

Hemodynamic changes in the infant cortex during the processing of featural and spatiotemporal information

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ABSTRACT

Over the last 20 years neuroscientists have learned a great deal about the ventral and dorsal object processing pathways in the adult brain, yet little is known about the functional development of these pathways. The present research assessed the extent to which different patterns of neural activation, as measured by changes in blood volume and oxygenation, are observed in infant visual and temporal cortex in response to events that involve processing of featural differences or spatiotemporal discontinuities. Infants aged 6.5 months were tested. Increased neural activation was observed in visual cortex in response to a featural-difference and a spatiotemporal-discontinuity event. In addition, increased neural activation was observed in temporal cortex in response to the featural-difference but not the spatiotemporal-discontinuity event. The outcome of this experiment reveals early functional specialization of temporal cortex and lays the foundation for future investigation of the maturation of object processing pathways in humans.

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1. Introduction

Over the last 20 years a great deal of research has been conducted on the neural basis of object processing. Early studies conducted with non-human primates suggested that there are two main routes for visual object processing (De Yoe & Van Essen, 1988; Goodale & Milner, 1992; Livingstone & Hubel, 1988; Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). The *ventral* route originates from the parvocellular layers of the lateral geniculate nucleus (LGN) and projects from the primary visual cortex to the temporal cortex and mediates processing of visual features important for the recognition and identification of objects. The *dorsal* route originates from the magnocellular layers of the LGN and projects from the primary visual cortex to the parietal cortex and is important for the analysis of motion, depth, and location. More recent studies with non-human (Orban, Van Essen, & Fanduffel, 2004; Tootell, Tsao, & Vanduffel, 2003; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001; Wang, Tanifuji, & Tanaka, 1998; Wang, Tanaka, & Tanifuji, 1996) and human (Bly & Kosslyn, 1997; Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector et al., 1998; Haxby et al., 1991; Kourtzi & Kanwisher, 2001; Kraut, Hart, Soher, & Gordon, 1997) primates, using more sophisticated neuroimaging techniques, provide

converging evidence for the functional distinction between these two pathways.

Although we now have extensive information about the neural correlates of object processing in the adult, little is known about the functional development of these pathways. Research conducted with infant monkeys suggests that the temporal cortex undergoes significant structural and neurophysiological development early in life (Bachevalier, Brickson, Hagger, & Mishkin, 1990; Rodman, Skelly, & Gross, 1991; Webster, Ungerleider, & Bachevalier, 1991, 1995). Metabolic, neurophysiological, and neuroanatomical data obtained with human infants also reveals significant neural maturation during the first year (e.g., Braddick, Atkinson, & Wattam-Bell, 2003; Braddick & Atkinson, 2007; Chugani & Phelps, 1986; Conel, 1939–1967; De Haan & Nelson, 1999; Franceschini, Thaker, Themelis, Krishnamoorthy & Bortfeld, 2007; Gunn et al., 2002; Purpura, 1975). However, because there are a limited number of non-invasive techniques available to measure localized functional brain activation in infants, little is known about the functional consequences of neural maturation. Recent advances in optical imaging, including near-infrared spectroscopy (NIRS), now offer the opportunity to study functional activation in human infants.

In NIRS, near-infrared light is projected through the scalp and skull into the brain and the intensity of the light that is diffusely reflected is recorded. Typically, during cortical activation local concentrations of oxyhemoglobin (HbO₂) increase, whereas concentrations of deoxyhemoglobin (HbR) decrease (Hoshi & Tamura, 1993; Jaszewski et al., 2003; Obrig et al., 1996; Strangman,

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Franceschini, & Boas, 2003; Villringer & Dirnagl, 1995). From the summated change in HbO₂ and HbR, the total change in hemoglobin (HbT) can be computed. Given that changes in HbT signal changes in regional cerebral blood flow (rCBF), having a measure of HbT is an important guide in the interpretation of NIRS data. While an increase in blood volume would result in an increase in HbO₂ and HbR, an increase in blood flow results in an increase in HbO₂ and a “washout” of HbR (i.e., an increase in relative concentration of HbO₂ and a decrease in relative concentration of HbR).

Predicting and interpreting changes in HbO₂ and HbR during cortical activation is not always straightforward, however. For example, an increase in rCBF (as indicated by HbT) produces an increase in HbO₂ and a decrease in HbR. At the same time, an increase in oxygen consumption produces a decrease in HbO₂ and an increase in HbR. Furthermore, the effect of these opposing mechanisms may be different in infants than adults (Hintz et al., 2001; Meek et al., 1998; Sakatani, Chen, Lichty, Zuo, & Wang, 1999). Hence it is important to remember that changes in relative concentrations of HbO₂ and HbR are produced by changes in blood volume, rCBF, and oxygen consumption and that the relation between these can be complex.

To capitalize on changes in HbO₂ and HbR, near-infrared light between approximately 650 and 950 nm is utilized. At these wavelengths, light is differentially absorbed by oxygenated and deoxygenated blood (Gratton, Sarno, Maclin, Corballis, & Fabiani, 2000; Villringer & Chance, 1997). Measuring the light intensity modulation during stimulus presentation, and comparing it to the light intensity during a baseline event in which no stimulus is presented, provides important information about the hemodynamic response to brain activation.

Recently, researchers have successfully applied NIRS technology to human infants in the experimental setting (e.g., Baird et al., 2002; Bortfeld, Wruck, & Boas, 2007; Pena et al., 2003; Taga, Asakawa, Maki, Konishi, & Koizumi, 2003; Wilcox, Bortfeld, Woods, Wruck, & Boas, 2005, 2008). Most of these studies have focused on region specific hemodynamic changes in the neocortex during perceptual and cognitive tasks. For example, Wilcox et al. (2005) assessed hemodynamic changes in the visual and the temporal cortex during a visual object processing task. In this task, 6.5-month-olds saw an event in which a green ball and a red box emerged successively to opposite sides of screen (Fig. 1A). Behavioral studies (Wilcox & Baillargeon, 1998a,b; Wilcox & Chapa, 2002) indicate that 4.5–11.5-month-old infants use the featural differences to interpret the event as involving two distinct objects. Analysis of the NIRS data revealed a significant increase in HbO₂ in visual and temporal cortex during the test event. Follow-up studies replicated and extended these findings to other events involving featurally distinct objects (Wilcox et al., 2008) and demonstrated that activation is observed in visual but not temporal cortex in response to control events (e.g., when the same object is seen to both sides of the screen). These data suggest that object processing is functionally localized: whereas visual cortex responds to all events involving visual objects temporal cortex responds only when the objects differ in their featural properties.

What these findings leave open to speculation, however, is the extent to which temporal cortex mediates the processing of other types of object information. For example, in adults the ventral pathway mediates processing of object features but does not typically mediate processing of the spatiotemporal properties of objects. If the ventral pathway in the infant is organized in a way similar to

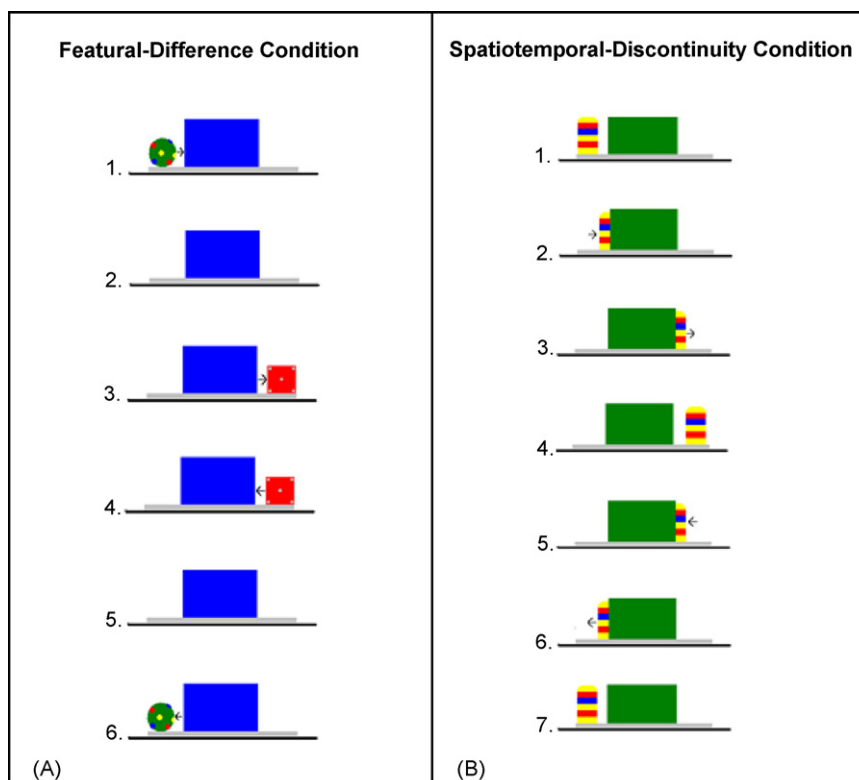


Fig. 1. The test events seen in the featural-difference (A) and spatiotemporal-discontinuity (B) condition. Although not pictured, a hand moved the objects. In the *featural-difference* condition, the ball moved right until it was fully hidden behind the occluder (2 s); the box then emerged and moved to the right edge of the platform (2 s). The box paused (1 s) and the 5 s sequence was seen in reverse. The entire 10 s ball-box cycle then repeated twice to conclude the 30 s trial. When in motion the objects moved at a rate of 12 cm/s and the occlusion interval was 1.8 s. In the *spatiotemporal-discontinuity* condition, the column moved right until it was fully occluded (2.5 s) and then the second column appeared immediately at the right edge of the occluder (the event was produced by two experimenters who had similar sized hands covered by identical white gloves) and moved right until it reached the right end of the platform (2.5 s). The column paused (1 s) and the 6 s sequence was reversed. The entire event was then repeated 1.5 times to conclude the 30 s trial. When visible, the object moved at a rate of 3 cm/s.

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