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Functional modular architecture underlying attentional control in aging

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ABSTRACT

Previous research suggests that age-related differences in attention reflect the interaction of top-down and bottom-up processes, but the cognitive and neural mechanisms underlying this interaction remain an active area of research. Here, within a sample of community-dwelling adults 19–78 years of age, we used diffusion reaction time (RT) modeling and multivariate functional connectivity to investigate the behavioral components and whole-brain functional networks, respectively, underlying bottom-up and top-down attentional processes during conjunction visual search. During functional MRI scanning, participants completed a conjunction visual search task in which each display contained one item that was larger than the other items (i.e., a size singleton) but was not informative regarding target identity. This design allowed us to examine in the RT components and functional network measures the influence of (a) additional bottom-up guidance when the target served as the size singleton, relative to when the distractor served as the size singleton (i.e., *size singleton effect*) and (b) top-down processes during target detection (i.e., *target detection effect*; target present vs. absent trials). We found that the size singleton effect (i.e., increased bottom-up guidance) was associated with RT components related to decision and nondecision processes, but these effects did not vary with age. Also, a modularity analysis revealed that frontoparietal module connectivity was important for both the size singleton and target detection effects, but this module became central to the networks through different mechanisms for each effect. Lastly, participants 42 years of age and older, in service of the target detection effect, relied more on between-frontoparietal module connections. Our results further elucidate mechanisms through which frontoparietal regions support attentional control and how these mechanisms vary in relation to adult age.

Introduction

Visual attention is hypothesized to be controlled by two processes – top-down and bottom-up (Connor et al., 2004; Yantis, 1998; 2005; however, for an opposing view, see Awh et al., 2012). Top-down attention refers to the *goal-oriented,* voluntary allocation of attention to an object or spatial location, whereas bottom-up attention refers to a less voluntary, *stimulus-driven* capture of attention (Theeuwes, 2010; Yantis, 1998). Although the relative contributions of top-down and bottom-up attention have been under investigation for several decades, exactly how these two processes interact is a topic of active investigation. This issue is especially relevant for conjunction visual search, which requires observers to detect a target that is a conjunction of nontarget (distractor) features (e.g., a right-tilted blue bar target among left-tilted blue bars and right-tilted green bars). Historically, conjunction search has been viewed as relying predominantly on top-down attention, because when salience is relatively constant across displays, a correct response relies on the observer's knowledge of the particular combination of features that define a target (Bacon and Egeth, 1997; Eckstein, 2011; Kristjansson and Campana, 2010; Kristjansson et al., 2002; Treisman, 1988; Wolfe, 1998). Some evidence, however, indicates that bottom-up processes may also influence conjunction search (Kaptein et al., 1995; Proulx, 2007).

This issue is further complicated in aging, where, in general, increased age is associated with a decline in visual search performance, especially when the task relies on visual sensory functioning (Hommel et al., 2004; Madden and Whiting, 2004). The specific processes underlying age-related decline in visual search performance, however, are still poorly understood. Several studies have demonstrated that top-down attentional processes are relatively preserved with age (Madden et al., 2004, 2005b; McAvinue et al., 2012; Whiting et al., 2005), but bottom-up attentional processes in aging remain understudied and

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may be a source of age-related decline in cognitive performance (Baltes and Lindenberger, 1997; Monge and Madden, 2016; Schneider and Pichora-Fuller, 2000).

Bottom-up guidance during conjunction search

The overall goal of the current study was to investigate age-related differences in the interaction of top-down and bottom-up attentional processes during conjunction search, using both behavioral and event-related functional MRI (fMRI) measures. We used a conjunction search task (Fig. 1), adapted from Proulx (2007), in which participants searched for a Color x Orientation conjunction target among distractors (e.g., a right-tilted blue bar among left-tilted blue bars and right-tilted green bars). Each display also included a salient feature (a size singleton) that was not part of the target definition and was not informative regarding target presence. Thus, size was a potential source of bottom-up guidance, but the size singleton was no more likely to be the target than nonsingleton display items. This *size singleton effect* is expressed as a decrease in reaction time (RT) for singleton target trials, relative to nonsingleton target trials, demonstrating that participants appeared to use salience (i.e., bottom-up processing) as the basis for their search strategy. In contrast, the *target detection effect,* defined as the increase in RT for nonsingleton target (i.e., target present) trials, relative to target-absent trials, primarily represents top-down processes of target identification and response selection, as salience does not provide any guidance or support on these trials.

Neural mechanisms underlying visual attention in aging

Researchers have attempted to further elucidate the role of top-down and bottom-up processes in visual search by examining the neural mechanisms underlying these processes. A large neuroimaging literature has demonstrated that top-down attentional processes rely more on a dorsal frontoparietal network, whereas bottom-up attentional processes rely more on a ventral frontoparietal network (Corbetta and Shulman, 2002; Miller and Buschman, 2013; Noudoost et al., 2010; Riddoch et al., 2010; Shipp, 2004; Shulman et al., 2004), but these network components are highly interconnected (Egner et al., 2008; Monge et al., 2016; Treue, 2003; Vossel et al., 2014). However, with regard to conjunction visual search, this interaction remains poorly understood, in terms of both (a) the extent of this interaction and (b) the neural mechanisms underlying this interaction.

Regarding aging, it appears that the previously described preservation of top-down attentional processes in older adults is often associated with increased activation in dorsal frontoparietal regions (Allen and Payne, 2012; Eyler et al., 2011; Madden et al., 2005a; Spreng et al., 2010), but how bottom-up attentional processes may influence dorsal frontoparietal functional properties in aging is largely unknown. Madden et al. (2017) recently explored this issue using the conjunction visual search task adapted from Proulx (2007), and found, in the examination of brain-behavior relations, that individuals 35 years of age and older (vs. relatively younger adults) exhibited greater engagement of the left frontal eye field (FEF) in service of the size singleton effect (i.e., increased bottom-up guidance). Thus, preliminary evidence indicates that age does have an effect on the neural mechanisms supporting bottom-up attentional guidance.

Graph theory: modularity and centrality

The Madden et al. (2017) study, as the majority of neuroimaging studies of attention, used univariate, event-related fMRI activation analyses. These univariate analyses, however, are limited in that they do not indicate how brain regions *interact* with each other in the context of whole-brain networks. A useful approach in this regard is *multivariate functional connectivity* (Bullmore and Sporns, 2009; van den Heuvel and Sporns, 2013). In the current study, we used multivariate functional connectivity to investigate the whole-brain functional networks underlying top-down and bottom-up attentional control during conjunction search in aging. We specifically used a multivariate framework, graph theory, which views the brain as a network consisting of discrete nodes (brain regions) and the edges between nodes (functional connections between brain regions). The analysis of the edges between nodes allows for the characterization of the topological properties of a functional network; these unique properties cannot be revealed with more traditional analysis approaches such as univariate activation or bivariate functional connectivity. Within the current study, we focused on two types of graph metrics – modularity and centrality.

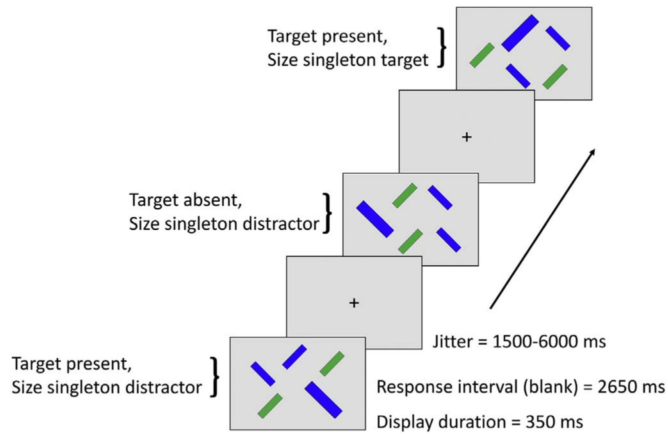

Fig. 1. Conjunction visual search task. Participants performed a conjunction visual search task in which the target shared one feature (either color or orientation) with each of the nontarget (distractor) items. The target could be either (a) a right tilted, blue bar among right-tilted green bars and left-titled blue bars (distractors); or (b) a left-titled green bar among left-tilted blue bars and right-titled green bars; in the scanner, display items were presented against a black background. The target was constant within participants and counterbalanced across participants. Display size was constant at five items. Participants made a yes/no response on each trial regarding the presence of the target. In each display, one of the distractors was 50% larger than the other items (i.e., a size singleton). On one-fifth of the target-present trials, the size singleton coincided with the target.

Functional and structural brain networks have been found to consist of distinct clusters of interconnected nodes (i.e., modules; for reviews, see Mišić and Sporns, 2016; Sporns and Betzel, 2016). *Modularity* describes the degree to which sets of nodes may be segregated into modules in a data-driven manner. It is hypothesized that modules allow the brain to efficiently adapt to cognitive demands of the environment (Crossley et al., 2013; Mišić and Sporns, 2016), making understanding the functional role of modules in service of cognition of great importance. The functional role of modules is especially important in the study of cognitive aging because of preliminary evidence, predominantly from resting-state functional connectivity analyses, indicating that with increased age, modules become less segregated and that this decreased segregation may have cognitive consequences (Betzel et al., 2014; Cao et al., 2014; Chan et al., 2014; Onoda and Yamaguchi, 2013; Song et al., 2014). However, since resting-state functional connectivity may not correspond to task-based connectivity (Campbell and Schacter, 2016; Cohen and D'Esposito, 2016; Davis et al., 2016), these studies do not inform how the modular topology of the brain adapts to cognitive demands of the environment. Task-based functional connectivity analyses, therefore, are necessary. Only two studies, to our knowledge, have examined modularity in aging using task-based functional connectivity, and found that (a) the modular topology of the brain adapts to executive function and cognitive control demands, and (b) older adults relied more on between-module connections in service of cognition (Gallen et al., 2016; Schlesinger et al., 2017)[1]. These studies, however, are