NeuroImage 53 (2010) 1256–1263

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Dissociation of processing of featural and spatiotemporal information in the infant cortex

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ARTICLE INFO

Article history:
Received 12 January 2010
Revised 1 June 2010
Accepted 24 June 2010
Available online 13 July 2010

Keywords:
Near-infrared spectroscopy
Infants
Featural information
Spatiotemporal information
Cortical development

ABSTRACT

A great deal is known about the development of visual object processing capacities and the neural structures that mediate these capacities in the mature observer. In contrast, little is known about the neural structures that mediate these capacities in the infant or how these structures eventually give rise to mature processing. The present research used near-infrared spectroscopy to investigate neural activation in visual, temporal, and parietal cortex during object processing tasks. Infants aged 5–7 months viewed visual events that required processing of the featural (Experiment 1) or the spatiotemporal (Experiment 2) properties of objects. In Experiment 1, different patterns of neural were obtained in temporal cortex in response to shape than color information. In Experiment 2, different patterns of neural activation were obtained in parietal cortex in response to spatiotemporal (speed and path of motion) than featural (shape and color) information. These results suggest a dissociation of processing of featural and spatiotemporal information in the infant cortex and provide evidence for early functional specification of the human brain. The outcome of these studies informs brain-behavior models of cognitive development and lays the foundation for systematic investigation of the functional maturation of object processing systems in the infant brain.

Our capacity to perceive objects as solid bounded entities that persist even when perceptual contact is lost is fundamental to human cognition. The development of looking time paradigms in the late 1960s and early 1970s provided researchers, for the first time, with a method with which to investigate visual object processing in preverbal and motorically limited infants. The outcome of many years of research has revealed that young infants recognize the persistence and continuity of physical objects and possess more sophisticated object knowledge than originally believed (Baillargeon et al., 2009; Spelke and Kinzler, 2007). At the same time, infants' object processing capacities undergo significant changes during the first year. For example, early in the first year infants use spatiotemporal information, such as speed and path of motion, to track the identity of objects as they move in and out of view (Aguiar and Baillargeon, 2002; Spelke et al., 1995; Wilcox and Schweinle, 2003). Young infants also use featural information, but this capacity is not as well developed (Wilcox and Baillargeon, 1998; Woods and Wilcox, 2006). By 4.5 months infants use shape information but it is not until 11.5 months that they use color information as the basis for individuating objects (Wilcox, 1999). This finding is intriguing because infants can perceive color differences, even though they fail to use these differences to individuate objects.

At about the time that developmental scientists first reported studies of object processing in infants, neuroscientists began to explore the neural basis of object processing in non-human primates. The outcome of neuro-anatomical, -physiological, and -behavioral studies indicated that there are two main routes for visual object processing (De Yoe and Van Essen, 1988; Desimone and Ungerleider, 1989; Ungerleider and 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. The dorsal route originates from the magnocellular layers of the LGN and projects from the primary visual cortex to the parietal cortex. Although there has been some debate about the precise function of the two routes (Goodale and Milner, 1992), most researchers agree that the ventral pathway mediates processing of visual features (e.g., shape and color) important for the recognition and identification of objects. In contrast, the dorsal pathway is important for the analysis of the motion, depth, and location (e.g., spatiotemporal) information.

The development of non-invasive neuroimaging techniques has provided neuroscientists with the opportunity to examine the extent to which there are analogous visual processing systems in the human brain (Haxby et al., 1991; Kriegeskorte et al., 2008; Tanaka, 1997; Tootell et al., 2003). Overall, studies have revealed that the functional map of the human brain is similar to that of the monkey brain. In the human visual cortex, V1 to V3 are important for the analysis of basic visual stimuli, such as lines and their orientation (Orban et al., 2004; Tootell et al., 2003). The ventral route, which is involved in the

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doi:10.1016/j.neuroimage.2010.06.064

processing of more complex visual stimuli such as objects, extends from the lateral occipital cortex (LOC), which lies near the occipital-temporal border, to the middle of the temporal cortex. The LOC encodes objects as whole entities, rather than as groups of independent features (Grill-Spector, 2003; Kanwisher, 2003; Malach et al., 1995) and is important for the recognition of objects on the basis of what they look like, rather than their spatiotemporal properties. More anterior or "higher" areas in the ventral stream, such as middle temporal cortex, mediate more sophisticated object processes, such as object individuation and identification, categorization, and naming (Devlin et al., 2002; Humphreys et al., 1999; Malach et al., 1995). The dorsal object processing route extends from the occipital-parietal border to the parietal cortex. Within this stream, the inferior parietal cortex and the inferior parietal sulcus mediate the processing of the spatiotemporal properties of objects, including location, depth, and motion-carried information (Haxby et al., 1991; Murray et al., 2003; Peuskens et al., 2004). More recent evidence suggests that the angular gyrus also mediates attention to and analysis of speed and path of object motion (Chambers et al., 2007; Nagel et al., 2008).

Although we now have extensive information about the neural correlates of object processing in human adults, little is known about the functional development of these pathways. There is evidence from structural, electrophysiological, and metabolic studies conducted with human and non-human primates that object processing areas in the temporal and parietal cortex are structurally and functionally intact early in development but that these areas also undergo significant neural maturation during infancy (Chugani and Phelps, 1987; Franceschini et al., 2007; Rodman et al., 1991; Webster et al., 1995). Unfortunately, the functional consequences of many of these maturational changes have not yet been fully specified. Scientists have attempted, for many years, to draw inferences about the relation between neural and cognitive development in humans but have lacked the techniques to study localized functional activation in the human infant.

With the recent application of near-infrared spectroscopy (NIRS), a non-invasive optical imaging technique, into the experimental setting (Baird et al., 2002; Meek et al., 1998; Pena et al., 2003; Taga et al., 2003; Wilcox et al., 2005) we now have the capacity to study functional activation during object processing in the human infant. 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. During cortical activation local concentrations of oxyhemoglobin (HbO) typically increase, whereas concentrations of deoxyhemoglobin (HbR) decrease (Strangman et al., 2003; Villringer and Dirnagl, 1995). From the summated change of HbO and HbR total hemoglobin (HbT) can be computed. The present research used NIRS with two goals. The first goal was to assess neural activation in temporal cortex in response to select object features. We expected to obtain different patterns of neural activation to shape differences, which young infants use to individuate objects, than to color differences, which young infants do not use to individuate objects. This outcome would firmly establish a link between object processing capacities and patterns of neural activity in the ventral object processing stream. The second goal was to assess the extent to which the temporal and parietal cortices are functionally specialized in the young infant. We expected different patterns of neural activation to spatiotemporal than featural information. Although this prediction is supported by behavioral data (Kaldy and Leslie, 2003; Mareschal and Johnson, 2003) it has yet to be directly tested with neurophysical data.

Two experiments were conducted using tasks that have been used previously and have yielded reliable behavioral results. In the first experiment, 5- to 7-month-old infants were shown an event (Fig. 1) in which objects emerged successively to opposites side of an occluder; the objects differed in their shape (shape difference event), their color (color difference event), or were identical in appearance (control event). Previous behavioral work indicates that infants 4.5 and older interpret the shape difference event as involving two numerically distinct objects; in contrast infants fail to use the color difference to individuate the objects until 11.5 months (Wilcox, 1999; Wilcox and Woods, 2009). Similar results favoring shape over color information have been obtained in object segregation and

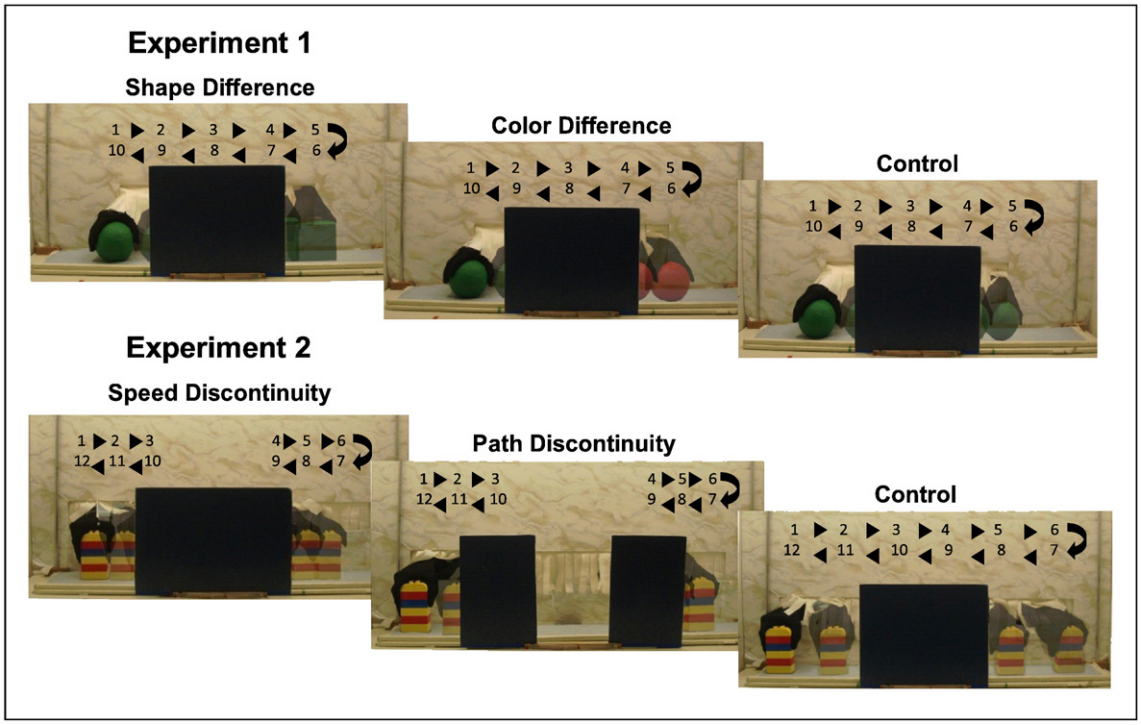

Fig. 1. Test events. In Experiment 1 each cycle of the test event was 10 s and infants saw 2 complete cycles during each test trial. Infants saw the following objects to the left and right sides of the screen, respectively: green ball-green box (shape difference); green ball-red ball (color difference); green ball-green ball (control). In Experiment 2 each cycle of the test event was 12 s and infants saw 2 complete cycles during each test trial.

identification tasks (for a review see Wilcox and Woods, 2009). In the second experiment, 5- to 7-month-old infants saw a speed-discontinuity, path-discontinuity, or control event (Fig. 1). Previous behavioral research (Aguiar and Baillargeon, 2002; Spelke et al., 1995; Wilcox and Schweinle, 2003) indicates that infants as young as 3.5 months interpret speed- and path-discontinuity events, but not the control event, as involving two objects.

In both experiments optodes were placed over infants' left visual, temporal, and parietal cortex at four skull locations using the International 10–20 system: O1, P3, T5, and T3 (Fig. 2). For O1, T3 and T5 the emitter was placed at the 10–20 coordinate; for P3 the emitter was placed 2 cm above the coordinate. According to cortical maps obtained with adults (Okamoto et al., 2004), O1 lies over visual cortex (middle occipital gyrus), P3 over the posterior parietal cortex (angular gyrus), T5 over the posterior surface of the temporal cortex (inferior temporal gyrus/middle temporal gyrus), and T3 over the anterior surface of the temporal cortex (middle temporal gyrus/superior temporal gyrus). Because cranio-cerebral correspondences have not yet been identified in infants, we use adult cortical maps as a general guide and exercise caution in our interpretation of the data until infant cortical maps become available. Optical imaging data were collected at nine channels (Fig. 2) as infants watched the events and relative changes in blood volume and oxygenation were used as an indicator of neural activation.

Materials and methods

Participants

Infants aged 5–7 months participated in Experiment 1 ($n=54$; 29 males, M age = 6 months, 19 days, range = 5 months, 1 days to 8 months, 14 days) and Experiment 2 ($n=54$; 22 males, M age = 6 months, 1 day, range = 5 months, 1 day to 7 months, 19 days). In Experiment 1, 27 additional infants were tested but excluded from analysis because of procedural problems ($n=6$), crying ($n=4$), difficulty in obtaining an optical signal ($n=3$), motion artifacts ($n=5$), or failure to look at least 15 s on two or more test trials ($n=9$). In Experiment 2, 31 additional infants were tested but excluded from analysis because of procedural problems ($n=9$), difficulty in obtaining an optical signal ($n=4$), motion artifacts ($n=6$), or failure to look at least 20 s on two or more test trials ($n=12$). The study protocol was approved by the Institutional Review Board at Texas A&M University and informed consent was obtained from all parents of participants. Parents received reimbursement for travel expenses and/or a lab t-shirt for their infant.

Task and procedure

Infants sat on their parent's lap or in a bumbo seat in a quiet and darkened room and watched the event appropriate for the condition presented in a puppet-stage apparatus. Trained experimenters produced the test events live following a precise script.

In Experiment 1, infants were presented with four trials of one of three events (Fig. 1): shape difference ($n=18$), color difference ($n=18$), or control ($n=18$). Each trial was 20 s in duration (each cycle of the test event was 10 s and infants saw 2 complete cycles during each test trial). Because analysis of the optical imaging data requires baseline recordings of the measured intensity of refracted light, each test trial was preceded by a 10 s baseline interval during which time a curtain covered the front opening and stage of the apparatus. The curtain was raised to begin each test trial. Previous studies using similar tasks (Wilcox et al., 2008, 2009) indicate that

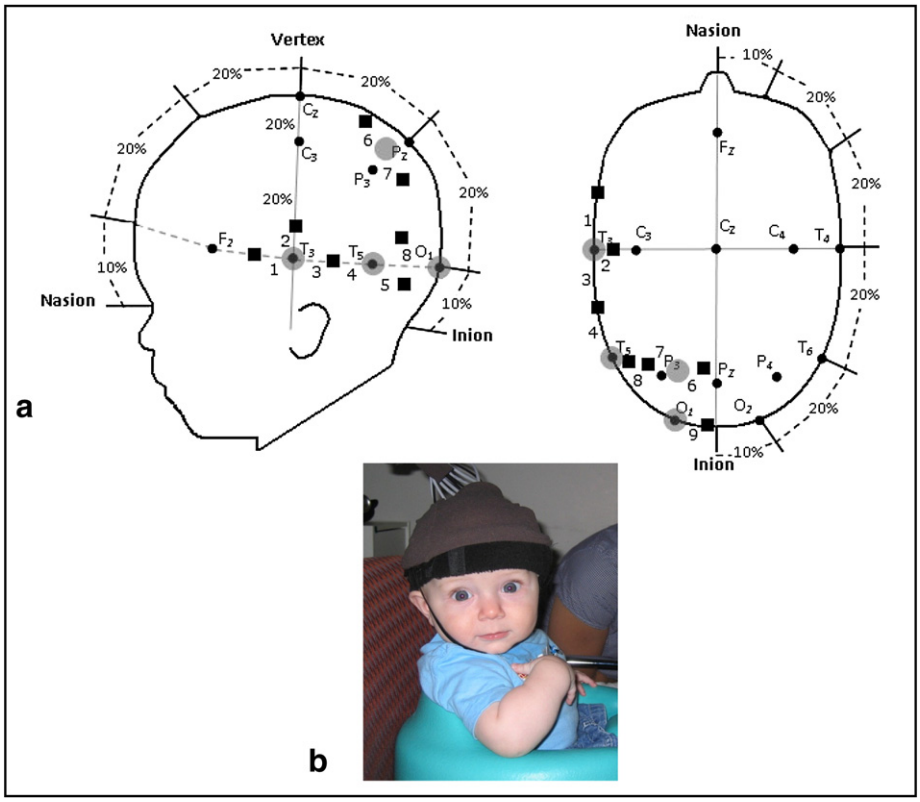

Fig. 2. Configuration and placement of optodes. (a) Location of emitters (large grey circles) and detectors (black squares) on the infant's head in relation to the 10–20 International EEG system (small black circles). Note that an emitter was placed directly over O1, T5, and T3. Also represented are the nine corresponding channels (numbers) from which data were collected. Emitter-detector distances were all 2 cm. Each detector read from a single emitter except for the detector between T3 and T5, which read from both emitters. The light was frequency modulated to prevent "cross-talk." (b) Infants sat in a supportive seat to restrain excess movement. Elasticized headband slid on and was secured by a chin strap.

10 s is sufficient for blood volume to return to baseline levels. Experiment 2 also consisted of a between-subjects design. Infants were presented with four trials of one of three events (Fig. 1): speed-discontinuity ($n=18$), path-discontinuity ($n=18$), or control ($n=18$). Each trial was 24 s in duration (each cycle of the test event was 12 s and infants saw 2 complete cycles during each test trial). As in Experiment 1, each test trial was preceded by a 10 s baseline interval.

Looking behavior was monitored by two independent observers who watched the infants through peepholes in cloth-covered frames attached to the side of the apparatus. Inter-observer agreement averaged 95% across the two experiments.

Instrumentation

The imaging equipment contained three major components: (1) four fiber optic cables that delivered near-infrared light to the scalp of the participant (emitters); (2) eight fiber optic cables that detected the diffusely reflected light at the scalp (detectors); and (3) an electronic control box that served as the source of the near-infrared light and the receiver of the reflected light. The control box produced light at 690 and 830 nm wavelengths with two laser-emitting diodes (TechEn Inc). At 690 nm light is more sensitive to deoxygenated blood and at 830 nm it is more sensitive to oxygenated blood. Laser power emitted from the end of the diode was 4 mW. Light was square wave modulated at audio frequencies of approximately 4–12 kHz. Each laser had a unique frequency so that synchronous detection could uniquely identify each laser source from the photodetector signal. Ambient illumination from the testing room did not interfere with the laser signals because environmental light sources modulate at a different frequency. All fiber optic cables were 1 mm in diameter and 5 m in length. Each emitter delivered both wavelengths of light and each detector responded to both wavelengths. The signals received by the electronic control box were processed and relayed to a DELL desktop computer. A custom computer program recorded and analyzed the signal.

Prior to test, infants were fitted with custom-made headgear that secured the fiber optics to the scalp. The configuration of the optic cables within the headgear and the placement of the headgear on the infants head are shown in Fig. 2.

Processing of the NIRS data

The NIRS data were processed, for each detector separately, using a procedure similar to that of Wilcox et al. (2005). Briefly, the raw signals were acquired at the rate of 200 samples per second, digitally low-pass-filtered at 10 Hz, a principal components analysis was used to design a filter for systemic physiology and motion artifacts, and the data were converted to relative concentrations of oxygenated (HbO) and deoxygenated (HbR) blood using the modified Beer–Lambert law. Changes in HbO and HbR were examined using the following time epochs: the 2 s prior to the onset of the test event, the 20 s (Experiment 1) or 24 s (Experiment 2) test event, and the 10 s following the test event. The mean optical signal from -2 to 0 s (baseline) was subtracted from the signals and other segments of the time epoch were interpreted relative to this zeroed baseline. Optical signals were averaged across trials and then infants for each event condition. Trials objectively categorized as containing motion artifacts (a change in the filtered intensity greater than 5% in 1/20 s during the 2 s baseline and test event) were eliminated from the mean. In addition, because neural activation depends on visual attention to the events, trials in which the infant cumulated less than 15 s (Experiment 1) or 20 s (Experiment 2) looking time were also eliminated from analysis. On the basis of these criteria, in Experiment 1, 25 (of 216 possible) trials were eliminated from analysis and in Experiment 2, 54 (of 216 possible) trials were eliminated.

Results

Looking time data

Looking time data were averaged across trials and infants for each event condition within each experiment. This was to ensure that visual attention did not vary by condition, which alone could lead to different patterns of neural activity. As expected, in Experiment 1 infants' looking times did not differ significantly by condition (shape difference, $M=18.21$, $SD=1.39$; color difference, $M=18.22$, $SD=0.56$; and control, $M=18.69$, $SD=0.90$) $F(2, 51)<1$. In Experiment 2 infants' looking times also did not differ significantly by condition (speed-discontinuity, $M=22.38$, $SD=1.01$; path-discontinuity, $M=22.49$, $SD=1.18$; and control, $M=22.51$, $SD=0.78$), $F(2, 51)<1$.

Neural responses to featural differences: Experiment 1

Hemodynamic response curves for each channel and event are presented in Fig. 3. Two types of analyses were conducted. First, relative changes in HbO and HbR were averaged over 6–20 s for each channel separately and compared to 0 (Table 1). These intervals were chosen because the object seen to the right of the screen first began its appearance at 4 s and, allowing 2 s for the hemodynamic response to become initiated, changes in HbO and HbR should be detectable by 6 s. Second, a one-way ANOVA was conducted for each channel with event as the between-subjects factor. When significant results were obtained follow up comparisons (shape difference vs. control and color difference vs. control) were performed (Table 1). Both HbO and HbR responses are reported, but given that HbO is a more sensitive and reliable response measure than HbR (Strangman et al., 2003) we focus our discussion on HbO.

For ease in description, we will move posterior to anterior in our presentation of the results. A significant increase in HbO relative to baseline was obtained at channels 8 and 9 and at channels 4 and 5 in response to all events. In addition, responses did not differ significantly by event. A significant increase in HbO was observed in channels 2 and 3 in response to the shape difference event but not the color difference and control events. In channel 3, the HbO response to the shape difference (but not color difference) event differed significantly from that to the control event.

In summary, two main findings emerged. First, activation was obtained in the visual cortex and in posterior areas of the temporal cortex in response to all events, and the magnitude of the responses did not vary significantly by event. Second, activation was obtained in more anterior areas of the temporal cortex in response to the event that infants interpret as involving two objects (shape difference) but not in response to the events that infants interpret as involving a single object (color difference and control). These findings suggest hierarchical organization of object processing within the infant temporal cortex and are consistent with the interpretation that posterior areas (e.g., inferior temporal gyrus and/or LOC) respond to events involving moving objects, more generally, and anterior areas (e.g., middle and/or superior temporal gyrus) respond when featural differences signal the presence of numerically distinct objects.

Neural responses to spatiotemporal discontinuities: Experiment 2

Hemodynamic response curves for each channel and event are presented in Fig. 3. Optical imaging data were analyzed in a manner identical to that of Experiment 1 except that changes in HbO and HbR were averaged over 7–24 s for all channels (the first emergence of the object occurred by 5 s and an additional 2 s was allowed for initiation of the hemodynamic response). These data are presented in Table 1.

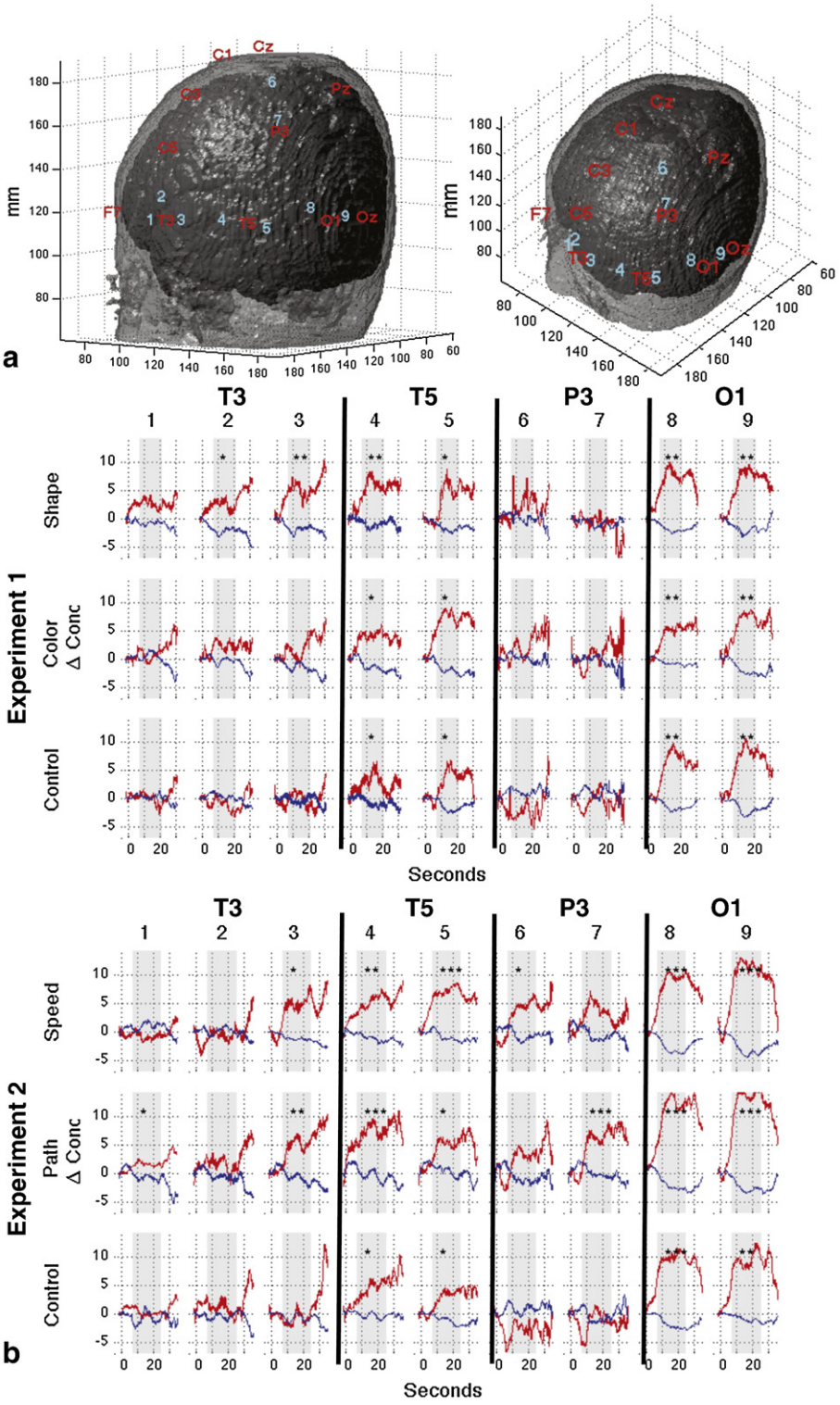

Fig. 3. Neuroimaging Data. (a) Relative skull location of each of the nine channels (blue numbers) in relation to the four 10–20 coordinates (red letters/numbers) are overlaid on a representative MRI of a 6-month-old infant. (b) Relative changes in HbO and HbR (red and blue lines respectively) during each test event at each of the nine channels are displayed for Experiment 1 and Experiment 2 separately. For each experiment and condition, $n = 18$. Time is on the x-axis and hemodynamic changes in μM cm on the y-axis. The bold lines separate channels associated with each of the four 10–20 coordinates. In Experiment 1, 1–20 s was the test event and 21–30 s was the silent pause (baseline). The hemodynamic response was averaged over 6–20 s, indicated by grey shading. In Experiment, 1–24 s was the test event and 25–34 s was the silent pause (baseline). The hemodynamic response was averaged over 7–24 s, again indicated by grey shading. Asterisks indicate M (SD) responses that differed significantly from baseline (*$p<.05$; **$p<.01$; and ***$p<.001$, two-tailed).

A significant increase in HbO relative to baseline was obtained at channels 8 and 9 in response to all events and responses did not vary significantly by event. A significant increase in HbO was also observed at channel 7 in response to the path-discontinuity event and at channel 6 in response to the speed-discontinuity event, and both of these responses differed significantly from control. We also obtained a significant increase in HbO at channels 4 and 5 in response to all events and the magnitude of the response did not differ

Table 1
Mean (SD) HbO and HbR responses during the test events. (a) and (b) Experiment 1, one sample *t*-tests comparing HbO and HbR responses (averaged over 6–20 s) to zero for each channel. One-way ANOVAs tested for differences between groups for each channel. Follow-up comparisons, using independent samples *t*-tests, were performed for those channels in which a significant effect was obtained. (c) and (d) Experiment 2, one sample *t*-tests comparing mean HbO and HbR responses (averaged over 7 s to 24 s) to zero. One-way ANOVAs tested for differences between groups. Follow-up comparisons, using independent samples *t*-tests, were performed for those channels in which a significant effect was obtained. In all cases $^{*}p<.05$; $^{**}p<.01$; $^{***}p<.001$, two-tailed.

Experiment 1 HBO		One sample *t*-tests *M* (*SD*)			One-way ANOVA (*df* = 51)
Neural region	Channel	Shape difference *n* = 18	Color difference *n* = 18	Control *n* = 18	Between subjects effects
T3	1	0.0025 (0.006)	**−0.00004 (0.004)**	−0.0002 (0.003)	*F* = 2.12
	2	0.0023 (0.004) *	0.0021 (0.009)	−0.0012 (0.006)	*F* = 1.53
	3	**0.0048 (0.006) ****	**0.0014 (0.007)**	−0.00001 (0.004)	***F* = 3.44 ***
					Shape vs. control *t* = 2.86**, *df* = 34
					Color vs. control *t* < 1, *df* = 34
T5	4	**0.0058 (0.007) ****	**0.0040 (0.007) ***	**0.0033 (0.006) ***	*F* < 1
	5	**0.0042 (0.007) ***	**0.0067 (0.010) ***	**0.0036 (0.006) ***	*F* < 1
P3	6	**0.0025 (0.007)**	0.0018 (0.010)	−0.0027 (0.007)	***F* = 2.22**
	7	−0.0006 (0.007)	**0.0006 (0.008)**	−0.0002 (0.007)	***F* < 1**
01	8	**0.007 (0.011) ****	**0.0046 (0.006) ****	**0.0068 (0.010) ****	*F* < 1
	9	**0.007 (0.011) ****	**0.0068 (0.009) ****	0.0077 (0.012) **	*F* < 1
Experiment 1 HBR		One sample *t*-tests *M* (*SD*)			One-way ANOVA (*df* = 51)
Neural region	Channel	Shape difference *n* = 18	Color difference *n* = 18	Control *n* = 18	Between subjects effects
T3	1	−0.0009 (0.002)	0.0004 (0.003)	0.0002 (0.002)	*F* = 1.5
	2	−0.0023 (0.002) ***	−0.0046 (0.002)	0.0002 (0.004)	*F* = 2.16
	3	−0.0020 (0.003) **	−0.0014 (0.003)	−0.0004 (0.006)	*F* < 1.5
T5	4	−0.0012 (0.003)	−0.0016 (0.003) *	−0.0010 (0.003)	*F* < 1
	5	−0.0019 (0.003) *	−0.0019 (0.003) *	−0.0018 (0.004) *	*F* < 1
P3	6	0.00002 (0.003)	0.0002 (0.004)	0.0009 (0.003)	*F* < 1
	7	−0.0009 (0.003)	−0.0001 (0.004)	0.0010 (0.005)	*F* < 1.5
O1	8	**−0.0020 (0.003) ***	**−0.0009 (0.003)**	**−0.0017 (0.002) ***	*F* < 1.5
	9	**−0.0021 (0.003) ***	**−0.0021 (0.005)**	−0.0022 (0.003) *	*F* < 1
Experiment 2 HBO		One sample *t*-tests *M* (*SD*)			One-way ANOVA (*df* = 51)
Neural region	Channel	Speed discontinuity *n* = 18	Path discontinuity *n* = 18	Control *n* = 18	Between subjects effects
T3	1	−0.0009 (0.002)	**0.0015 (0.003) ***	0.0001 (0.004)	*F* = 2.39
	2	−0.0006 (0.008)	0.0014 (0.005)	0.0006 (0.008)	*F* < 1
	3	**0.0049 (0.008) ***	**0.0047 (0.007) ****	−0.0010 (0.008)	***F* = 3.48 ***
					Speed vs. control *t* = 2.21*, *df* = 34
					Path vs. control *t* = 2.32*, *df* = 34
T5	4	**0.0052 (0.006) ****	**0.0072 (0.008) *****	**0.0044 (0.008) ***	*F* < 1
	5	**0.0071 (0.007) *****	**0.0050 (0.009) ***	**0.0031 (0.006) ***	*F* < 1.5
P3	6	**0.0043 (0.008) ***	0.0028 (0.009)	−0.0027 (0.009)	***F* = 3.25 ***
					Speed vs. control *t* = 2.48*, *df* = 34
					Path vs. control *t* = 1.83, *df* = 34
	7	0.0040 (0.010)	**0.0060 (0.006) *****	−0.0011 (0.009)	***F* = 3.35 ***
					Speed vs. control *t* = 1.67, *df* = 34
					Path vs. control *t* = 2.88**, *df* = 34
01	8	**0.0090 (0.009) *****	**0.0115 (0.011) *****	**0.0098 (0.009) *****	*F* < 1
	9	**0.0111 (0.010) *****	**0.0133 (0.013) *****	**0.0093 (0.011) ****	*F* < 1
Experiment 2 HBR		One sample *t*-tests *M* (*SD*)			One-way ANOVA (*df* = 51)
Neural region	Channel	Speed discontinuity *n* = 18	Path discontinuity *n* = 18	Control *n* = 18	Between subjects effects
T3	1	0.0009 (0.003)	−0.0009 (0.003)	−0.0010 (0.007)	*F* < 1
	2	−0.0001 (0.003)	−0.0008 (0.003)	−0.0006 (0.004)	*F* < 1
	3	−0.0014 (0.003)	−0.0010 (0.003)	−0.0010 (0.003)	*F* < 1
T5	4	−0.0012 (0.003)	−0.0006 (0.005)	−0.0006 (0.003)	*F* < 1
	5	−0.0010 (0.005)	0.0002 (0.004)	−0.0013 (0.003)	*F* < 1
P3	6	−0.0009 (0.004)	−0.0012 (0.004)	0.0007 (0.004)	*F* < 1.5
	7	−0.0010 (0.005)	−0.0002 (0.003)	−0.0009 (0.004)	*F* < 1
O1	8	**−0.0032 (0.004) ****	**−0.0023 (0.003) ***	**−0.0021 (0.003) ****	*F* < 1
	9	**−0.0035 (0.003) *****	**−0.0027 (0.004) ***	−0.0010 (0.003)	*F* = 2.59

significantly by condition. Finally, a significant increase in relative concentrations of HbO was observed at channel 3 in response to the speed- and path-discontinuity events and these responses different significantly from that obtained in the control condition.

To summarize, three main findings emerged. First, activation was obtained in the parietal cortex in response to spatiotemporal discontinuities. However, the two parietal detectors were differentially sensitive: greater activation was obtained at channel 7 in response to the path-discontinuity event, whereas greater activation was obtained at channel 6 in response to the speed-discontinuity event. Second, activation was obtained in the posterior area of the temporal cortex in response to all events, and the magnitude of the response did not differ by event. These data are consistent with those obtained in Experiment 1 and with other studies reporting activation to moving, complex objects in occipitotemporal regions in infants (Watanabe et al., 2008). Finally, activation was obtained in an anterior section of the temporal cortex in response to the events in which infants are known to individuate objects (speed- and path-discontinuity) but not in response to events that do not engage the individuation process (control).

General discussion

The results of these two experiments provide insight into the neural basis of object processing in the infant and reveal new information about the organization of the immature brain. First, a greater magnitude of neural activation was obtained in the anterior temporal cortex in response to shape than color differences, a finding consistent with behavioral data indicating that young infants are more likely to use shape than color information to individuate objects. In contrast, a greater magnitude of activation was obtained in the parietal cortex in response to objects that underwent spatiotemporal discontinuities than objects that moved smoothly, a finding consistent with evidence that parietal areas are sensitive to changes in the path or speed of moving objects in the adult. Furthermore, activation was observed in parietal cortex in response to spatiotemporal discontinuities but not to featural differences. Together, these findings suggest that the ventral and dorsal object processing systems of the infant brain, like that of the adult, are specialized for the analysis of the featural and spatiotemporal properties of objects, respectively. This is the first direct evidence for dissociation of object processing areas in the immature brain.

Second, cortical areas within the ventral stream evidenced distinct patterns of neural activation. Neural activation was obtained in visual cortex and posterior areas of the temporal cortex in response to all test events. However, a different pattern of results was obtained in anterior areas of the temporal cortex. Significant activation was obtained in response to events that infants interpret as involving two objects but not to events that infants interpret as involving one object. This pattern of activation was observed regardless of how the objects were individuated (e.g., on the basis of featural differences or spatiotemporal discontinuities). Two interpretations of these data are possible. One interpretation is that this temporal area mediates the individuation process and when this process is invoked and objects are individuated, neural activation is obtained. This interpretation is consistent with fMRI data in adults implicating areas in the temporal cortex as important for mediating higher level object processes, such as object identification and categorization (Devlin et al., 2002; Humphreys et al., 1999; Malach et al., 1995). The other possibility is that this temporal area is involved in the analysis of small sets of objects and the representation "two objects" evokes neural activation. Although most fMRI data implicate parietal areas as important for numerical processing in the adult brain (Dehaene, 2007), there is behavioral and electrophysiological evidence suggesting that small sets of objects (e.g., 2) and large sets of objects (e.g., 24) are processed differently, at least in infants (Feigenson et al., 2004; Hyde and Spelke, 2008). For example, small sets are represented as a group of distinct entities (object *x* and object *y*) rather than as a cardinal value (two objects). Perhaps the processing of small sets, which is intimately linked to the objects themselves, is mediated by temporal areas. Regardless of which explanation is supported by future research, this is the first evidence for differential processing within the ventral stream in the young infant, with posterior areas responding to events involving moving objects more generally and anterior areas responding to objects as numerically distinct individuals.

Finally, the results of the current experiments demonstrate how neural imaging can inform developmental theory. Developmental scientists have reported that there is sometimes a discrepancy between infants' capacity to perceive information and the extent to which they use this information to interpret physical events (Baillargeon et al., 2009; Wang and Baillargeon, 2008; Wilcox and Woods, 2009). Most relevant to the present discussion is that infants can detect shape and color differences by 4.5 months, but fail to use color differences to individuate objects until 11.5 months. The current results reveal a neural response consistent with behavioral findings and support the idea that infants can include information about objects at one level of analysis that they do not bring to bear when interpreting physical events involving those objects (Baillargeon et al., 2009; Wang and Baillargeon, 2008). Findings such as these are critical to the development of brain-behavior models of perceptual and cognitive development and allow us, for the first time, to specify the relation between neural activation and specific components of object processing in the human infant.

Acknowledgments

We thank Tracy Smith, Kayla Boone, Jennifer Norvell, and the staff of the Infant Cognition Lab at Texas A&M University for help with data collection and management, Lesley Wheeler for preparation of figures, and the infants and parents who so graciously participated in the research. This work was supported by NSF grants 0518986 and 0642996 to T.W., NIH grant 5R21HD048943 to T.W., and NIH grant P41-RR14075 to D.A.B.

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