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Age differences in gain- and loss-motivated attention

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ABSTRACT

Adaptive gain theory (Aston-Jones & Cohen, 2005) suggests that the phasic release of norepinephrine (NE) to cortical areas reflects changes in the utility of ongoing tasks. In the context of aging, this theory raises interesting questions, given that the motivations of older adults differ from those of younger adults. According to socioemotional selectivity theory (Carstensen, Isaacowitz, & Charles, 1999), aging is associated with greater emphasis on emotion-regulation goals, leading older adults to prioritize positive over negative information. This suggests that the phasic release of NE in response to threatening stimuli may be diminished in older adults. In the present study, younger adults (aged 18–34 years) and older adults (60–82 years) completed the Attention Network Test (ANT), modified to include an incentive manipulation. A behavioral index of attentional alerting served as a marker of phasic arousal. For younger adults, this marker correlated with the effect of both gain and loss incentives on performance. For older adults, in contrast, the correlation between phasic arousal and incentive sensitivity held for gain incentives only. These findings suggest that the enlistment of phasic NE activity may be specific to approach-oriented motivation in older adults.

1. Introduction

In our day-to-day lives, we are constantly bombarded with sensory information that competes for our limited attentional capacities. Despite this sensory overload, we tend to navigate our environments successfully. The ability to identify meaningful cues in the environment to guide selective attention towards high-priority information is critical in this regard. This capacity emerges early in human development, as even infants show an attentional bias for objects cued as threatening by fearful adult gazes (Hoehl, Palumbo, Heinisch, & Striano, 2008; Hoehl, Wiese, & Striano, 2008; LoBue & DeLoache, 2010). In the current study, the objective was to examine motivational effects on attention in healthy younger and older adults.

1.1. Motivated attention and aging

In recent years, the goal-directed nature of attention has received considerable investigation within the domain of aging. Notably, numerous studies have reported an age-related positivity effect, with healthy older adults showing preference for positive over negative or neutral stimuli (for a recent meta-analysis, see Reed, Chan, & Mikels, 2014). In fact, older adults may actively avoid the processing of negative or aversive information, suppressing amygdala activity in the presence of such stimuli (Mather & Carstensen, 2005; Ochsner et al., 2004; Sakaki, Nga, & Mather, 2013; St. Jacques, Dolcos, & Cabeza, 2010). Such observations are in line with socioemotional selectivity theory, which holds that in later adulthood individuals prioritize emotion regulation goals aimed towards the attainment of meaningful, positive experiences and improved well-being (Carstensen, 1992, 2006; Carstensen, Isaacowitz, & Charles, 1999).

When examining the influence of motivation on attention in the laboratory, it is common to offer opportunities to gain, or in some cases lose, monetary incentives within cognitive tasks (e.g., Ashare, Hawk, & Mazzullo, 2007; Della Libera & Chelazzi, 2006; Engelmann & Pessoa, 2007). Such designs are valuable as they allow for comparisons of behavioral performance when such incentives are present versus when they are absent, with differences presumably attributable to goal-based modulations of attention. When applied to older adults, there have been findings of an age-related reduction in loss sensitivity, but preserved sensitivity to gains, consistent with a "positivity effect" (e.g. Bagurdes, Mesulam, Gitelman, Weintraub, & Small, 2008; Mikels & Reed, 2009; Samanez-Larkin

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et al., 2007). However this decreased responsiveness to losses is not always exhibited by this population (e.g., Ebner, Freund, & Baltes, 2006; Eppinger, Schuck, Nystrom, & Cohen, 2013; Spaniol, Bowen, Wegier, & Grady, 2015; Spaniol, Voss, Bowen, & Grady, 2011). Generally, differences involving responsiveness to monetary incentives are attributed to an age-related reduction of dopamine (DA) transmission in the brain's reward circuit (e.g., Chowdhury et al., 2013; Eppinger, Nystrom, & Cohen, 2012; Mell et al., 2009). However, it may also be useful to consider contributions from other neural sources.

1.2. Adaptive gain theory

One promising candidate that may help clarify age-related differences in attentional sensitivity to gains and losses is the neurotransmitter norepinephrine (NE), which has long been hypothesized to influence attention through its association with wakefulness and arousal (e.g., Aston-Jones & Bloom, 1981; Foote, Berridge, Adams, & Pineda, 1991; Squire, Bunsey, & Strupp, 1995). The principal source of this neurotransmitter in the brain is the locus coeruleus (LC), a small nucleus located in the brainstem, which projects to a number of cortical and subcortical regions, collectively referred to as the LC-NE system (Schwarz & Luo, 2015). Current understanding of this network distinguishes two primary modes of activation, which differentially affect attentional processes: (a) a phasic firing mode, and (b) a tonic firing mode (Aston-Jones, Rajkowski, & Cohen, 1999; Aston-Jones, Rajkowski, Kubiak, & Alexinsky, 1994; Rajkowski, Kubiak, & Aston-Jones, 1994; Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999). The phasic firing mode is associated with moderate levels of global NE, in combination with bursts of activity occurring shortly after the presentation of task-relevant stimuli, or just before a behavioral response is made. The tonic firing mode, on the other hand, maintains high levels of global NE, but shows a marked reduction, if not absence, in the bursts of activity observed in the phasic mode. Enhanced task performance is observed in the phasic mode, possibly due to an increased signal-to-noise ratio for high-priority stimuli (Mather, Clewett, Sakaki, & Harley, in press). In contrast, the tonic firing mode of the LC is associated with increased distractibility and task disengagement.

Research on the role of the LC-NE system in goal-directed attention in older adults is currently lacking. Yet, there is reason to expect age differences in LC-NE system modulation of the attentional system. According to adaptive gain theory (Aston-Jones & Cohen, 2005), the firing mode of the LC-NE system is directly influenced by motivational states. This theory draws on the exploration-exploitation tradeoff described by reinforcement learning models, in which organisms balance between persisting at a behavior with a known set of outcomes (exploitation), and seeking alternative behaviors that may produce greater value (exploration) as they attempt to maximize utility (See Cohen, McClure, & Yu, 2007, for review). The phasic mode of LC activation promotes exploitation by directing attentional resources towards a specific task, optimizing performance and task outcomes. In contrast, the task disengagement and distractibility that characterize the tonic firing mode of the LC is well suited for exploration behavior.

Aston-Jones and Cohen (2005) argue that utility-based shifts in LC-NE firing are mediated by prefrontal structures. Specifically, this role is attributed to the orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC), which have both consistently been shown to encode and represent value (for rewards and costs) during associative learning and economic decision-making (e.g. Bush et al., 2002; Gallagher, McMahan, & Schoenbaum, 1999; Kahnt, Heinzle, Park, & Haynes, 2010; Kennerley, Behrens, & Wallis, 2011; Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006; O'Doherty et al., 2001). When the utility of a task is perceived as high, these evaluation structures mobilize the phasic LC firing mode, optimizing task performance. However, when the perceived utility of a task is low or diminishes, they bias the LC-NE system to fire tonically, prompting the individual to disengage from the task and search for alternative sources of utility.

1.3. Phasic alerting as a marker of NE activity

Presently, direct observations of LC-NE activity in humans are difficult to obtain non-invasively. Support for adaptive gain theory thus mostly stems from studies involving non-human species. Anatomical rodent studies, for example, have shown that electrical and chemical stimulation of medial prefrontal regions produce an excitatory influence on LC neurons, with projections from this region innervating an area nearby the LC (Jodoj, Chiang, & Aston-Jones, 1998; Shipley, Fu, Ennis, Liu, & Aston-Jones, 1996). Similarly, the central nucleus of the amygdala has been shown to innervate and activate the LC (Bouret, Duvel, Onat, & Sara, 2003; Cedarbaum & Aghajanian, 1978; Wallace, Magnuson, & Gray, 1992). Along with its well-known role in processing emotional stimuli, the amygdala is also involved in encoding and representing value, and may thus play an analogous role to that of the OFC and ACC (Blair, Sotres-Bayon, Moita, & Ledoux, 2005; Gottfried, O'Doherty, & Dolan, 2003; Paton, Belova, Morrison, & Salzman, 2006; Schoenbaum, Chiba, & Gallagher, 1998). Lastly, rhesus monkeys exhibit phasic bursts of LC-NE activity, preceded by OFC activity, in response to reward-signaling cues, with this activity being greater for high-reward cues than low reward cues, but diminishing with increased satiation (Bouret & Richmond, 2010, 2015).

While direct measures of LC-NE activity are difficult to obtain in humans, non-invasive observations are possible through indirect physiological indices such as pupil dilation (Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Jepma & Nieuwenhuis, 2011; Joshi, Li, Kalwani, & Gold, 2016; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014; Phillips, Szabadi, & Bradshaw, 2000). Potential behavioral indices are also available. In their model of attention, Posner and Petersen (1990) describe three distinct attention networks: alerting, orienting, and executive control. Particularly noteworthy here is the alerting network, which the authors implicate in maintaining vigilance. The orienting and executive control networks, in contrast, are involved in directing attention to spatial locations and conflict monitoring processes, respectively. Preparatory cues signaling target onset activate a phasic alerting response which facilitates faster responding relative to when no cue is presented (Fernandez-Duque & Posner, 1997; Thiel, Zilles, & Fink, 2004). This phasic alerting response likely corresponds to phasic activation of the LC-NE system, as administration of clonidine, an α2-adrenoceptor agonist which works to inhibit the release of NE, selectively diminishes alerting, but not orienting effects (Coull, Nobre, & Frith, 2001; Witte & Marrocco, 1997). As such, a behavioral measure of phasic alerting may be indicative of the extent to which the phasic LC firing mode is engaged during a task.

The Attention Network Test (ANT; Fan, McCandliss, Sommer, Raz, & Posner, 2002) is ideal for obtaining a behavioral measure of phasic alerting, as it purports to capture network scores for the three attention networks outlined by Posner and Petersen (1990). It combines an attentional-cueing paradigm (Posner, 1980) with the Eriksen-flanker task (Eriksen & Eriksen, 1974). The network score for alerting is measured by comparing responses to targets cued by a non-spatial warning cue to responses to non-cued targets, consistent with the studies described above.