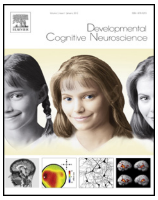
Developmental Cognitive Neuroscience 5 (2013) 40–50

Contents lists available at SciVerse ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: http://www.elsevier.com/locate/dcn



Dimensional Change Card Sort performance associated with age-related differences in functional connectivity of lateral prefrontal cortex

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ARTICLE INFO

Article history:
Received 5 April 2012
Received in revised form 7 December 2012
Accepted 18 December 2012

Keywords:
Development
Cognitive flexibility
fMRI
Brain networks
ICA

ABSTRACT

The Dimensional Change Card Sort (DCCS) is a standard procedure for assessing executive functioning early in development. In the task, participants switch from sorting cards one way (e.g., by color) to sorting them a different way (e.g., by shape). Traditional accounts associate age-related changes in DCCS performance with circumscribed changes in lateral prefrontal cortex (lPFC) functioning, but evidence of age-related differences in the modulation of lPFC activity by switching is mixed. The current study therefore tested for possible age-related differences in functional connectivity of lPFC with regions that comprise a larger cognitive control network. Functional magnetic resonance imaging (fMRI) data collected from children and adults performing the DCCS were analyzed by means of independent components analysis (ICA). The analysis revealed several important age-related differences in functional connectivity of lPFC. In particular, lPFC was more strongly connected with the anterior cingulate, inferior parietal cortex, and the ventral tegmental area in adults than in children. Theoretical implications are discussed.

The Dimensional Change Card Sort (DCCS; Zelazo, 2006) is a standard procedure for assessing executive functioning early in development. In the task, participants sort bivalent cards (e.g., red trucks) one way (e.g., by color) and then are instructed to switch and sort the same cards a new way (e.g., by shape). Exercising flexibility of this kind is particularly difficult for children. Three- and 4-year-olds typically perseverate by repeatedly sorting by old rules after being instructed to switch and sort by new rules, and err in this way despite apparent knowledge of the correct response (Zelazo, 2006). Later in development, most children correctly switch, but show larger switch-related behavioral costs relative to adolescents and adults (Cepeda et al., 2001; Crone et al., 2006; Davidson et al., 2006; Huizinga and van der Molen, 2011; Lehto et al., 2003; Waxer and Morton, 2011b; Weed et al., 2008).

Age-related changes in DCCS performance have traditionally been associated with the functional development of the lateral prefrontal cortex (Bunge and Zelazo, 2006; Dempster, 1992; Diamond, 2002; Kirkham et al., 2003; Morton and Munakata, 2002). First, like mental flexibility specifically and cognitive control generally, dorso- and ventrolateral prefrontal cortex follow a protracted developmental trajectory, showing continued change in synaptogenesis (Huttenlocher and Dabholkar, 1997), gray matter density (Sowell et al., 2001), cortical thickness (Shaw et al., 2008), and myelination (Nagy et al., 2004) into early adulthood. Second, lesions to lPFC lead to inflexibility reminiscent of that observed in young children. For example, lesions to lPFC, but not other cortical areas, lead to increased perseveration in the Wisconsin Card Sorting Task (Berg, 1948), an inferential rule use task similar in its demands to the DCCS. And third, switching tasks, including

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http://dx.doi.org/10.1016/j.dcn.2012.12.001

the DCCS (Moriguchi and Hiraki, 2009, 2011), are commonly associated with activity in lPFC (Barber and Carter, 2005; Cole and Schneider, 2007). Taken together then, there is support for the idea that the development of flexible rule use in the DCCS is associated with age-related changes in lPFC activity.

There is, however, also countervailing evidence that speaks against this basic association (Morton et al., 2009; Wendelken et al., 2012). In one study, children and adults were administered a modified version of the DCCS as changes in blood oxygenation were measured by means of fMRI (Morton et al., 2009). Although all participants showed greater activity in dorso- and ventrolateral PFC in conditions that required rule-switching as compared to conditions that did not require rule-switching, age-related differences in brain activity were confined to the dorsal premotor and superior parietal cortices, regions that fall well-outside lPFC proper. In a second fMRI study, children and adults switched between rules based on color and spatial orientation (Wendelken et al., 2012). Rule-switching was associated with greater activity in dlPFC as compared to rule repetition, but the effect of rule switching on dlPFC activity was equivalent for both groups, as reflected in a statistically non-significant interaction of Switching and Age in dlPFC activity. One possibility, suggested by Wendelken et al. (2012), is that there are age-related changes in the temporal dynamics of activation in dlPFC such that rule updating in dlPFC occurs more slowly in children than in adults.

A related possibility that we investigated in the present study is that there are age-related changes in lPFC's functional integration with a larger cognitive control network. Despite a predominant focus on lPFC in theoretical (Dempster, 1992; Diamond, 2002; Kirkham et al., 2003) and empirical (Moriguchi and Hiraki, 2009, 2011) work on the development of dimensional switching, recent evidence suggests that, in the context of higher-order mental operations, lPFC does not function independently, but forms part of a larger cognitive control network. First, switching generally (Barber and Carter, 2005; Cole and Schneider, 2007; Liston et al., 2006; Wendelken et al., 2012), and DCCS performance specifically (Morton et al., 2009), is associated with activity in many regions beyond lPFC, including the anterior cingulate cortex, dorsal premotor cortex, inferior frontal junction, inferior and superior parietal cortex, the caudate nucleus, and the thalamus. These regions co-activate across a broad range of executive tasks (Duncan, 2010; Duncan and Owen, 2000), are densely interconnected by white matter fiber tracts (Olesen et al., 2003), have intrinsically correlated signal timecourses (Cole and Schneider, 2007; Seeley et al., 2007), and rapidly exchange information in the context of attentionally demanding tasks (Buschman and Miller, 2007). Functional connectivity of lPFC with these regions is associated with individual differences in higher-order cognitive functioning (Danielmeier et al., 2011; Langen et al., 2012; Mulder et al., 2011; Nagy et al., 2004; van den Bos et al., 2012), including switching (Cole and Schneider, 2007), and changes considerably in early development (Allen et al., 2011; Fair et al., 2007; Kelly et al., 2008; Langen et al., 2012; Mulder et al., 2011; Stevens et al., 2009).

The present investigation therefore tested whether DCCS performance is associated with age-related differences in the functional connectivity of lateral prefrontal cortex with a larger cognitive control network. To test this possibility, fMRI data acquired from children and adults performing the DCCS (Morton et al., 2009) were re-analyzed using spatial independent component analysis (or spatial ICA; Calhoun et al., 2009). Spatial ICA is a statistical procedure for revealing hidden sources underlying a set of observations such that the revealed sources are maximally independent. Applied to the analysis of an fMRI volumetric time-series, the procedure assumes that each volume of the series is a mixture of a finite number of spatially independent sources. ICA then blindly decomposes or un-mixes the observed data to reveal a set of spatial components, each with an associated timecourse. Objective selection of theoretically meaningful components (e.g., components that show an effect of switching or are otherwise associated with cognitive control) can be achieved by using predictors from a standard fMRI design matrix to predict variance in component timecourses in the context of a GLM, spatially correlating component topographies with a network template, or both. Isolating a network of interest in this way carries several advantages. First, because artifacts like those associated with subject motion (Power et al., 2012) or biological rhythms have unique spatiotemporal profiles, ICA can isolate and assign these artifacts to separate components, leaving remaining components relatively free of these unwelcome sources of variance. Second, through the use of objective component selection procedures, components that are directly associated with dimensional switching can be identified. Group differences in connectivity and activation of this network can then be revealed by means of group contrasts on the spatial and temporal components respectively. Finally, because ICA is computed on all voxels comprising a volumetric time series, the resulting characterization of network organization is not biased by an a priori selection of regions of interest.

Therefore, the current study used spatial ICA to test for age-related differences in the functional connectivity of networks selected on the basis of their association with DCCS performance. Children and adults performed the DCCS as T2*-weighted images were acquired by means of a 4-Tesla MRI scanner (Morton et al., 2009). Resulting images were decomposed into a set of 20 maximally independent spatial components by means of spatial ICA. Switch-related components were then identified by means of an objective component selection procedure. Of interest was whether functional connectivity in selected task-related executive networks would differ across adults and children.

On the basis of previous analyses, we expected lPFC and its associated network to show greater activity during switch blocks than repeat blocks, but that the magnitude of this effect would be equivalent across children and adults. At the same time, we predicted that functional connectivity between lPFC and other cognitive control regions including the anterior cingulate cortex, parietal cortex, and subcortical structures, would be stronger in adults than in children.