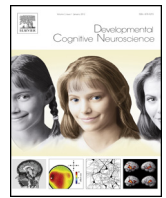




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Developmental Cognitive Neuroscience

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



The transition from childhood to adolescence is marked by a general decrease in amygdala reactivity and an affect-specific ventral-to-dorsal shift in medial prefrontal recruitment

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ARTICLE INFO

Article history:

Received 1 May 2016

Received in revised form 8 June 2016

Accepted 27 June 2016

Available online xxx

Keywords:

Emotion
Neurodevelopment
Prefrontal cortex
Amygdala
fMRI

ABSTRACT

Understanding how and why affective responses change with age is central to characterizing typical and atypical emotional development. Prior work has emphasized the role of the amygdala and prefrontal cortex (PFC), which show age-related changes in function and connectivity. However, developmental neuroimaging research has only recently begun to unpack whether age effects in the amygdala and PFC are specific to affective stimuli or may be found for neutral stimuli as well, a possibility that would support a general, rather than affect-specific, account of amygdala-PFC development. To examine this, 112 individuals ranging from 6 to 23 years of age viewed aversive and neutral images while undergoing fMRI scanning. Across age, participants reported more negative affect and showed greater amygdala responses for aversive than neutral stimuli. However, children were generally more sensitive to both neutral and aversive stimuli, as indexed by affective reports and amygdala responses. At the same time, the transition from childhood to adolescence was marked by a ventral-to-dorsal shift in medial prefrontal responses to aversive, but not neutral, stimuli. Given the role that dmPFC plays in executive control and higher-level representations of emotion, these results suggest that adolescence is characterized by a shift towards representing emotional events in increasingly cognitive terms.

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1. Introduction

Current neurodevelopmental models posit that changes in amygdala and prefrontal function – or in their connectivity (Casey, 2015) – underlie changes in affective responding in childhood and adolescence (Casey et al., 2008; Ernst et al., 2006). Such models are bolstered by a rich body of animal work demonstrating developmental changes in prefrontal-amygdala dynamics (Bouwmeester et al., 2002a,b; McCallum et al., 2010; Pattwell et al., 2012), as well as extensive adult neuroimaging research linking the amygdala and prefrontal cortex to a host of emotional processes (Buhle et al.,

2014; Costafreda et al., 2008; Kober et al., 2008). However, there is also emerging evidence that the amygdala does not exclusively respond to aversive, or even affective stimuli (Cunningham and Brosch, 2012). As such, it is possible that developmental changes in amygdala and prefrontal function are related not only to emotional development, but also to a broader set of developmental processes (e.g., salience processing, social appraisals) (Pfeifer and Blakemore, 2012; van den Bulk et al., 2013). The present study sought to examine two non-competing possibilities for how amygdala and prefrontal function relate to general and affect-specific changes in development.

The first possibility was that age would predict general changes in the way individuals respond to both negative affective and neutral stimuli. Specifically, it was hypothesized that age would be associated with diminished engagement of subcortical systems like the amygdala which has been broadly implicated in responding to motivationally salient (Cunningham and Brosch, 2012), intense

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<http://dx.doi.org/10.1016/j.dcn.2016.06.005>

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Please cite this article in press as: Silvers, J.A., et al., The transition from childhood to adolescence is marked by a general decrease in amygdala reactivity and an affect-specific ventral-to-dorsal shift in medial prefrontal recruitment. *Dev. Cogn. Neurosci.* (2016), <http://dx.doi.org/10.1016/j.dcn.2016.06.005>

(Anderson et al., 2003), and emotion-eliciting – both positive and negative (Breiter et al., 1996) – stimuli (Costafreda et al., 2008). A sizeable body of neuroimaging work suggests that amygdala responses to aversive stimuli including fearful faces and emotionally evocative scenes are elevated in childhood (Gee et al., 2013; Silvers et al., 2015) and adolescence (Guyer et al., 2008; Hare et al., 2008; Monk et al., 2003; Passarotti et al., 2009) and decrease in adulthood. However, the evidence that age-related changes in amygdala responses are emotion-specific is more mixed (Helfinstein and Casey, 2014). Indeed, neuroimaging studies have revealed age-related decreases in amygdala responding for neutral (Forbes et al., 2011; Thomas et al., 2001), positive (Vasa et al., 2011), or a combination of different types of stimuli (Hare et al., 2008; Swartz et al., 2014; Vink et al., 2014). This suggests that perhaps children interpret a broader variety of affective and neutral stimuli as being salient or personally relevant than do adults and thus show elevated amygdala responses for both aversive and non-aversive stimuli. Among studies that have specifically examined age-related effects in the amygdala for aversive stimuli, most have focused on contrasts between aversive stimuli and fixation (Gee et al., 2013), or, in the case of our own work, on the effects of different regulatory conditions on responses to aversive stimuli (Silvers et al., in press; Silvers et al., 2015). While such approaches are useful for characterizing changes in amygdala function in affective contexts, they do not address whether or not such age-related changes are *unique* to affective contexts. As such, this prior research leaves open the possibility that the amygdala shows general, rather than negative affect-specific, age-related decreases in responding.

The second possibility we sought to explore was whether age is associated with dynamic changes in how medial prefrontal cortex (mPFC) responds to negative affective stimuli. mPFC presents itself as a strong candidate region for such age-related changes for two reasons. The first is that converging evidence from animal studies and neuroimaging work in adult humans has strongly implicated mPFC in the top-down generation and regulation of emotion, both of which require relatively mature cognitive skills. Within mPFC, dorsal regions (dmPFC) appear to be preferentially involved in generating fear responses (Etkin et al., 2011; Mechias et al., 2010; Sotres-Bayon and Quirk, 2010), though they are also implicated in top-down cognitive regulation of emotion (Buhle et al., 2014) as well as mentalizing processes more generally (Denny et al., 2012; Van Overwalle and Baetens, 2009). Together, this suggests that dmPFC supports abstract and conceptual representations of affective states (Ochsner and Gross, 2014; Satpute et al., 2013). Ventral mPFC (vmPFC) recruitment, by contrast, scales with perceived value (Hare et al., 2009; Kable and Glimcher, 2007), decreases under conditions of stress and threat (Mobbs et al., 2007; Wager et al., 2009), and is strongly implicated in fear extinction (Diekhof et al., 2011; Milad et al., 2006; Quirk et al., 2006), suggesting it may play a key role in regulating the expression of affective responses based on contextual constraints (Ochsner and Gross, 2014; Roy et al., 2012). As such, while dmPFC and vmPFC play complementary roles in shaping affective experiences in adults, each contributes to conceptual and contextual representations of emotion. This ability to consider emotional events in more cognitive terms is central to mature emotion regulatory processes and is therefore likely to be specifically related to changes in affective development.

A second reason to suspect that mPFC underlies negative affect-specific changes in development comes from prior work showing that mPFC responses to aversive stimuli change in striking ways across development (Cohen et al., 2016). With regards to vmPFC, prior neuroimaging studies have revealed that vmPFC responses to aversive stimuli decrease during adolescence (McRae et al., 2012), and that functional connectivity between vmPFC and the amygdala in response to aversive stimuli is initially positive but becomes negative during the transition from childhood to adolescence (Gee

Table 1
Age-independent effects of stimulus valence on brain recruitment.

Region	Hemisphere	# Voxels	F	MNI Coordinates		
				x	y	z
<i>Aversive > Neutral and Neutral > Aversive*</i>						
<i>Aversive > Neutral:</i>						
Temporoparietal junction, middle occipital gyri	R	10401	280.64	51	-63	6
Inferior frontal gyrus	R	199	45.56	42	24	-15
Inferior frontal gyrus	R	217	66.33	45	3	30
Inferior frontal gyrus	R	205	53.35	51	27	-3
Inferior and middle frontal gyri	R	70	37.76	54	15	39
Inferior frontal gyrus	R	199	53.58	54	33	6
Inferior frontal gyrus	R	253	79.79	57	18	27
Middle frontal gyrus	R	234	86.96	39	0	42
Superior temporal gyrus	R	309	66.22	57	-45	15
Superior temporal gyrus	R	103	56.30	45	-45	15
Temporoparietal junction, middle occipital gyri	L	1381	248.06	-48	-72	6
Superior parietal lobule	R	142	40.20	27	-72	33
Fusiform gyrus	R	285	268.15	45	-54	-15
Fusiform gyrus	R	594	236.82	45	-66	-9
Fusiform gyrus	L	265	106.82	-39	-51	-18
Cerebellum	L	342	72.21	-15	-78	-30
<i>Neutral > Aversive:</i>						
Anterior insula	R	133	77.29	36	6	9
Mid insula	R	75	29.97	42	3	-9
Posterior insula	R	317	100.53	51	-3	3
Posterior insula	R	273	56.96	39	-15	12
Posterior insula	R	168	51.38	42	-33	21
Posterior insula	R	99	32.68	36	-24	3
Hippocampus, parahippocampal gyrus	L	192	73.17	-30	-48	-3
Hippocampus, parahippocampal gyrus	R	62	49.88	33	-42	-6
Parahippocampal gyrus	L	71	33.17	-21	-33	-21
Parahippocampal gyrus	R	89	33.07	27	-36	-18
Parahippocampal gyrus, fusiform gyrus	R	195	59.87	27	-51	0
Precentral gyrus	R	496	70.81	57	-9	12
Cuneus	L	311	124.17	-12	-69	21
Cuneus	R	323	112.79	12	-57	6
Cuneus	R	421	106.26	12	-69	21
Cuneus	L	316	105.78	-6	-78	27
Cuneus	L	347	87.14	-9	-57	3
Cuneus	R	192	81.41	9	-69	0
Cuneus	L	229	72.57	-9	-81	3
Cuneus	L	230	68.63	-6	-87	18
Cuneus, cerebellum	L	149	103.93	-6	-72	-6
Cerebellum	R	85	62.56	9	-69	-9
Cerebellum	L	121	26.70	-21	-57	-18
<i>Aversive > Neutral</i>						
Inferior frontal gyrus	L	201	29.03	-54	15	24
Inferior frontal gyrus	L	34	23.70	-54	15	33
Inferior frontal gyrus	L	37	23.53	-48	3	33

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