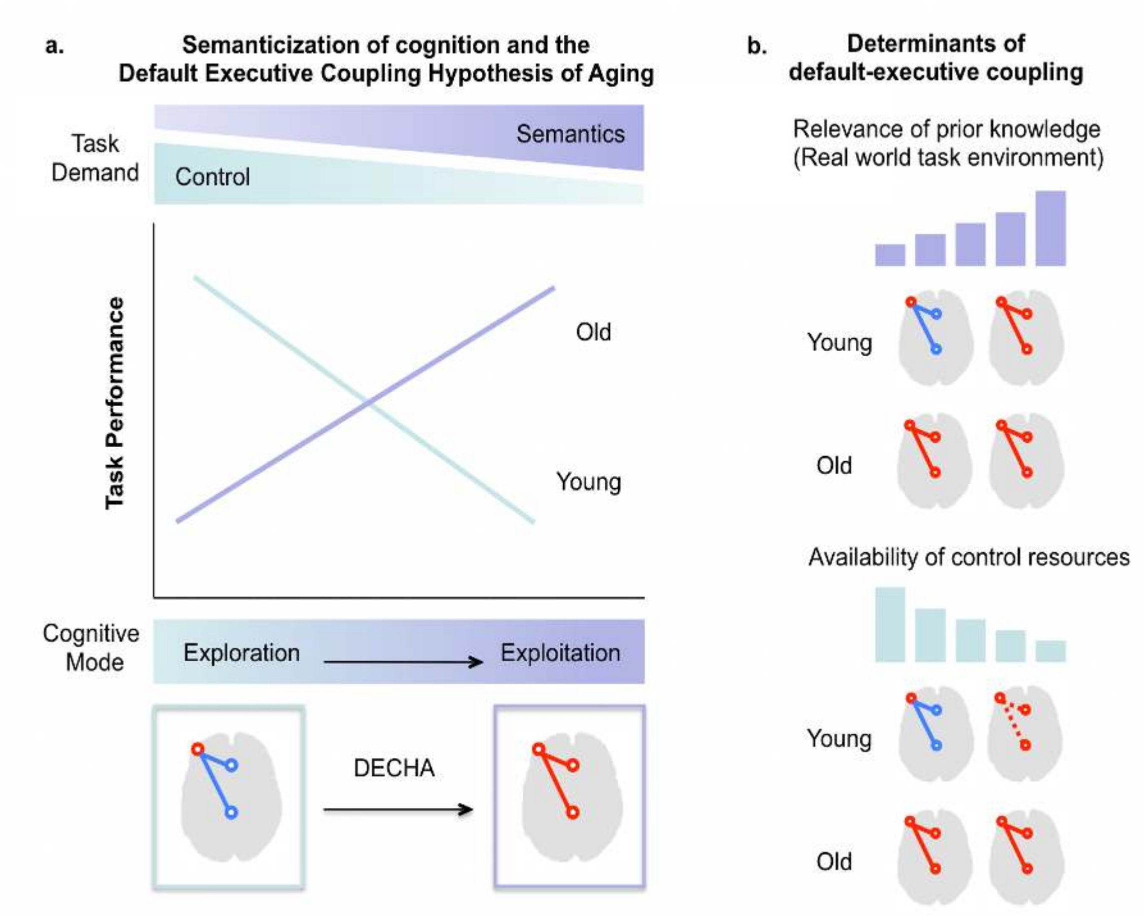

Figure 2. Integrated model of cognitive and brain aging. A.) Shifting task demands, from controlled processing to greater reliance on semantics (prior knowledge), impacts task performance differently for younger and older adults. When control demands are high, there is a relative performance benefit for young (leftward aspect of the graph). As prior knowledge becomes more goal relevant, the performance advantage shifts to older adults (rightward aspect of the graph). Greater reliance on semantic knowledge representations, in the context of declining control resources (see Figure 1), results in a shift in cognitive mode from exploration to exploitation in later life. Brain schematics (bottom of panel A) represent the Default to Executive Hypothesis of Aging (DECHA). Left schematic reflects greater reliance on cognitive control processes, or exploratory cognitive mode. This is associated with engagement of lateral prefrontal brain regions (red circle) and suppression of default network brain regions (blue circles). Blue lines reflect negative functional connectivity between default and executive regions (i.e. greater frontal activation in the context of default network suppression). Right schematic reflects greater reliance on prior knowledge, or an exploitative cognitive mode. This is associated with increased and positive functional connectivity between lateral prefrontal regions and the default network. We hypothesize that this pattern of increased functional connectivity serves as a neural network mechanism promoting the semanticization of cognition in later

life. B.) Upper schematic demonstrates that as the relevance of prior knowledge changes, default to executive coupling is modulated in younger adults (from negative to positive correlations). In contrast, default to executive coupling is poorly modulated in older adults. Lower schematic demonstrates that as access to cognitive control resources change, default to executive coupling shows a similar pattern of context-dependent modulation in young. (Direct evidence for this network pattern in the young is lacking in the literature these, therefore the associations are represented by dotted lines). The pattern of default to executive coupling is less flexible in older adults and poorly and is modulated by access to control resources. Figure adapted from Samanez-Larkin and Knutson (2014).