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Cortical activation to object shape and speed of motion during the first year

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ABSTRACT

A great deal is known about the functional organization of cortical networks that mediate visual object processing in the adult. The current research is part of a growing effort to identify the functional maturation of these pathways in the developing brain. The current research used near-infrared spectroscopy to investigate functional activation of the infant cortex during the processing of featural information (shape) and spatiotemporal information (speed of motion) during the first year of life. Our investigation focused on two areas that were implicated in previous studies: anterior temporal cortex and posterior parietal cortex. Neuroimaging data were collected with 207 infants across three age groups: 3–6 months (Experiment 1), 7–8 months (Experiment 2), and 10–12 months (Experiments 3 and 4). The neuroimaging data revealed age-related changes in patterns of activation to shape and speed information, mostly involving posterior parietal areas, some of which were predicted and others that were not. We suggest that these changes reflect age-related differences in the perceptual and/or cognitive processes engaged during the task.

Introduction

There is a substantial body of research suggesting that in the human brain, information about the spatiotemporal and featural properties of objects are processed by different cortical systems, similar to those first identified in the non-human primate (Mishkin et al., 1983; Ungerleider and Mishkin, 1982). The *ventral system* extends from the visual cortex through the temporal cortex and mediates processing of the featural attributes of objects. For example, areas in the primary visual cortex respond to specific features, such as lines, orientation, or color (Bartels and Zeki, 2000; Orban et al., 2004; Tootell et al., 2003), whereas areas in the occipito-temporal cortex integrate these features and code objects as wholes, independent of visual perspective (Grill-Spector, 2003; Kourtzi and Kanwisher, 2001). Finally, more anterior areas in temporal cortex are important for higher level object processing, such as object recognition, identification, and naming (Devlin et al., 2002; Humphreys et al., 1999; Malach et al., 1995). The *dorsal system* extends from the visual cortex through the parietal cortex and mediates processing of the spatiotemporal attributes of objects. For example, area MT/V5 responds selectively to moving (as compared to static) stimuli and is sensitive to coherent motion of randomly distributed dots (Kolster et al., 2010; Murray et al., 2003, 2004; Paradis et al., 2000), whereas the angular gyrus mediates attention to and analysis of speed and path of object motion (Chambers et al., 2007; Nagel et al., 2008) and the inferior parietal cortex mediates the extraction of 3-D object structure from coherent motion displays (Denys et al., 2004; Murray et al., 2003, 2004; Paradis et al., 2000; Peuskens et al., 2004). These and related findings (for reviews see Bell et al., 2013; Orban, 2011) support the functional distinction proposed by Ungerleider and colleagues that the ventral stream is dedicated to the recognition, identification, and categorization of objects, or the "what" of objects, whereas the dorsal stream is dedicated to the processing of information about motion, depth, and location, or the “where” of objects (for an alternative viewpoint see Milner and Goodale, 1995). Claims about the functional specificity of these two pathways have been tempered somewhat, however, by evidence that ventral and dorsal cortical areas may be less specialized (or at least more interactive) than originally proposed (Borst et al., 2011; Konen and Kastner, 2008; Kravitz et al., 2010; Zachariou et al., 2014).

What has remained unspecified is the functional development of these visual object-processing pathways, largely because of a lack of neuroimaging techniques that can be used successfully with infants. With the introduction of functional near-infrared spectroscopy (fNIRS) into the experimental setting, however, developmental scientists now have the opportunity to investigate functional organization of the infant cortex. A growing number of studies (for a review see Lloyd-Fox et al., 2010) have focused on identifying cortical substrates that mediate processing of distinct types of objects and/or object properties, many of which are theoretically important to cognitive and developmental neuroscientists. The outcome of such studies have allowed us to better

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understand how the human brain is functionally organized from the early days of life (Honda et al., 2010; Lloyd-Fox et al., 2009; Watanabe et al., 2008; Wilcox et al., 2010) and provide insight into how this might change with time and experience (Wilcox et al., 2012). Most relevant to the present research are studies that have focused on the cortical substrates that support infants' emerging capacity to use featural and spatiotemporal information to track the identity of objects (Wilcox et al., 2009, 2012, 2014).

Object Individuation: cortical activation to featural differences

Several studies have investigated the cortical basis of infants' capacity to use featural information to track the identity of objects through occlusion. In one group of studies (Wilcox et al., 2012), infants 3–5 months (M age = 5, 8) and 11–12 months (M age = 11, 21) were shown occlusion events (Fig. 1) in which the objects that emerged successively from behind the screen differed in shape (green ball-green box), color (green ball-red ball) or were identical in appearance (green ball-green ball). The cortical areas targeted were anterior temporal, posterior temporal, posterior parietal, and occipital cortex. Two main findings relevant to the present research emerged. First, infants 3–5 months of age, who use shape but not color information to individuate objects (Wilcox, 1999), showed activation in the anterior temporal cortex when viewing the shape difference but not the color difference test event (see also Wilcox et al., 2010). It is not until 11–12 months, when infants first individuate-by-color (Wilcox, 1999; Wilcox et al., 2007), that infants showed activation in the anterior temporal cortex when viewing the different-color event. Neither age group showed activation in anterior temporal cortex when viewing the control (green ball-green ball) test event, an event that infants interpret as involving a single object that moves back and forth behind the screen (Wilcox, 1999). More recent studies (Wilcox et al., 2014) have revealed that infants younger than 11–12 months, if first primed to attend to color differences (i.e., given experiences that lead them to individuate-by-color), show activation in anterior temporal cortex to the color difference test event. These results provide converging evidence for the conclusion that in the infant the anterior temporal cortex is involved in the object individuation process.

The second main finding was of age-related changes in patterns of cortical activation to the different-shape event. One interesting characteristic of shape processing is that either ventral or dorsal cortical areas can mediate it, depending on the visual cues that give rise to object shape. For example, ventral areas extract object structure from contour whereas dorsal areas extract object structure from motion-carried information (De Yoe and Van Essen, 1988; Denys et al., 2004; Desimone et al., 1985; Kraut et al., 1997; Livingstone and Hubel, 1987, 1988; Murray et al., 2004; Paradis et al., 2000; Peuskens et al., 2004). On the basis of these findings, one might expect younger infants, whose visual acuity is less well developed and hence depend more on motion-carried information to perceive object shape, to show greater activation in dorsal areas than older infants. Consistent with this hypothesis, Wilcox et al. (2012) found that infants 3–5 months, but not infants aged 11–12 months, evidence activation in posterior parietal cortex during the different-shape event. Recall that from the early months of life infants individuate on the basis of shape (Wilcox, 1999) and both 3–5-month-olds and 11–12-month-olds show activation in anterior temporal cortex to the shape difference test event (Wilcox et al., 2012). Yet, only the 3–5-month-olds show activation in posterior parietal cortex. (The younger infants did not show activation in the posterior parietal cortex to the control event, indicating that this response was specific to the shape difference and was not obtained for events involving moving objects more generally.) According to the visual acuity hypothesis, at what age would we expect infants to no longer show activation in parietal cortex to shape differences? Visual acuity matures significantly during the first 6 months of life, and by 7–8 months approaches that of an adult (Dobson and Teller, 1978; Norica and Tyler, 1985; Teller and Movshon, 1985). Hence, by this time we would expect infants to show cortical activation patterns similar to those of the older (and not the younger) infants. The current research tested this prediction.

Object Individuation: cortical activation to spatiotemporal discontinuities

Much less research has been conducted on the cortical basis of infants' use of spatiotemporal information to individuate objects. In a recent study conducted with infants 5–7 months (Wilcox et al., 2010), participants were shown a speed discontinuity, path discontinuity, or control event (Fig. 2). Previous behavioral studies conducted with 3.5–9.5-month-olds have demonstrated that infants interpret the speed discontinuity and path discontinuity event (but not the control event) as involving two distinct objects; that is, they use the spatiotemporal discontinuities to individuate the objects seen in the occlusion sequence (Schweinle and Wilcox, 2004; Wilcox and Schweinle, 2003). During the test session, neural activation, as measured by changes in HbO, was assessed at the same four locations as that of Wilcox et al. (2012). Two main findings emerged. First, the infants in the speed and path discontinuity conditions, but not the control condition, evidenced significant activation in the anterior temporal cortex. When spatiotemporal information embedded in the occlusion sequence signaled the presence of distinct objects, anterior temporal cortex was activated. These results provide converging evidence, using a different type of event – an event involving spatiotemporal discontinuities rather than featural differences – that the anterior temporal cortex mediates the individuation process in the infant. Second, the infants in the speed and path discontinuity conditions, but not the control condition, evidenced activation in the posterior parietal cortex. This finding supports prevailing hypotheses (Johnson and Mareschal, 2003; Kaufman et al., 2003) that from an early age dorsal cortical areas mediate processing of the spatiotemporal properties of objects. The extent to which cortical responses to spatiotemporal discontinuities change during the first year

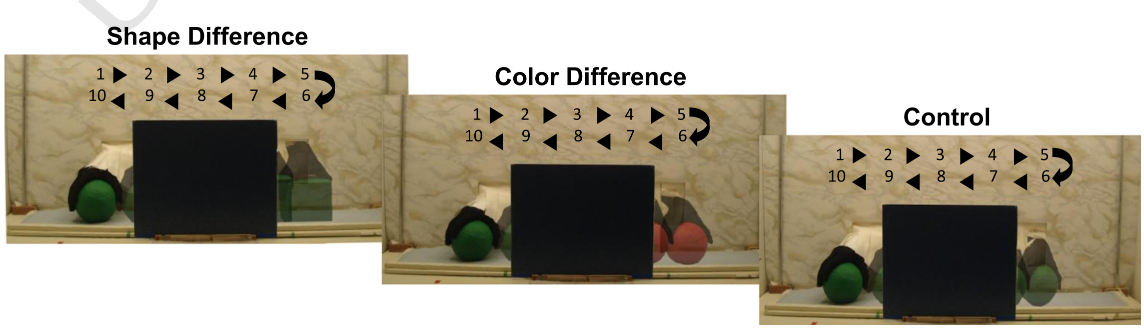

Fig. 1. The shape difference, color difference, and control test events of Wilcox et al. (2012). Each cycle of the test event was 10 s and infants saw 2 complete cycles during each test trial.

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