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Life was meant to be lived, and curiosity must be kept alive. One must never, for whatever reason, turn his back on life.

- Eleanor Roosevelt (1961)

Curiosity is a fundamental motivation in humans. Although the literature still lacks a widely accepted definition of curiosity and there have been several variations in its definition (Berlyne, 1954; Collins, Litman, & Spielberger, 2004; Kidd & Hayden, 2015; Litman, 2008; Loewenstein, 1994; Oudeyer, Gottlieb, & Lopes, 2016; Silvia, 2005, 2008), most researchers agree that curiosity represents a motivation or desire to seek and learn new information by exploring novel or uncertain environments (Kashdan & Silvia, 2009). Especially visible in early childhood, curiosity has received attention in the literature of child development (Engel, 2011; Smock & Holt, 1962) and education (Grossnickle, 2016; Klahr, Zimmerman, & Jirout, 2011; Oudeyer et al., 2016). These studies have found that curiosity plays a central role in children's learning, predicting academic achievement and achievement motivation (Renninger & Hidi, 2016; Von Stumm, Hell, & Chamorro-Premuzic, 2011). Curiosity also plays critical roles beyond the context of child development and education, supporting a variety of activities like consumer behaviors (Steenkamp & Baumgartner, 1992), job performance (Mussel, 2013), and scientific discoveries (Simon, 2001).

In the current paper, we provide a literature overview of one of the most underappreciated topics on curiosity—curiosity in old age. We argue that, although curiosity generally declines with age, it plays an important role in maintaining cognitive function, mental health, and physical health in older adults. In contrast to the literature in

child development and education, the existing literature on curiosity in older adults is rather sparse and the few relevant topics are largely isolated from each other. Furthermore, whereas some studies examine curiosity by focusing on a phasic emotional and motivational state evoked when faced with novel and interesting stimuli, other studies measure individual differences in trait curiosity (individual differences in a tendency to experience curiousity; Litman & Spielberger, 2003) using self-reported questions, with little attempt to compare or reconcile findings across the different methodologies. In addition, studies on similar concepts (e.g., novelty seeking, experience seeking and sensation seeking) provide useful insights into curiosity, but this link tends to be overlooked in the existing literature. Our aim in the current paper is to join these different lines of research and assert the importance of curiosity in the aging population.

1. Effects of Age on Curiosity

Previous studies on subjective feelings of curiosity and aging suggest that normal aging leads to a decline in at least some aspects of curiosity. For example, in a cross-sectional survey study on a nationally representative sample in the UK, Robinson, Demetre, and Litman (2017) showed a decline from early to late adulthood in three distinct dimensions of curiosity: interpersonal curiosity, a desire to find out information about other people, such as feelings of other people and what other people do; epistemic curiosity, an intellectual desire for new knowledge; and intrapersonal curiosity, a desire to find out new information about the self (see also Renner, 2006).

This age-related decline in curiosity is consistent with findings from studies of personality traits that are related to individual differences in trait curiosity. One example

is openness to experience from the Big Five personality traits (Kashdan et al., 2009; Kashdan, Rose, & Fincham, 2004), which refers to individuals' willingness to explore, tolerate, and consider new and unfamiliar ideas and experiences (McCrae & Costa, 1987). Previous research has shown that, although scores for some personality traits increase with age (e.g., agreeableness; conscientiousness), openness to experience decreases with age (Costa, Herbst, McCrae, & Siegler, 2000; McCrae et al., 1999; McCrae et al., 2000; Ziegler, Cengia, Mussel, & Gerstorf, 2015). Another trait which is related to curiosity is sensation seeking. Sensation seeking represents individual differences in the 'optimal level of stimulation' and refers to one's tendency to seek varied, novel, complex, and intense sensations and experiences (Zuckerman, Buchsbaum, & Murphy, 1980). Like openness to experience, sensation seeking appears to decrease with age (Lawton, Kleban, Rajagopal, & Dean, 1992; Zuckerman, Eysenck, & Eysenck, 1978). Closely related to sensation seeking, age-related declines in subjective feelings of stimulation seeking (i.e., a tendency to take part in stimulating activities) have also been confirmed via longitudinal study (Giambra, Camp, & Grodsky, 1992). Research on apathy—a *lack* of motivation and interest, including indifference towards having new experiences—further reveals that normal aging is associated with increased apathy (Brodaty, Altendorf, Withall, & Sachdev, 2010), consistent with age-related declines in curiosity.

Age-related reductions in exploratory behaviors in novel situations are also evident in animal research (e.g., Mroczek & Kolarz, 1998; Van Waas & Soffié, 1996). In one study, for example, young and old rats were habituated to two bottles with water for five days; on the sixth day, water in one of the bottles was replaced by a saccharin

solution (Collier, Greene, Felten, Stevens, & Collier, 2004). While young rats preferred the saccharin solution over the water in the other bottle despite its novelty, old rats showed reduced preference for the novel saccharin solution over the water bottle (see also Dellu, Mayo, Valleé, Le Moal, & Simon, 1994). In summary, previous research suggests that normal aging is associated with reduced curiosity and reduced exploration behaviors in novel environments.

2. Brain Mechanisms underlying Curiosity in Old Age

What are the brain mechanisms underlying these age-related changes? To address this question, we will first provide a brief review of the brain mechanisms underlying curiosity and then explain how normal aging affects these brain regions.

2.1. Brain mechanisms of curiosity

While research on the neural mechanisms underlying subjective feelings of curiosity is still sparse, substantial research has addressed the neural mechanisms underlying exploration driven by novelty and uncertainty (for a review see Schomaker & Meeter, 2015). Novelty is defined as per the number of times that the stimulus has been previously encountered, while uncertainty is defined as per the unreliability of consequent outcomes (Gottlieb, Oudeyer, Lopes, & Baranes, 2013; Yu & Dayan, 2005). Thus, these two concepts are related but can be independently operationalized (e.g., one can feel uncertain about an outcome irrespective of whether the outcome is familiar or novel). Nevertheless, previous studies show some overlap in the brain regions involved in these processes and indicate the possibility that brain regions implicated in rewards and emotion play important roles in curiosity.

The first set of regions implicated in curiosity is the mesolimbic dopaminergic

system (Figure 1A). Exposure to novel stimuli induces activation of subcortical reward-related regions, including the nucleus accumbens (NAc), substantia nigra (SN), and ventral tegmental area (VTA; Axmacher et al., 2010; Bunzeck & Düzel, 2006; Bunzeck, Guitart-Masip, Dolan, & Duzel, 2014; Krebs, Heipertz, Schuetze, & Duzel, 2011; Wittmann, Bunzeck, Dolan, & Düzel, 2007; Wittmann, Daw, Seymour, & Dolan, 2008). Individuals with high novelty-seeking tendencies also show greater activity in these regions than those with low novelty-seeking tendencies when exposed to novel stimuli (Krebs, Schott, & Düzel, 2009). Animal research provides further support for the role of the dopaminergic system in curiosity (Bardo, Donohew, & Harrington, 1996): when animals are exposed to a novel environment, they show increased dopaminergic signals in the NAc (Legault & Wise, 2001; Piazza et al., 1991; Rebec, Christensen, Guerra, & Bardo, 1997; Rebec, Grabner, Johnson, Pierce, & Bardo, 1996) and increased firing rates of dopaminergic neurons in the SN (Ljungberg, Apicella, & Schultz, 1992).

Recent neuroimaging studies have examined the neural mechanisms underlying curiosity more directly by employing tasks that induce subjective feelings of curiosity. These studies also indicate the importance of the dopaminergic system in curiosity (Kang et al., 2009; for a review see Kidd & Hayden, 2015). For example, Gruber and colleagues presented participants with trivia questions that differed in curiosity levels and found that trivia questions with higher curiosity was associated with stronger activity in the striatum and SN/VTA (Gruber, Gelman, & Ranganath, 2014). The striatum has been also implicated in the relief of perceptual curiosity (i.e., when curiosity triggered by the presentation of ambiguous visual input was satisfied by disambiguation; Jepma, Verdonschot, van Steenbergen, Rombouts, & Nieuwenhuis, 2012).

The studies described so far have focused on the dopaminergic reward-related areas, but accumulating evidence suggests that processing of novel and uncertain stimuli is also associated with the noradrenergic system (Figure 1B), in particular the locus coeruleus (LC), a primary source of norepinephrine in the brain (e.g., Devauges & Sara, 1990; Gompf et al., 2010). Indeed, pupil dilation, a peripheral measure of LC activity (Joshi, Li, Kalwani, & Gold, 2016; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014), tracks unpredictability during tasks (Lavin, San Martín, & Rosales Jubal, 2014). A recent neuroimaging study suggests that the LC is involved in processing uncertainty in humans (Payzan-LeNestour, Dunne, Bossaerts, & O'Doherty, 2013). In addition, changes in pupil dilation owing to uncertainty have been associated with better learning rates (Nassar et al., 2012). Likewise, phasic arousal induced by something emotional (which is associated with the LC activity) modulates learning and hippocampal functioning (Mather, Clewett, Sakaki, & Harley, 2016; Sakaki, Fryer, & Mather, 2014). Thus, the LC may also be related to curiosity-enhanced learning.

Animal studies further support the role of the LC in processing novelty and uncertainty (Delini-Stula, Mogilnicka, Hunn, & Dooley, 1984; Harro, Oreland, Vasar, & Bradwejn, 1995). In one study, rats were habituated to a box which included nine holes symmetrically cut in the floor (Devauges & Sara, 1990). After habituation, objects were added in four holes and the rats were given idazoxan (an alpha2 adrenergic antagonist) or a control treatment. Idazoxan increased the time that rats spent exploring the holes with novel and unexpected objects, particularly those with complex objects, but did not affect exploration of the empty holes. Subsequent research confirms that administration of alpha2 adrenergic receptor agonists and beta receptor antagonists eliminate this

preference towards holes with novel objects (Sara, Dyon-Laurent, & Hervé, 1995; see also Vankov, Hervé-Minvielle, & Sara, 1995).

2. 2. Effects of age on brain regions important for curiosity

As reviewed in the previous section, the dopaminergic system and the noradrenergic system underlie exploration behaviors based on novelty and uncertainty in young adults and animals. Previous research also suggests that similar brain regions play critical roles in curiosity in older adults. For example, exposure to novel stimuli evoked activation in the SN/VTA in older adults like that seen in younger adults (Bunzeck & Düzel, 2006; Bunzeck et al., 2007). Norepinephrine release in the cingulate cortex—a region which has strong projections from the LC (B. E. Jones & Moore, 1977)—was also associated with intact exploratory behaviors in novel environments in old rats (Collier, Greene, Felten, Stevens, & Collier, 2004).

The dopaminergic system and the noradrenergic system are also susceptible to age-related decline. Past research has documented age-related declines in the striatum structure (Raz et al., 2003; Walhovd et al., 2005), striatal dopamine levels (Collier et al., 2007; Haycock et al., 2003), the number of dopaminergic D1 and D2 receptors in the striatum (Rinne et al., 1993; Rinne, Lönnberg, & Marjamäki, 1990), responsivity of the striatum to reward learning (Chowdhury et al., 2013; Eppinger, Schuck, Nystrom, & Cohen, 2013; Schott et al., 2007), and D2 receptor binding in the striatum (Bäckman et al., 2000; for reviews see Bäckman, Lindenberger, Li, & Nyberg, 2010; Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010; Kaasinen & Rinne, 2002; Reeves, Bench, & Howard, 2002). Previous research has also shown increased iron accumulation in the striatum with age (Steiger, Weiskopf, & Bunzeck, 2016), as well as high exposure of SN neurons

to iron (Zecca, Stroppolo, et al., 2004). Given that iron exposure leads to oxidative stress and neuronal loss (Zecca, Youdim, Riederer, Connor, & Crichton, 2004), these results further suggest that the dopaminergic neurons are particularly vulnerable to oxidative stress during aging. Furthermore, animal research reveals reduced dopamine concentration levels in the striatum (Míguez, Aldegunde, Paz-Valiñas, Recio, & Sánchez-Barceló, 1999) and neuronal loss in the SN (Emborg et al., 1998) in aged brains. The age-related change in the dopaminergic function was not limited to the striatum and the SN (Bach et al., 1999; Míguez et al., 1999). For example, studies have shown the reduced density of D2 receptors in the hippocampus (Amenta et al., 2001) and reduced mRNA levels for D1-D5 receptors in the CA1 neurons in the hippocampus with age (Hemby, Trojanowski, & Ginsberg, 2003).

The noradrenergic system also shows decline with age. The density of alpha2 receptors declines in aging in monkeys (Bigham & Lidow, 1995). Likewise, alpha1 and alpha2 noradrenergic receptor bindings in the prefrontal cortex (PFC) were lower in older monkeys than in younger monkeys (Moore et al., 2005). Aging was also associated with reduced firing rates of LC neurons (Olpe & Steinmann, 1982), reduced density of beta adrenergic receptors (Greenberg & Weiss, 1978), the impaired synthesis of alpha1 and alpha2 receptors (Zhou, Weiss, Freilich, & Greenberg, 1984), and altered sensitivity of neurons to norepinephrine in rodents (R. S. G. Jones & Olpe, 1984; R. S. G. Jones & Olpe, 1983). The density of norepinephrine transporter (NET) in LC also declines with age in humans (Ding et al., 2010). Since NET plays critical roles in NE signaling (Jayanthi & Ramamoorthy, 2005), these results further suggest that normal aging is associated with changes in the action of norepinephrine in the brain.

Furthermore, exposure to novel stimuli often induces the P3 component of the event related potential (ERP), but normal aging is associated with a decline in the amplitude of the P3 component (Czigler, Pató, Poszet, & Balázs, 2006; Fabiani & Friedman, 1995; Friedman, Kazmerski, & Cycowicz, 1998). Though the exact neural mechanisms underlying the P3 component are not yet known, the LC is a candidate region (Murphy, Robertson, Balsters, & O'Connell, 2011; Nieuwenhuis, Aston-Jones, & Cohen, 2005). Thus, the age-related decline in P3 amplitude suggests that aging is linked to impaired LC function. The impaired function and structure of the brain regions critical for curiosity in older adults may in turn lead to the aforementioned reductions in subjective feelings of curiosity.

3. Motivational Factors that Affect Curiosity in Old Age

Aging is associated not only with changes in neural structure and function, but also with changes in one's motivation. According to the socioemotional selectivity theory (SST) (Carstensen, 1995; Carstensen, Isaacowitz, & Charles, 1999; Carstensen & Turk-Charles, 1994), people have two broad goal categories: a) to acquire knowledge, seek novelty, and expand breadth of knowledge and b) to regulate negative, and maintain positive, emotional states. These goals operate across the lifespan, such that people are generally motivated to learn new knowledge and maintain positive emotional states.

SST further posits that when individuals are young or perceive their future time as more open-ended, they are more likely to focus on information-seeking goals over emotion-regulation goals in preparation for the uncertain future. In contrast, people are more likely to favor emotion-regulation goals and optimizing their psychological wellbeing when they perceive time as being limited. Consistent with the predictions of

SST, older adults, relative to younger adults, tend to prefer interactions with familiar people over new people (Fredrickson & Carstensen, 1990), have a smaller size of social networks than do younger adults (Fung, Carstensen, & Lang, 2001; Lang & Carstensen, 1994; Lang & Carstensen, 2002; Wrzus, Hanel, Wagner, & Neyer, 2013), and show reduced exploration behaviors in their social life. Older adults also tend to remember and pay attention to more positive information than negative information (Löckenhoff & Carstensen, 2004; Löckenhoff & Carstensen, 2007; Mikels et al., 2010). These age-related differences can be weakened when motivations are manipulated to elicit the information-gathering goal or time perspectives are manipulated to think of time as being expansive (Barber, Opitz, Martins, Sakaki, & Mather, 2016; Kellough & Knight, 2012; Löckenhoff & Carstensen, 2007). These results suggest that at least some of the effects of age on curiosity are driven by motivational shifts with age, rather than structural or functional changes in the brain.

4. Curiosity as a Proxy for Adaptive Aging

As reviewed so far, previous studies with respect to personality psychology, animal behavior, neuroimaging, and social psychology are consistent with the notion that curiosity declines with advanced age. However, accumulating evidence also suggests that curiosity may actually play a critical role in maintaining cognitive functioning, wellbeing and physical health in older adults.

In this section, we argue that momentary feelings of curiosity can help older adults' mental functions, because phasic activation of the noradrenergic and dopaminergic systems modulate brain functioning, facilitating our mental processing which often declines with age (Figure 2). In addition to the short-term effects of

curiosity, we also point out that a chronic tendency to experience curiosity can have benefits over the course of aging (Figure 3). Below we first provide an explanation about possible mechanisms by which curiosity can have life-long effects, followed by discussions of each domain curiosity appears to help: memory, general cognition, wellbeing, and physical health.

4.1. Mechanisms underlying the cumulative effects of curiosity

When one has a general tendency to experience curiosity, such experiences can have cumulative effects and long-term consequences via several mechanisms. First, trait curiosity can affect one's behaviors and facilitate behaviors that are beneficial for adaptive aging. For example, cognitively stimulating activities protect against age-related declines in cognitive functioning, such as reasoning and episodic memory (Corbett et al., 2016; Ferreira, Owen, Mohan, Corbett, & Ballard, 2015; Robertson, 2013). Curiosity is often the primary predictor for older adults' engagement in such activities in the first place (Romaniuk & Romaniuk, 1982). Therefore, those with lower curiosity may engage in fewer stimulating activities and learning opportunities as they age, thus leading to poorer cognitive performance.

Second, accumulating evidence suggests that both norepinephrine and dopamine have neuroprotective effects. Norepinephrine is known to reduce inflammatory responses (for reviews see Braun, Madrigal, & Feinstein, 2014; Feinstein et al., 2002; Mather & Harley, 2016; O'Donnell, Zeppenfeld, McConnell, Pena, & Nedergaard, 2012). For example, norepinephrine depletion facilitates inflammatory reactions and inhibits clearance of beta-amyloid (which is toxic to neurons) in the hippocampus and frontal cortex (Heneka et al., 2010). Likewise, dopamine has an anti-

inflammatory function (Elgueta et al., 2017; Torres-Rosas et al., 2014; Yan et al., 2014). Increased inflammation has been associated not only with physical pathologies (e.g., infection, stroke) but also with cognitive decline and emotional disorder (e.g., depression; Kuo et al., 2005; McAfoose & Baune, 2009; Miller, Maletic, & Raison, 2009). Thus, individuals with a chronic tendency to experience curiosity and seek novel or unexpected events can benefit from the anti-neurodegenerative effects of norepinephrine and dopamine, possibly leading to better cognitive functioning, wellbeing and physical health.

4.2. Effects of curiosity on memory

The first type of cognitive processing related to curiosity is memory. The hippocampus receives projections of the dopaminergic (Lisman & Grace, 2005) and the noradrenergic systems (Figure 1; B. E. Jones & Moore, 1977). Thus, when individuals encounter something novel/unexpected and experience curiosity, dopamine and norepinephrine can facilitate learning by modulating the hippocampal activity (Oudeyer et al., 2016). Given that the hippocampus is susceptible to age-related declines (Allen, Bruss, Brown, & Damasio, 2005; Mitchell, Johnson, Raye, & D'Esposito, 2000; Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010; Walhovd et al., 2005), curiosity may help mitigate impairments to memory functioning due to age. In fact, processing of novel stimuli, relative to familiar stimuli, is associated with increased activity in the hippocampus and enhanced learning in both younger and older adults (Axmacher et al., 2010; Bunzeck, Doeller, Dolan, & Duzel, 2012; Bunzeck & Düzel, 2006; Bunzeck et al., 2007; Li, Cullen, Anwyl, & Rowan, 2003; for a review see Lisman & Grace, 2005). Younger and older adults also show greater learning when they are uncertain about

cue-outcome contingencies (Nassar et al., 2016; Nassar et al., 2012). Likewise, younger and older adults remember materials that they find curious better than more boring materials (Fastrich, Kerr, Castel, & Murayama, in press; McGillivray, Murayama, & Castel, 2015).

Studies discussed so far focused on memories for materials that evoked curiosity or uncertainty, but the mnemonic effects of curiosity also carry over to other irrelevant materials. In one study, participants explored a novel versus familiar situation in virtual reality followed by a word learning task; exposure to the novel situation facilitated participants' memory for the subsequent words, despite their being irrelevant to the situation itself (Schomaker, van Bronkhorst, & Meeter, 2014). In another study, trivia questions about which participants were highly curious led to better incidental memory for subsequent (irrelevant) images of faces than did less interesting trivia questions (Gruber, Gelman, & Ranganath, 2014). In animals, exposure to novel environments facilitates long-term potentiation (LTP), which are mediated by dopaminergic and noradrenergic systems (Li et al., 2003; Li et al., 2013). Exposure to novel environments also facilitates the transition from early LTP to late LTP, which is mediated by noradrenergic (Straube, Korz, Balschun, & Frey, 2003) and dopaminergic activities (Moncada & Viola, 2007). Thus, curiosity not only helps individuals remember things they feel curious about but also allow them to remember other temporally proximal information.

In addition to these effects of momentary feelings of curiosity, individuals with a greater tendency to experience curiosity benefit from the protective effects of norepinephrine and dopamine more often throughout their lives (Heneka et al., 2010),

leading to preserved structural organization in the hippocampus and thereby aiding memory functioning. In fact, a longitudinal study in rodents suggests that greater exploratory behaviors in novel situations during youth predict better memory performance in old age (Dellu et al., 1994). Likewise, in rodents, exposure to novel environments leads to better spatial memory performance (Yang & Tang, 2011) and a larger volume in the hippocampus (Scholz, Allemang-Grand, Dazai, & Lerch, 2015). In humans, individual differences in experience seeking—which is related to trait curiosity—correlate with individual differences in hippocampal volume (Martin et al., 2007). Curiosity is thus posited to have lifelong benefits for memory by affecting hippocampal performance and structure.

4.3. Effects of curiosity on general cognitive performance

The effects of curiosity on cognition are not limited to memory. Both the dopaminergic and noradrenergic systems project to the PFC (Figure 1) and affect its function, such as top-down regulation, working memory and goal-directed behavior (Arnsten, 2011; Arnsten, Wang, & Paspalas, 2015; Cools, Sheridan, Jacobs, & D'Esposito, 2007; Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999). Therefore, when individuals encounter something novel or uncertain, a momentary feeling of curiosity may help their PFC functioning, which typically declines with age (Allen et al., 2005; Nyberg et al., 2010; Raz et al., 2010). In line with this idea, working memory performance is better for novel stimuli than familiar stimuli (Mayer, Kim, & Park, 2011). Presentation of novel stimuli also facilitates processing of other stimuli that are presented either at the same time or shortly after the novel stimuli (Hoffing & Seitz, 2015; Wetzel, Widmann, & Schroger, 2012). Such effects are associated with changes

in pupil dilation (Hoffing & Seitz, 2015), suggesting that the noradrenergic system may play roles in the novelty-induced facilitation effects in the PFC functioning (for a review see Schomaker & Meeter, 2015).

In addition to these documented phasic effects of novelty, studies on individual differences also suggest a link between curiosity and general cognitive functioning. For example, both the noradrenergic (Clewett et al., 2016; Robertson, 2013; Wilson et al., 2013) and dopaminergic systems (MacDonald, Karlsson, Rieckmann, Nyberg, & Bäckman, 2012; Nagel et al., 2008; Papenberg, Lindenberger, & Bäckman, 2015) have been associated with cognitive preservation in older adults. In addition, previous research reveals that preference for novel stimuli is associated with better cognitive function in older adults (Daffner et al., 2007; Daffner et al., 2006a, 2006b; Pontifex, Hillman, & Polich, 2009) and even a reduced risk of Alzheimer's disease (Daffner, Scinto, Weintraub, Guinessey, & Mesulam, 1992; Fritsch, Smyth, Debanne, Petot, & Friedland, 2005). In one study, older adults were shown a sequence of stimuli: a standard (a triangle; 70% of frequency), a target (an inverted triangle; 15% of frequency), and novel stimuli randomly drawn from a set of unusual line drawings (15% of frequency; Daffner et al., 2006b). Participants were told to view each picture for however long they wanted and to control the viewing duration by a button press. Across older adults, longer viewing durations of novel stimuli was correlated with better performance on neuropsychological tests, especially those involving attention/executive functions (Daffner et al., 2006b). In the same study, cognitive performance in older adults was associated with P3 ERP amplitudes to novel stimuli, considered a non-invasive measure of LC activity (Murphy et al., 2011; Nieuwenhuis et al., 2005; Pineda,

Foote, & Neville, 1989; Pineda & Westerfield, 1993). Thus, results from this study suggest that higher curiosity levels in old age reflect the preserved noradrenergic system as well as preserved cognitive functioning in older adults.

While these studies do not tell us whether the preserved curiosity or the preserved noradrenergic and dopaminergic system lead to cognitive preservation or the other way around, there is increasing evidence from longitudinal research that curiosity is not only correlated to but also *predicts* better cognitive functioning. Longitudinal research on openness to experience indicates that individuals with relatively higher openness to experience tend to seek more educational and stimulating opportunities throughout their lives and ultimately exhibit smaller age-related cognitive decline (Chapman et al., 2012; Hogan, Staff, Bunting, Deary, & Whalley, 2012; Sutin et al., 2011; Williams, Suchy, & Kraybill, 2013; Ziegler et al., 2015) (but see Sharp, Reynolds, Pedersen, & Gatz, 2010). Additionally, a recent study of recently retired individuals showed that cognitive performance was predicted by a need for cognition—a tendency to seek and enjoy intellectual activities (Baer et al., 2013). As one's need for cognition is correlated to curiosity (Olson, Camp, & Fuller, 1984), these results again support the notion that curiosity is protective against age-related cognitive decline. Furthermore, in patients with Mild Cognitive Impairment (MCI), those who experienced apathy were more likely to develop dementia than other MCI patients later (Lanctôt et al., 2017; Robert et al., 2008; Starkstein, Jorge, Mizrahi, & Robinson, 2006).

4.4. Effects of curiosity on mental and physical health

Brain regions critical for curiosity are important not only for cognitive processing but also for wellbeing. In fact, dopaminergic signals in the striatum are associated with

various positive affective states (for a review see Burgdorf & Panksepp, 2006). Given that subjective feelings of curiosity are accompanied by striatum activity (Gruber et al., 2014), it is not surprising that individuals feel positive affective states towards novel or uncertain stimuli (Berlyne, 1970).

In addition to these short-term effects, previous research suggests that the noradrenergic and dopaminergic mechanisms implicated in curiosity have a long-term effect on mental health and wellbeing. For example, recent research shows that LC neuronal loss leads to depression-like behaviors in rodents (Szot et al., 2016). Depression is also associated with smaller P3 ERPs to novel stimuli (Bruder et al., 2009), which, as stated above, has been associated with noradrenergic mechanisms. In fact, depression often co-occurs with apathy (Levy et al., 1998; Marin, Firinciogullari, & Biedrzycki, 1993) and apathy is often a precursor of depression, such that severe apathy is predictive of subsequent depression (Pedersen, Alves, Aarsland, & Larsen, 2009; Starkstein et al., 2006). Thus, it appears that levels of curiosity predict not only cognitive performance but also depression.

Past research reports positive correlations between trait curiosity and wellbeing (Park, Peterson, & Seligman, 2004; Vittersø & Søholt, 2011). Openness to experience also positively predicts life satisfaction (Vittersø, 2003) and is associated with greater resilience (Caska & Renshaw, 2013; Williams, Rau, Cribbet, & Gunn, 2009). A diary study on college students further showed that greater curiosity on one day predicted greater life satisfaction on the following day (Kashdan & Steger, 2007). Animal research also supports the role of curiosity in wellbeing; low novelty-seeking rats exposed to chronic stress for four weeks, for instance, tended to develop anhedonia (i.e., lack of

reward and pleasure in positive stimuli) more quickly than did high novelty-seeking rats (Stedenfeld et al., 2011). Rats with high novelty-seeking tendencies were also more resilient to maternal separation stress during early life (Clinton, Watson, & Akil, 2014).

Although the exact mechanisms underlying the effects of curiosity on mental health are unknown, one possibility is that high curiosity leads to greater tendencies to employ flexible and adaptive responses to age-related challenges (Swan & Carmelli, 1996). Indeed, higher levels of openness to experience have been associated with a greater tendency to gather information about health (Sörensen, Duberstein, Chapman, Lyness, & Pinquart, 2008), and with enhanced creativity (Feist, 1998). In another study, children's curiosity level was predictive of their tendency to come up with flexible solutions to problems (Greenberger, O'Connor, & Sorensen, 1971). In addition, high curiosity was predictive of improved efficiency in stopping negative thoughts over time in veterans with suicidal ideation (Denneson, Smolenski, Bush, & Dobscha, 2017), suggesting that curiosity might help individuals to develop coping skills flexibly.

If curiosity encourages more flexible problem solving, the effects of curiosity should not be limited to mental health and should be observed in other domains. In fact, the effects of curiosity have also been observed in physical function and health (Consedine & Moskowitz, 2007; Peterson, Park, & Seligman, 2006). One striking finding in relation to this issue is that higher curiosity predicts a better 5-year survival rate in older adults even after controlling for a number of other risk factors, such as age, education level, and smoking behaviors (Swan & Carmelli, 1996). Curiosity also appears to be predictive of physical functioning. For example, apathy (an *absence* of curiosity) is predictive of daily disabilities such as difficulty in walking,

dressing/undressing, and taking a bath or shower (Clarke, Ko, Lyketsos, Rebok, & Eaton, 2010). Higher curiosity was also shown to protect against hypertension and diabetes (Richman et al., 2005). Openness to experience is also predictive of preserved walking abilities (Tolea et al., 2012) and better physical functioning in older adults (Chapman, Duberstein, & Lyness, 2007; Duberstein et al., 2003), as well as reduced mortality rates (Ferguson & Bibby, 2012; Jonassaint et al., 2007; Turiano, Avron Spiro, & Mroczek, 2012).

These results are consistent with the proposed notion that curiosity encourages flexible problem solving and may help people effectively cope with physical and mental problems. Another possible explanation for curiosity's influence on physical health is that the effects of curiosity on mental health mediate the relationship between curiosity and physical health. As described earlier, curiosity appears to reduce negative emotion, enhance positive emotion, and help maintain wellbeing. Critically, negative emotional states are known to be detrimental to physical health (DeSteno, Gross, & Kubzansky, 2013). For example, higher levels of anxiety and distress predict risk of coronary heart disease approximately 10 years later (Kubzansky, Cole, Kawachi, Vokonas, & Sparrow, 2006), and individuals with symptoms of posttraumatic stress disorder (PTSD) were more likely to develop coronary heart disease during a 14-year follow-up period than those without PTSD symptoms (Kubzansky, Koenen, Jones, & Eaton, 2009). Stress-induced activation of the hypothalamus-pituitary-adrenal (HPA) axis also leads to proinflammatory activity, thereby negatively affecting physical health (Eisenberger & Cole, 2012). In contrast to these negative effects, dopamine (which is released when curiosity is evoked) can attenuate excessive HPA axis activation (Sullivan & Dufresne,

2006). Thus, through downregulation of negative emotion and stress, curiosity might help to prevent detrimental effects of negative emotion and stress on physical health.

4.5. Positive-feedback loop based on curiosity

In summary, curiosity has diverse positive effects in the course of aging. Momentary feelings of curiosity have positive effects on memory, general cognitive functioning, and wellbeing via engagement of the noradrenergic and dopaminergic systems (Figure 2). In addition, one's chronic tendency to experience curiosity has a life-long impact on memory, general cognitive functioning, wellbeing, and physical health both by changing behaviors and altering the brain function or structure (Figure 3).

We believe this adaptive functioning of curiosity during aging is further supported by a positive feedback loop between curiosity and dopamine/norepinephrine that strengthens the effects of curiosity over time (Figure 4). As reviewed in Section 2, the dopaminergic system and noradrenergic system are critical to support one's curiosity. When one feels curious about uncertain stimuli or an individual has a tendency to experience curiosity and explore novel environments, this will increase his/her exposure to novel or uncertain stimuli—which typically results in increased release of dopamine and norepinephrine in the brain. These neuromodulators in turn have the anti-inflammatory and the anti-neurodegenerative effects, helping individuals to maintain their ability to experience curiosity and boost their cognition, wellbeing, and physical health (Figures 2-3), which may further support their exploratory behaviors. This positive feedback loop should play a critical role in sustaining the anti-neurodegenerative mechanisms in the brain and achieving successful and adaptive aging.

5. Future questions

In the current paper, we treated curiosity as if it is a unitary concept. However, this concept is more nuanced and multifaceted (Kashdan & Silvia, 2009). For future research, it would be fruitful to take into account this multifaceted nature of curiosity when examining the role of curiosity in aging. For example, we have argued that aging leads to a decline in curiosity. However, this does not mean that aging leads to decline in all *domains* of curiosity. Studies often distinguish curiosity for different types of objects or domains (Kidd & Hayden, 2015; Litman & Spielberger, 2003)—knowledge (epistemic curiosity), perception (perceptual curiosity), and social issues (interpersonal/social curiosity). In a study by Robinson et al. (2017), whereas the researchers found decline in epistemic and interpersonal curiosity, they did not observe significant effects of age in perceptual curiosity (i.e., individuals' tendency to seek new visual, auditory or tactile experiences; Collins et al., 2004). Thus, there might be some unique characteristics about perceptual curiosity that can result in different age effects. In fact, neuroimaging studies suggest that while feelings of epistemic curiosity are rather rewarding and pleasant (Gruber et al., 2014; Kang et al., 2009), feelings of perceptual curiosity are unpleasant due to lack of something wanted (Jepma et al., 2012). In addition, high curiosity is often accompanied with greater activity of the PFC (Gruber et al., 2014; Kang et al., 2009) but the PFC might be required less for perceptual curiosity than for epistemic curiosity which requires integration of information and existing knowledge. Future research should examine the effects of age on curiosity while considering these different types of curiosity.

Relatedly, the current paper incorporated a range of constructs related to curiosity such as novelty seeking, sensation seeking, apathy and openness to

experiences. But there is another related but different concept: interest (Grossnickle, 2016; Renninger & Hidi, 2016). Although researchers have not yet reached consensus on the distinction between curiosity and interest (Grossnickle, 2016), one major view is that, while curiosity represents a motivation or desire to seek and learn new information by exploring novel and uncertain environments, interest (especially what is often called "individual interest", Hidi & Renninger, 2006) is an enduring affective and psychological state that engages ones to learn information that is linked to the *existing knowledge* and *values of that individual* (Hidi & Renninger, 2006; Izard, 2009). Thus, interest and curiosity certainly overlap, but interest is characterized more by the knowledge and values individual possesses (rather than mere uncertainty reduction or novelty seeking), and is considered to develop over time as the knowledge and values accumulate. Given that people typically acquire more knowledge and elaborated personal values as they age (Salthouse, 2010), interest might not show age-related declines or could even show age-related increase. In fact, previous studies on vocational interests reveal stability of vocational interests across the adult lifespan (Costa, McCrae, & Holland, 1984; Low, Yoon, Roberts, & Rounds, 2005). Furthermore, in one study, researchers measured both participants' curiosity (a desire to know the answer to trivia questions) and interest (positive feelings associated with knowledge of the answer) as well as their memory (McGillivray et al., 2015). In this study, while curiosity and interest were positively correlated, their memory performance was more strongly determined by interest than curiosity. Although this study focused on a transient aspect of interest, this result suggests the potential differential role of curiosity and interest in predicting memory performance. Future research should clearly operationalize these different but related

concepts and address whether they have the same or different mechanisms in affecting our mental processing.

6. Conclusion

What helps you to stay healthy and happy as you age? For the past decades, this question has spurred a large number of empirical studies in the literature of aging, but these studies have mainly focused on cognitive, social, or physical factors, such as executive functioning (e.g., Grigsby, Kaye, Baxter, Shetterly, & Hamman, 1998), social relationships (e.g., Cacioppo, Hawkley, & Thisted, 2010), and physical exercise (e.g., Colcombe et al., 2004). The current review points to the importance of also considering motivational factors, especially curiosity. While curiosity seems to decline with advancing age, it can also be a proxy for maintaining cognitive functioning, mental health, and physical health in older adults, thus serving as a conduit for “successful aging.” Despite the growing interest in curiosity in recent neuroscientific research, empirical research on curiosity and aging remains limited and there are still many unanswered questions concerning the neural mechanisms underlying curiosity and its functional consequences. Continued research addressing these questions about curiosity and aging should improve our understanding of how we can support older adults to age healthily, happily and optimally.

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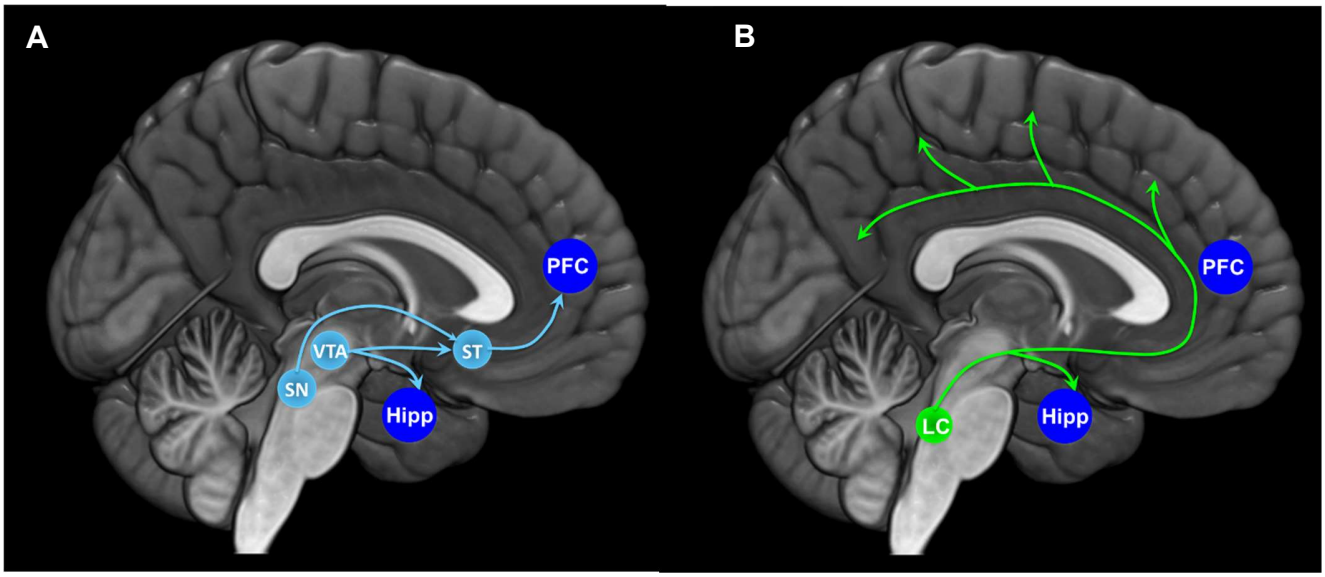

Figure 1. Brain regions important for curiosity. (A) The dopaminergic and (B) the noradrenergic systems play critical roles in curiosity. (SN: Substantia Nigra, VTA: Ventral Tegmental Area, ST: Striatum, Hipp: Hippocampus, LC: Locus Coeruleus, PFC: Prefrontal Cortex.)

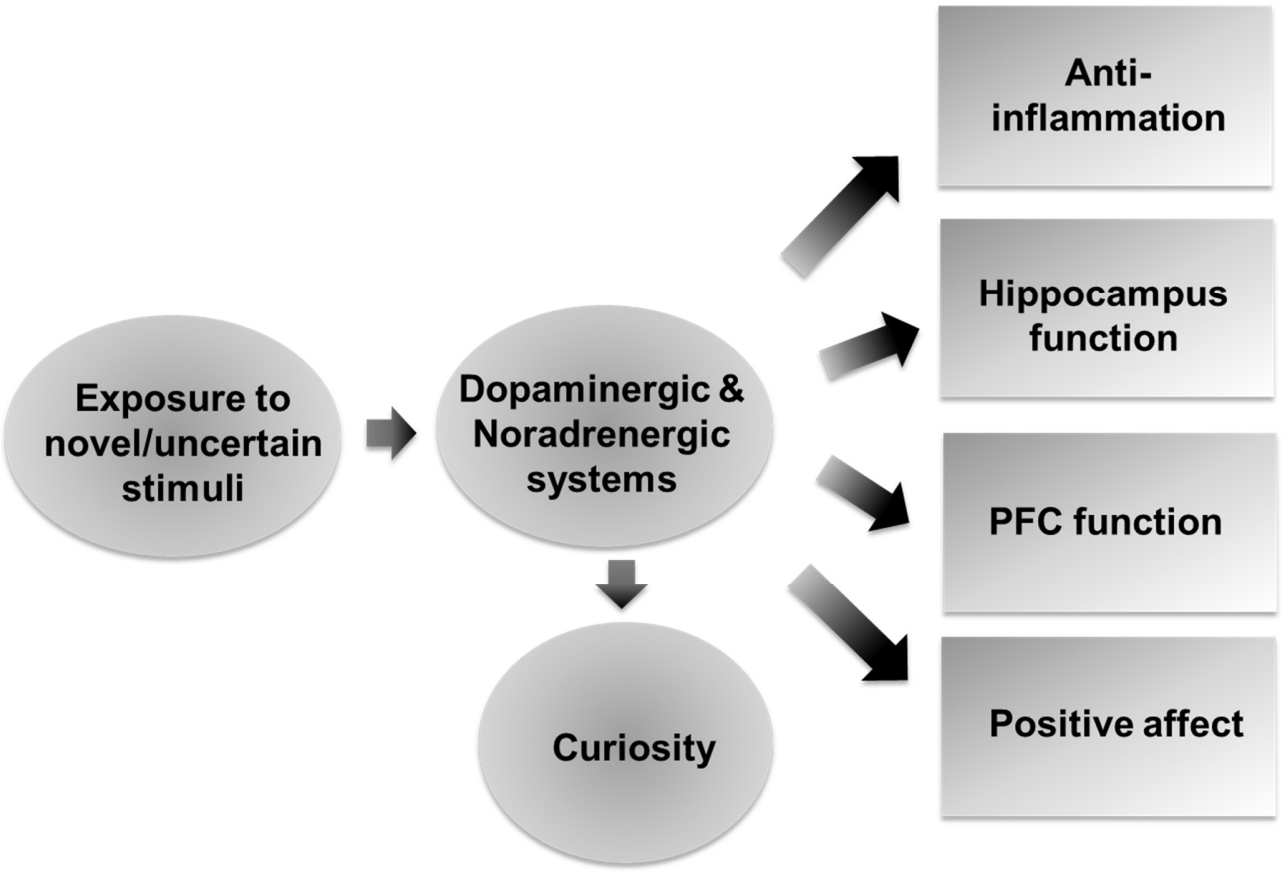

Figure 2. Effects of momentary feelings of curiosity when exposed to something novel and/or uncertain.

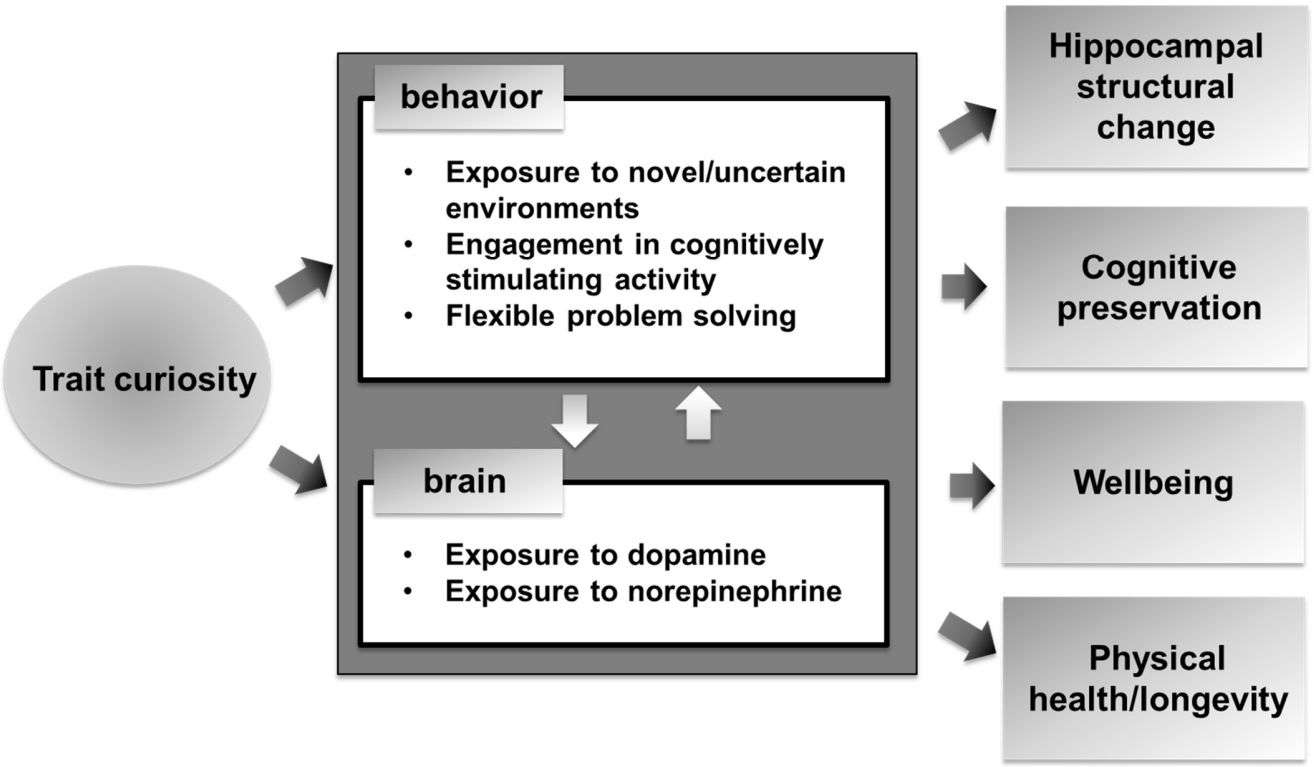

Figure 3. Effects of chronic tendency to experience curiosity on cognition, wellbeing, and physical functioning.

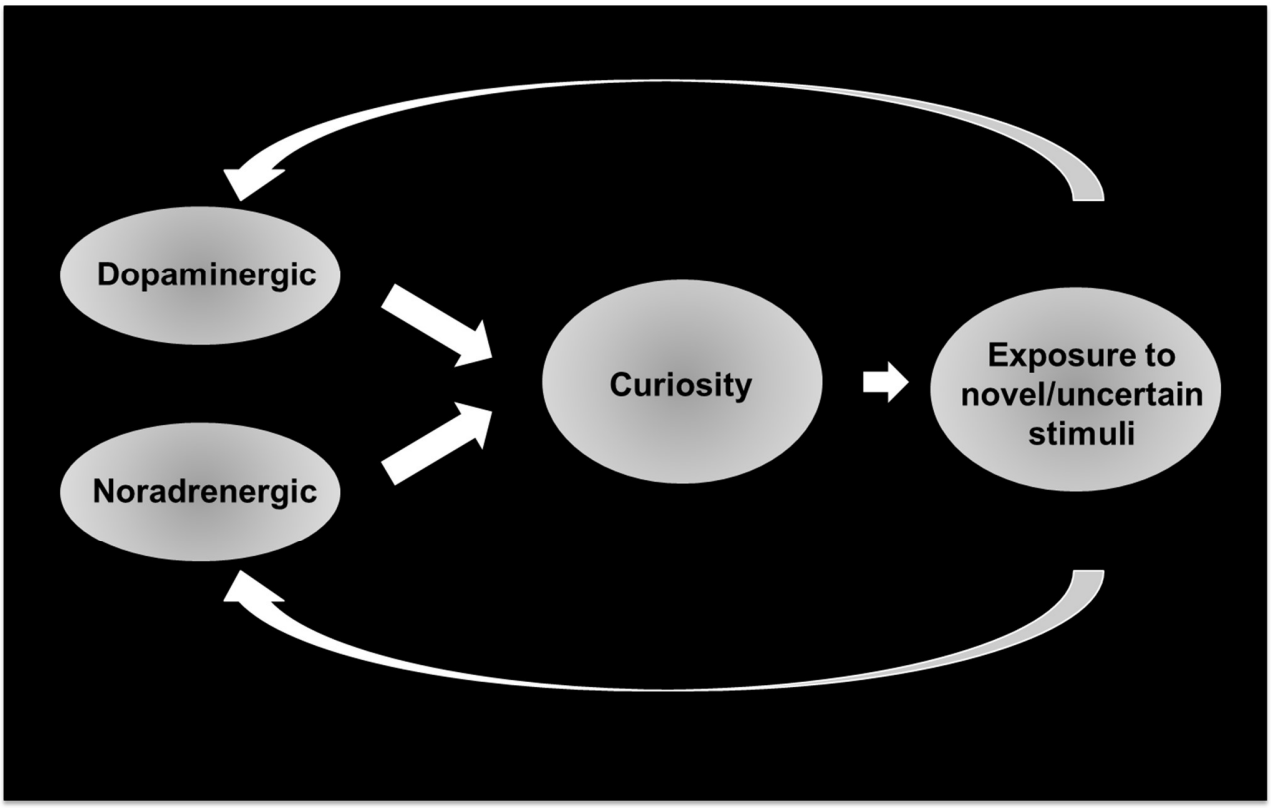

Figure 4. Positive feedback loop based on curiosity in aging.