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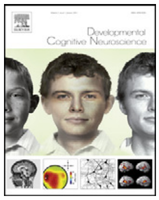

How the aging brain translates motivational incentive into action: The role of individual differences in striato-cortical white matter pathways

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ABSTRACT

The anticipation of reward enhances actions that lead to those rewards, but individuals differ in how effectively motivational incentives modulate their actions. Such individual differences are particularly prominent in aging. In order to account for such inter-individual variability among older adults, we approach the neurobiological mechanisms of motivated behavior from an individual differences perspective focusing on white matter pathways in the aging brain. Using analyses of probabilistic tractography seeded in the striatum, we report that the estimated strength of cortico-striatal and intra-striatal white matter pathways among older adults correlated with how effectively motivational incentives modulated their actions. Specifically, individual differences in the extent to which elderly participants utilized reward cues to prepare and perform more efficient antisaccades predicted structural connectivity of the striatum with cortical areas involved in reward anticipation and oculomotor control. These striatal connectivity profiles endow us with a network account for individual differences in motivated behavior among older adults. More generally, the data suggest that capturing individual differences may be crucial to better understand developmental trajectories in motivated behavior.

1. Introduction

Developmental models of motivated behavior can be constrained and better articulated with knowledge of structural and functional brain systems. However, interpreting brain–behavior correlations across age groups is difficult because of large inter-individual differences in performance (Crone and Ridderinkhof, 2011). This holds especially for the study of the elderly (Hedden and Gabrieli, 2004). Brain-imaging studies (Berkman et al., 1993; Cabeza et al., 2002; Rosen et al., 2002) have stimulated a growing interest in the neurobiological basis for individual differences among high-performing older adults. For example, "successful aging" refers to adaptive resources that sustain mental capacities in some older adults more than in others (Gallagher et al., 2006). A characterization of individual differences in adaptive behavior among older adults may allow a more sensitive approach to detect adaptive neuroanatomical circuitry that might be disguised by simply comparing old participants with young.

One area of research that might benefit from an individual-differences approach is motivation, or the incentives that energize goal-directed behavior. Humans adapt the degree of effort they expend according to the magnitude of reward they anticipate (Pessiglione et al., 2007). Such a process has been proposed as an operant concept of motivation (Robbins and Everitt, 1996;

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Schultz, 2006; Berridge, 2004) and seems to remain intact in old age (Harsay et al., 2010). Here we investigated the white matter circuitry in older adults that allows motivational incentives to facilitate goal-directed behavior. Specifically, we tested whether individual differences in the white matter pathways of the striatum (measured through diffusion-weighted MRI) predicted individual differences in reward-guided action. We focused on action control within the oculomotor system, using an antisaccade task in which participants inhibited an eye movement toward a peripheral stimulus and instead generated an eye movement in the opposite direction. This requires the appropriate selection of a volitional command over the predominantly automatic command (Hallett, 1978; Munoz and Everling, 2004). Even successful aging entails impairments in planning and initiating many day-to-day activities (Hedden and Gabrieli, 2005). Experimentally, these impairments can be captured using the antisaccade task. We previously showed that although antisaccade performance declines with age, antisaccade action modulation by reward seems to be spared (Harsay et al., 2010). This provides a useful context for examining the neuroanatomical basis for linking motivation-based action preparation with neuroanatomical circuits underlying reward and oculomotor functioning, and individual differences therein.

The anatomically well-characterized oculomotor network controls the volitional movement of the eyes, and includes subcortical (caudate, substantia nigra pars reticulata, pulvinar nucleus of the thalamus, superior colliculus) and cortical (frontal-, supplementary- and parietal eye fields, and parts of the lateral prefrontal cortex) regions (Law et al., 1997; Lynch and Tian, 2006; Petit et al., 1996; Pierrot-Deseilligny et al., 2003). For simplicity, we use the term “oculomotor control structures,” although in addition to their shared eye-movement control functions, the described regions contribute to other functions such as attention, decision-making, memory, and planning of motor movements (Lynch and Tian, 2006). Cortical oculomotor control structures can modulate saccade behavior by targeting saccade generators in the superior colliculus directly, as well as indirectly through the caudate. Anatomically, the caudate is connected with several cortical eye fields in the frontal and parietal cortices, in part via the thalamus, and with the superior colliculi via the substantia nigra pars reticulata (Alexander and Crutcher, 1990; Alexander et al., 1990; Grahn et al., 2008; Haber, 2003; Hikosaka et al., 2000, 2006).

Reward anticipation also recruits a widespread network including the striatum (nucleus accumbens, putamen and caudate). According to neuroimaging and fiber tracing, reward-related information may access the striatum either by a subcortical route via the amygdala and/or hippocampus or by a cortical route via the orbitofrontal and/or anterior cingulate (Friedman et al., 2002; Lehericy et al., 2004; Pessiglione et al., 2007). The caudate is directly connected to cortical oculomotor-control structures, and therefore is a likely candidate for modulating saccades according to motivation/reward anticipation.

The nucleus accumbens, although a key component in reward-processing networks, is not considered part of the oculomotor network and has no connections in a strong position to directly initiate or control eye movements (Zahm, 2000). The putamen, similarly, has been found to encode reward value and directions for actions (Haruno and Kawato, 2006; Hori et al., 2009) but is also not considered as part of the oculomotor circuit, despite its direct connections to the frontal eyefields, which are less dense than the connections between caudate and frontal eyefields (Cui et al., 2003). In reward-guided oculomotor control, the putamen is hypothesized to guide actions toward their expected outcomes mainly by forwarding reward value and directions for actions via intra-striatal connections to the caudate that can directly mediate cortical oculomotor control.

Thus, interestingly, the striato-limbic reward network and the oculomotor network show strongest overlap in the caudate. Recent neuro-imaging findings in young adults show that functional connectivity of the caudate predicts individual differences in the extent to which motivational incentive modulates goal-directed oculomotor behavior (Harsay et al., in press). Based on observations that stable individual differences in behavioral characteristics such as personality traits and reward-based learning are related to striato-cortical white matter connectivity (Cohen et al., 2008, 2009), we hypothesized here that by combining structural white matter imaging of striato-cortical connectivity with individual differences in reward-modulated oculomotor performance, we can better understand the neural circuitry underlying the interface between motivation and action among older adults.

Specifically, if the striatum is the interface between the reward and the oculomotor system then the white matter pathways linking the striatum to both reward- and oculomotor structures might be stronger in individuals who are more effective in using reward anticipation to improve oculomotor performance. Specifically, we hypothesized that in such individuals the caudate shows stronger white matter pathways to cortical oculomotor structures, whereas the putamen and the nucleus accumbens show stronger intrastriatal white matter pathways and stronger pathways to limbic reward evaluation structures. We quantified the white matter pathways of the caudate, accumbens and putamen in older adults using probabilistic tractography based on diffusion tensor imaging (DTI), and we examined whether individual differences in the strength of the striatal white matter pathways predicts individual differences in the efficacy of motivational incentives on oculomotor responses in the antisaccade task.

2. Methods

2.1. Participants

16 Healthy right-handed volunteers (age 64–76, $M = 68 \pm 4$, 11 female), with normal or corrected-to-normal vision participated in the experiment. They were recruited from a database of healthy elderly participants (www.SeniorLab.nl) who had previously expressed their interest in participation in cognitive aging research. All participants were screened with a standard vision test for normal or corrected-to-normal vision for short and for