CORTICAL ACTIVATION DURING SPATIOTEMPORAL PROCESSING IN THE INFANT BRAIN

A Thesis

by

JENNIFER RUTH ARMSTRONG

Submitted to the Office of Graduate Studies of Texas A&M University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2008

Major Subject: Psychology

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Approved by:

Chair of Committee, Teresa Wilcox Committee Members, Heather Bortfeld

Louis Tassinary

Head of Department, Les Morey

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ABSTRACT

Cortical Activation During Spatiotemporal Processing in the Infant Brain.

(December 2008)

Jennifer Ruth Armstrong, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Teresa Wilcox

Neuroscientists have uncovered much about the dorsal and ventral visual object processing pathways. However, little is understood about the functional development of these pathways in human infants. Behavioral data has shown that as early as 2.5 months, infants are sensitive to spatiotemporal information for object individuation in occlusion events. This study used Near Infrared Spectroscopy to assess neural activation (as evidenced by an increase in HbO₂) in four areas of the pathways: primary visual cortex (O1), posterior parietal cortex (P3), lateral occipital (T5), and inferior temporal (T3) in awake human infants aged 5.5 months while they view either a spatiotemporaldiscontinuity event or a control event. Three major predictions were made: 1) since the events contain visually distinct objects, there should be significant neural activation in O1 to both events, 2) if the dorsal route mediates the processing of spatiotemporal discontinuities, then there should also be a significant increase in P3 in response to the spatiotemporal-discontinuity event but not to the control event, and 3) activation present in T3 and T5 should not vary by condition if the ventral pathway is not responsible for the processing of spatiotemporal discontinuities. Results supported all three predictions.

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1. INTRODUCTION

Over the past few decades, researchers have uncovered much about object processing in infancy. Most of this research has relied on behavioral measures to assess infants' capacity to mentally represent objects (e.g., Baillargeon, 1986, 1987; Baillargeon & Graber, 1987; Baillargeon, Spelke, & Wasserman, 1985; Hood & Willatts, 1986). There is now evidence that as early as 2.5 months of age, out of sight does not mean out of mind; infants can represent objects that are not being directly experienced (e.g., Aguiar & Baillargeon, 1999, 2000, 2002; Baillargeon, 1991; Baillargeon & DeVos, 1991; Baillargeon et al. 1990; Goubet & Clifton, 1998; Hespos & Baillargeon, 2001a,b; Hespos & Rochat, 1997; Hofstadter & Reznick, 1996; Koechlin, Dehaene, & Mehler, 1998; Newcombe, Huttenlocher, & Learmonth, 1999; Rochat & Hespos, 1996; Simon, Hespos, & Rochat, 1995; Wilcox, 1999; Wilcox & Baillargeon, 1998b; Wilcox, Nadel, & Rosser, 1996; Wynn, 1992). Spelke and her colleagues (e.g., Spelke, 1990, 1996; Spelke et al., 1992) have theorized that infants possess, possibly at birth, a set of core principles that guide them through perceiving and reasoning about the world around them. Each principle obeys the basic laws of Newtonian physics. For example, physical objects move as cohesive wholes, on spatiotemporally continuous paths, and they cannot occupy the same space at the same time. These principles continue to be the solid foundation for which we perceive and reason about the world as mature adults.

This thesis follows the style of *Infancy*.

Several studies have also shown that mental representation is a complex cognitive ability that develops in a complex manner (see Baillargeon, 1994. 1995, 2004). For example, evidence exists that, when building representations of objects, infants are more sensitive to some types of information than others, and that the type of information to which they attend to can be situation specific (Needham, 1999; Needham, Baillargeon, & Kaufman, 1997; Tremoulet, Leslie, & Hall, 2001; Wilcox, 1999; Woods & Wilcox, 2006). However, little is understood about the neural mechanisms that underlie these cognitive capacities. Presently, near-infrared spectroscopy (NIRS), an optical imaging technique, is beginning to bridge the gap between the brain and cognitive development.

Behavioral Findings

The ability to represent the world in terms of numerically distinct objects (i.e. object individuation) is a complex cognitive capacity that emerges early in the first year of life. An extensive line of research conducted by Wilcox and her colleagues has assessed the types of information that infants will use to individuate objects using multiple behavioral paradigms including violation-of-expectation studies, reaching tasks, and eye tracking (Wilcox & Baillargeon, 1998b; Wilcox & Chapa, 2002; Wilcox & Schweinle, 2002; McCurry, Wilcox, & Woods, 2008; Woods et al., 2008). Behavioral findings have revealed that even very young infants are sensitive to motion and location (i.e., spatiotemporal) information for object individuation. For example, one set of studies (Wilcox & Schweinle, 2003; see also Schweinle & Wilcox, 2004) investigated infants' sensitivity to a discontinuity in speed of motion. Infants were presented with a

spatiotemporal-discontinuity event in which an object disappeared behind a wide screen and immediately emerged at the opposite end, too quickly to have traveled the entire length of the screen (Figure 1A). Infants as young as 3.5 months interpreted this event as involving two objects, one that disappeared behind one edge of the screen and a second identical object that appeared immediately at the opposite edge. This assumption was based on a combination of looking time data from 3 experiments each including experimental and control conditions. These findings provide support for the hypothesis that young infants are sensitive to at least one of Spelke's (1995) core principles: that objects will continue to move on a continuous path and speed of motion.

Young infants are also sensitive to spatiotemporal discontinuities in an object's path of motion. There are two lines of evidence that support this conclusion. First, in Spelke et al. (1995) infants viewed an event involving a discontinuity in path. In this event an object disappears at point A and then jumps out at point B without ever traveling the area in between. Four-month-old infants were surprised by this event suggesting that they could infer that there must be two separate yet identical objects present in order for the event to occur. Second, Wynn (1992) presented infants with a spatiotemporal-discontinuity event in which a Mickey Mouse doll stood on a stage and then disappeared behind a screen. Subsequently, infants viewed an experimenter placing another doll behind the screen. Infants were surprised when the screen was removed and revealed only one object. Wynn argues that there was not a continuous path to unite the first and second doll, and therefore infants derive the presence of two dolls and are surprised to see only one. They must use the spatiotemporal information of the dolls to

form a representation of two distinct dolls. In summary, there are a number of studies in object individuation research that signify that young infants possess an early sensitivity to spatiotemporal discontinuities.

Cortical Processing of Spatiotemporal Information

Where should one begin to search for the cortical areas that mediate the processing of spatiotemporal-discontinuities? Over the past two decades, scientists have been studying the neural basis of object processing with non-human primates. Behavioral and neuro-imaging studies reveal two main visual object processing routes: the "what" and the "where" (Livingstone & Hubel, 1987, 1988; De Yoe & Van Essen, 1988; Desimone & Ungerleider, 1989; Goodale & Milner, 1992; Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982; Van Essen, Anderson, & Felleman, 1992). The ventral system, i.e. the "what" pathway, projects from the primary visual cortex (V) to the inferior temporal cortex (IT). It is thought to process complex object features and aids in identifying objects. The dorsal system, i.e. the "where" pathway, projects from V to the posterior parietal cortex (PP). It is thought to be responsible for processing motion and location information. The functional and anatomical segregation of these two pathways has been upheld by recent studies utilizing more advanced imaging techniques (Dubowitz et al., 2001; Orban, Van Essen, & Vanduffel, 2004; Sereno & Tootell, 2005; Tanaka, 1997, 2000; Tootell, Tsao, & Vanduffel, 2003; Tsunoda et al., 2001; Wang, Tanifuji, & Tanaka, 1998; Van Essen et al., 2001; Wang, Tanaka, Tanifuji, 1996).

On the basis of adult functional neuro-imaging data (Haxby et al., 1991; Murray, Olshausen, & Woods, 2003; Paradis et al., 2000; Peuskens et al., 2004), we would expect to see neural activation in poster parietal and adjoining neural regions in response to events that require analysis of motion-carried information (i.e., spatiotemporaldiscontinuities). I will review a few of these studies below. First, Haxby et al. (1991) assessed neural activation with PET scans during both a face-matching task and a dot location matching task. The primary visual cortex and the superior parietal cortex were the only areas to become activated during the dot location matching task, and visual and temporal cortices were the only areas activated during the face-matching task. Secondly, Murray, Olshausen, & Woods (2003) assessed neural activation using fMRI while adult subjects viewed several events including stationary dots, dots with random motion, dots with motion that cued a rotating 3-D shape, known as shape-from-motion (SFM), and 2-D and 3-D line drawings. The parietal cortex displayed activation to two of these events: the 3-D SFM event and the 3-D line drawings. This suggests that the parietal cortex is responsible for processing complex motion-carried information (i.e. SFM) and the processing of 3-D spatial information. Finally, Peuskens et al., 2004 replicated and extended upon these findings. Using fMRI with healthy adults, they found that the processing of 3-D SFM information activated the parietal and occipito-temporal regions. Additionally, the processing of 3-D shape is linked to processing 3-D motion information in the parietal cortex, and the processing of surface texture is associated with the temporal-occipital area. These studies about 3-D SFM processing highlight the

importance of the parietal cortex as the area responsible for spatial and motion carried information.

With further examination and technological advances in neuro-imaging techniques, researchers have uncovered much about the nature and complexity of spatiotemporal representations in the human parietal cortex. The posterior parietal cortex, which includes both the superior and inferior parietal lobes, is thought to be important for spatial working memory. Colby & Goldberg (1999) discovered that spatial information is encoded in multiple frames of reference in the parietal cortex in reference to different coordinate systems (i.e., in relation to the eye or the hand). These representations are important for determining the salience of objects. Only if an object is highly salient will its spatial location information be encoded into spatial working memory in the parietal cortex. Additionally, PET scans with human adults have shown that tasks involving spatial working memory elicit significant changes in cerebral blood flow in both the superior and inferior parietal cortex (Courtney et al. 1996). Finally, in a meta-analysis of neuro-imaging studies utilizing fMRI and PET scans in adults between the years of 1993 and 2002, Wager & Smith (2003) found an expected dissociation of spatial and object working memory. The storage of spatial information most often activated the superior parietal cortex, whereas the storage of object information activated the inferior temporal cortex. In summary, researchers are in wide agreement that PP is of upmost importance for the processing of spatiotemporal information and that IT is most essential to the processing of object information.

Development of NIRS Technology

Now that non-invasive neuroimaging techniques like NIRS are available, researchers are able to investigate the functional development of the areas most important for the processing of spatiotemporal information. Scientists have been developing near-infrared spectroscopy (NIRS) technology for over three decades, and it is now becoming available to research and clinical communities. This technique uses near-infrared light to measure changes in cerebral blood flow. The basic assumption of this technique is that neural activation creates a metabolic demand for oxygenated blood. This results in a surge of oxygenated blood (HbO₂) and an overall increase in blood volume (HBT) to an activated area of the cortex. Changes in blood volume can be assessed by measuring relative concentrations of oxygenated hemoglobin [HbO₂] and deoxygenated hemoglobin [HbR]. Typically, [HbO₂] increases and [HbR] decreases during neural activation (Bartocci et al, 2000; Hoshi & Tamura, 1993; Jasdzewski et al., 2003; Obrig et al., 1996; Strangman, Franceschini, & Boas, 2003; Villringer & Dirnagl, 1995). Additionally, during cortical activation there will be an increase in total hemoglobin [HbT] indicating an overall increase in regional cerebral blood flow (rCBF).

Researchers have capitalized on the optical property of near-IR light to easily travel through tissue and bone. To demonstrate this property, hold your hand up to a white light bulb, and you will see only red light shining through. This is because near-IR light, as opposed to other wavelengths, is better able to travel through the tissue in your hand. Another optical property utilized in NIRS is the absorption spectrum of near-IR light to oxygenated and deoxygenated blood. For instance, HbR absorbs larger amounts

of lower wavelengths of light (approx. 690-750 nm) where as HbO₂ is more sensitive to the higher wavelengths (approx. 830-900 nm). Light emitters placed directly onto the scalp project two wavelengths, one high (830 nm) and one low (690 nm), of near-IR light simultaneously into the skull. Detectors adjacent to these emitters measure the relative amounts of light at each wavelength reflected back out. The Beer-Lambert law then converts changes in amounts of light to relative changes in [HbO₂] and [HbR]. The validity of this technique as an indicator of neural activation has been upheld by studies in the medical and clinical scientific arenas. It has been demonstrated that NIRS shows activation patterns similar to those obtained with fMRI or PET scans conducted simultaneously with NIRS (Kleinschmidt et al., 1996; Strangman et al., 2002; Villringer et al. 1997). Additionally, several studies have demonstrated that NIRS is non-invasive and sufficiently robust to use with awake and active human infants (Meek, 2002; Grinvald et al., 1991; Strangman, Boas, & Sutton, 2002; Villringer & Chance, 1997; Villringer & Dirnagl, 1995; Baird et al., 2002; Bortfeld, Wruck, & Boas, 2007; Pena et al., 2003; Taga et al., 2003; Wilcox et al., 2005, in press).

Previous NIRS Findings

Previous studies have examined neural activation in visual and inferior temporal cortex, the two major components of the ventral pathway, during processing of spatiotemporal and featural discontinuities. For example, in one experiment (Wilcox, Bortfeld, Armstrong, Woods, & Boas, 2008) infants aged 6.5 months were presented with two events: a spatiotemporal-discontinuity (Figure 1A) and a featural-difference (Figure 1B) event. The spatiotemporal-discontinuity event was identical to Wilcox &

Schweinle (2003) described above, in which a rectangular object disappeared behind one edge of a wide screen and then immediately reappeared at the other edge, too quickly to have traveled the length of the screen. In the featural-difference event, a ball and a box that differed on many dimensions emerged successively to opposite sides of a screen.

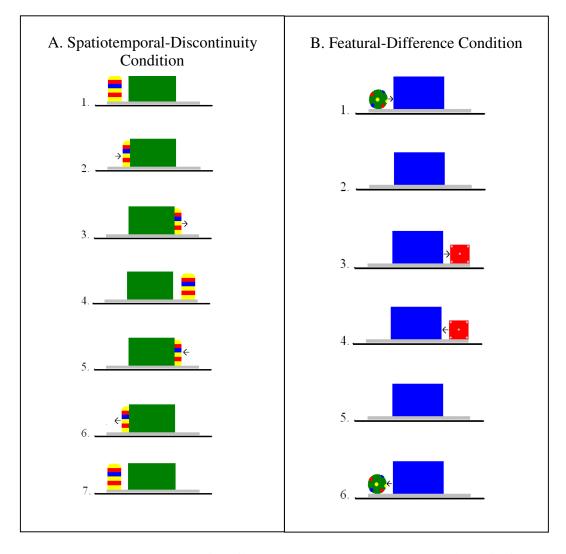


Figure 1. Test Events Seen in Wilcox et al. (2008). Spatiotemporal-Discontinuity Condition (A) and Featural-Difference Condition (B). Although not pictured, a hand moved the objects in both events.

Two predictions were made. If the visual cortex mediates the processing of visual events, regardless of whether the objects involved in the events differ in their featural properties or show spatiotemporal discontinuities, then increased activation should be observed in O1 in response to both events. That is, an increase in HbO2 and a decrease in HbR should be observed. Furthermore, the magnitude of the responses to the two events should not differ significantly. Second, if IT mediates the processing of the featural properties of objects, but not analysis of the spatiotemporal characteristics of objects, then a significant increase in neural activation should be observed in IT in response to the featural-difference but not the spatiotemporal-discontinuity event. Furthermore, the hemodynamic patterns observed in response to the two events should differ reliably from each other. The results supported all of these predictions. There was significant activation in V to both events and there was significant activation in IT only in response to the multi-feature change event. From this, we can conclude that at 6.5 months IT is responsible for processing multiple object features but not spatiotemporal information about objects.

Current Research Goals

The current research seeks to replicate and extend upon these previous findings by investigating the patterns of neural activation in response to spatiotemporal discontinuities in four neural areas, including O1, P3, T3, and T5. The spatiotemporal-discontinuity included in this study was a discontinuity in speed similar to the conditions of Wilcox and Schweinle (2003), and Wilcox et al. (2008). In this event, an object identical to previous studies (a column made of yellow, blue, and red duplo® bricks)

disappeared behind a wide screen, and an identical object appeared immediately on the opposite end of the screen, too quickly to have traversed the entire length of the screen. In a control event, using the same objects, the object disappeared behind a smaller screen and an identical object appeared at the other end of the screen, after a sufficient occlusion period that matches the speed at which the object is traveling. These events were designed to be as similar as possible and to differ solely on the basis of spatiotemporal information. For example, the objects in each event possess the same trajectory, but they differ in the speed of that trajectory. Additionally, the larger screen in the spatiotemporal-discontinuity event intensifies the amount of space that must be traveled by the more slowly moving object that appears immediately on the other end. Pilot studies suggested that viewing one event can influence infants' response to the other event. Therefore, a between subjects design was used in which infants view either the spatiotemporal-discontinuity event or the control event.

Predictions

Based on the NIRS results reported above and on current literature on the neural basis of the processing of spatiotemporal information, the following predictions are made: 1) there should be activation in V (O1) to both events since they involve visually distinct objects, 2) there is will be significant activation in PP (P3) to the spatiotemporal-discontinuity event but not to the control event, 3) patterns of activation in both lateral occipital (T5) and in inferior temporal (T3) should not vary across conditions since the objects did not vary on any featural dimension. In order to test these predictions, we will place the lasers and detectors on the visual cortex at O1, posterior parietal at P3, lateral

occipital (LOC) at T5, and inferior temporal at T3. This array of lasers and detectors is different from those of previous studies because it includes not only areas of the ventral pathway, but of the dorsal and ventral pathways simultaneously.

2. METHOD

Participants

Participants were 31 infants (14 boys and 17 girls) who were 5.5 months old (M = 5 months, 24 days; range = 4 months, 22 days-6 months, 17 days). Infants were randomly assigned to either the spatiotemporal-discontinuity event (8 boys and 8 girls; M = 5 months, 24 days) or the control event (6 boys and 9 girls; M = 5 months, 24 days). Infants were all healthy and born full-term. An additional 22 infants were eliminated from the analyses: 5 due to looking times lower than 20s on all of the trials, 14 due to either motion artifacts or noise in the signal, 1 due to hair preventing the acquisition of a good signal, and 2 due to movement of the headband during trials.

Apparatus and Stimuli

The apparatus and stimuli were similar to those in Wilcox et al. (2008). The apparatus consists of a wooden cubicle 213 cm high, 105 cm wide and 43.5 cm deep. The infant sat on a parent's lap or in a seat facing an opening 51 cm high and 93 cm wide in the front wall of the apparatus; the infant's head was approximately 78 cm from the objects on the platform (see Figure 2 for a schematic of Experimental Set-Up). The floor and walls of the apparatus were cream or covered with lightly-patterned contact paper. A cream-colored platform 1.5 cm high, 91 cm wide, and 19 cm deep laid 4.5 cm from the back wall and be centered between the left and right walls. To allow for smooth and quiet movement of the objects, a strip of light blue felt laid lengthwise down the center of the platform. A slit in the back wall enabled the experimenter to reach into the

apparatus and move the objects during the test events. The slit was 6.5 cm high, 52.5 cm long and was located 10 cm above the apparatus floor; cream-color fringe helped conceal the slit.

Experimental Set-up

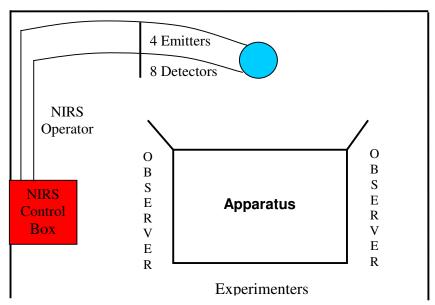


Figure 2. Experimental Set-up. The infant sat in his or her parent's lap facing the front opening of the apparatus and viewed the test event as it was presented on the apparatus stage. Observers sat behind tall muslin-covered wood frames and recorded infants' looking behavior. Another tall muslin-covered frame separated the NIRS operator and the NIRS control box from the infant.

Two rectangular-shaped objects were used to produce the spatiotemporal-discontinuity event. The objects were made of alternating rows of red, yellow, and blue duplo® bricks and were 12 cm high, 6 cm wide, and 3 cm deep. The occluding screen used in the spatiotemporal-discontinuity event was 24 cm high and 35 cm wide, made of dark blue matboard, and held upright by the wooden base. The same rectangular-shaped

objects were used in the control event. The occluding screen was 21.5 cm high and 30 cm wide, made of dark blue cardboard, and was held upright by a wooden base.

At the beginning of each test session, a muslin-covered shade covered the front opening of the apparatus, concealing the apparatus stage. At the beginning of each test trial, the shade was raised and the test event appropriate for that trial was presented. At the end of each trial, the shade was lowered and remained lowered for 10 s, which constituted baseline. Two muslin-covered wooden frames, each 213 cm high and 68 cm wide, stood at an angle on either side of the apparatus (Figure 2). These frames isolated the infant from the experimental room. Observers watched the infant through dime-sized holes that were covered with gauze. Another muslin-covered wood frame separated the infant from the experimental room. To illuminate the stage, a 20-watt fluorescent bulb was affixed inside each wall of the apparatus. No other lighting was used.

Test Events

Three experimenters worked together to produce the spatiotemporal-discontinuity test event. The first two each wore a black elbow-length glove on their right hands and moved the objects. The third raised and lowered the shade that covered the front opening of the apparatus. Two experimenters worked together to produce the control test event. The first wore a black elbow-length glove on her right hand and moved the objects. The second experimenter operated the screen. The numbers in parentheses (see below) indicate the time taken to produce the actions described for each event. A metronome attached to the back of the apparatus blinked once per second to help the experimenters adhere to the events' scripts (because we do not want to have an

auditory component, the metronome was set to blink, rather than to tick, once per second). Prior to the first block of test trials (spatiotemporal-discontinuity or control) the experimenter showed her gloved-hand to the infant.

Spatiotemporal-Discontinuity Event. Prior to the start of each test trial, the first experimenter held a column at the left edge of the platform (IPOV) gently tilting it to the left and right as the shade was raised. The blue occluding screen stood upright at the center of the platform and the second experimenter held the second column in her right hand behind the right half of the screen (out of the infant's view). When the shade was fully raised, the first experimenter held the column upright (1 s), and then moved it to the right along the platform at a rate of 3 cm per s until it was fully occluded by the screen (2.5 s). Immediately after the first column became fully occluded, the second experimenter moved the second column from behind the right edge of the screen (the two experimenters had similar sized hands covered by identical black gloves) until its center was 6 cm from the right edge of the screen (2.5 s). This 6 s sequence was then reversed. Finally, the entire event was repeated to conclude the 24 s trial. When visible, the object moved at a rate of 3 cm pers. In order to create an immediate-reappearance event that was perceptually surprising, it was necessary to move the visible objects at a slower rate in the spatiotemporal-discontinuity than control event (see Wilcox & Schweinle, 2003 for supporting data obtained with adults).

Control Event. Prior to the start of each test trial, the first experimenter held the column 15.5 cm from the left edge of the platform (infant point of view), and gently tilted it to the left and to the right (one tilt per s) to gain the infant's attention as the

shade was raised. The blue occluding screen stood upright at the center of the platform. Another identical column was hidden behind the right side of the screen. When the shade was fully raised, the first experimenter stopped tilting the column and moved it to the left along the platform until it became fully occluded behind the left edge of the screen (2.5 s). After an interval appropriate for the column's rate of motion (during which time the first experimenter released the first column and grasped the second one), the second column emerged from behind the right edge of the screen and was moved by the experimenter until it was 15.5 cm from the right edge of the platform (2.5 s). The ball paused (1 s) and then this sequence was reversed. The entire 12 s column-column cycle then repeated to conclude the 24 s trial. When in motion the objects moved at a rate of 12 cm/s and the occlusion interval is 1.8 s.

Procedure

The amount of time infants spent looking during each test trial was recorded and looking time data was time-locked to the NIRS data. Looking behavior was monitored by two observers who watched the infant through peepholes in the muslin-covered frames on either side of the apparatus. Each observer held a button that was connected to a DELL computer. When the infant attended to the event, the observer pressed the button, and when the infant stopped attending, depressed the button. Each trial was divided into 100-ms intervals, and the computer determined in each interval whether the two observers agreed on the direction of the infants' gaze. Inter-observer agreement is measured for all testing sessions in which two observers are present. It is calculated for each test trial on the basis of the number of intervals in which the computer registered

agreement out of the total number of intervals in the trial. Infants are presented with four test trials of one event.

Each test trial was 24 s in duration. Because analysis of the NIRS data required baseline recordings of the measured intensity of refracted light, prior to each trial infants were also be presented with a 10 s silent pause during which time no event was presented (the shade of the apparatus was down, occluding the apparatus stage). A final 10 s silent pause followed the last trial. Because failure to visually attend to the event could result in a decrease in hemodynamic response, the looking time data were inspected for trials in which the infant accumulates less than a 20 s looking time.

Instrumentation

The imaging equipment contained three major components: (1) four fiber optic cables that delivered near-infrared light to the scalp of the participant (i.e., sources); (2) eight fiber optic cables that detected the diffusely reflected light at the scalp (i.e., detectors); and (3) an electronic control box that served both as the source of the near-infrared light and the receiver of the reflected light.

The electronic control box produced light at 690 and 830 nm wavelengths with four laser-emitting diodes (Boas et al., 2002. TechEn Inc.). Laser power emitted from the end of the diode was approximately 4 mW. Light was square wave modulated at audio frequencies of approximately 4 to 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 does not interfere with the laser signals because environmental light sources modulate at a different frequency.

The four fiber optic cables that delivered the light from the control box to the headgear (described below) were 1 mm in diameter and 9 m in length. The eight fiber optic cables that detected the diffusely reflected light at the scalp and transmited it to the control box were also 1 mm in diameter and 9 m in length. Each emitter delivered both wavelengths of light (690 and 830 nm) and each detector responded to both wavelengths. The signals received by the electronic control box were processed and relayed to a DELL desktop computer with an Intel Pentium 4 processor. A custom computer program recorded and analyzed the signal. Additional details about the NIRS equipment can be found in Franceschini et al. (2006) and Joseph et al. (2006), who used a similar instrument except with a larger number of emitters and detectors.

Prior to presentation of the test events, infants were fitted with a custom-made headgear that secures the fiber optics to the scalp. The four sources were placed directly above areas O1, P3, T5, and T3 (S1, S2, S3, and S4 respectively, see Figure 3) as determined by the International 10-20 system for electrophysiological recording. Each source was surrounded by two or three detectors and embedded in non-elastic rubberized material. Detectors were positioned equidistant from the emitters with an emitter-detector distance of 2 cm. The plastic material was then attached to an elasticized terry cloth headband. Two detectors (D1 and D2) were placed to the right and left of O1. Two detectors (D4 and D3) laid above and below P3 on a vertical plane. Detectors (D5 and D6) were placed to the right and left of T5. Detectors (D6, D7, and D8) lay posterior, anterior, and above T3 respectively. D6 was able to detect and discriminate light from

both sources (S3 and S4) due to the different frequency modulation of the light from each source.

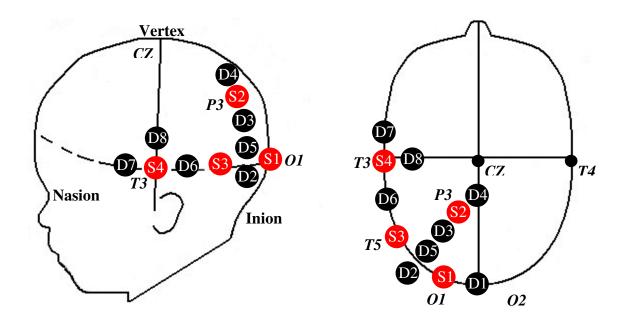


Figure 3. Probe Placement of Light Sources and Detectors. Locations of the four light sources (S1-S4) are denoted in the red circles, and the eight detectors (D1-D8) are denoted in the black circles. Placement of the sources was made relative to the International 10-20 system for electrophysiological recording. Inter-detector distance was 4 cm.

Processing of NIRS Data

The NIRS data was 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 filtered at 0 to 10.0 Hz, a principal components analysis was used to design a filter for systemic physiology and motion artifacts, and the

data was converted to relative concentrations of oxygenated (HbO₂) and deoxygenated (HbR) blood using the modified Beer-Lambert law (Strangman et al., 2002). Changes in HbO₂ and HbR were examined using 35 s time epochs: the 1 s immediately prior to the onset of the test event, the 24 s test event, and the 10 s following the test event. The optical signal obtained at -1 to 0 was set to 0 (this is referred to as baseline) and all other segments of the 35 s time epoch are interpreted relative to baseline. Optical signals were averaged across the 4 test trials for each participant and then across participants for each condition. Trials objectively categorized as containing motion artifacts (a change in the filtered intensity greater than 5% in 1/20 s during the 1 s baseline and 24 s test event) were eliminated from the mean.

3. RESULTS

Looking Time Data

Infants who looked 20s on at least one of the trials were included in analyses. This threshold was administered to ensure that only those infants who were visually attending to the test events were included in the analysis of the NIRS data. Of the infants who met this criteria, the looking times were similar for both the spatiotemporal-discontinuity (M = 22.6) and control conditions (M = 22.6). Inter-observer reliability was .96, and the number of trials that each infant contributed was M = 3.03 trials; St. Dev. = .91.

NIRS Data

The hemoglobin concentration response curves (Figure 4) include the relative changes in HbT, HbO₂, and HbR. Since we do not have precise estimates of path length, the values will be presented in terms of mM x length in cm (mM x cm), an approach used by other researchers (e.g., Taga et al., 2003). In both conditions, relative changes in [HbO₂] and [HbR] from 6 to 24 s following initiation of the event are compared to baseline. This time period was chosen because (a) the first emergence of the second column occurs at approximately 4 s and, allowing 2 s for the hemodynamic response to become initiated, changes in [HbO₂] and [HbR] should be detectable by 6 s and (b) the hemodynamic response should continue as the event repeats during the 24 s trial.

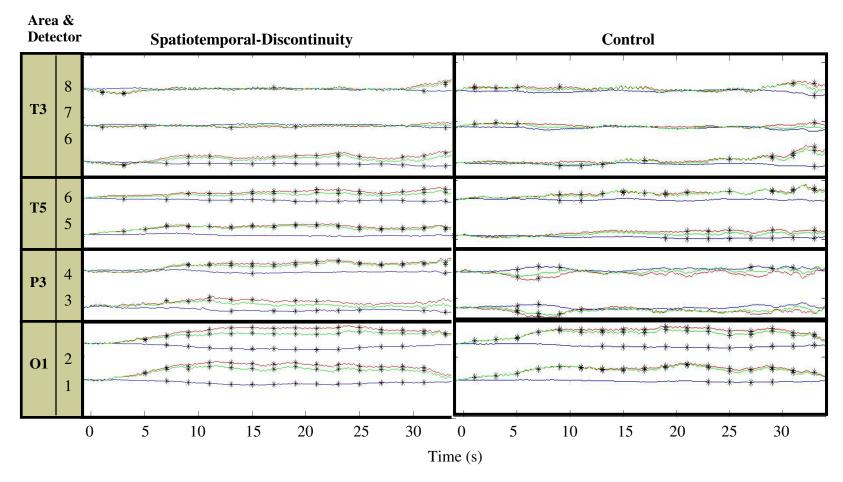


Figure 4. Hemoglobin Response Curves for the Spatiotemporal-Discontinuity and the Control Conditions. Y-axis is in optical density units, averaged across participants and trials for the detectors that surround primary visual (O1), posterior parietal (P3), lateral occipital (T5), and inferior temporal (T3). The timing of the event was as follows: baseline -1 to 0 s, test event 0 to 24 s, and post-stimulus (silent pause) 25 to 35 s. HbO₂, HbR, and HbT are indicated by the red, blue, and green lines respectively. The asterisks indicate points along the response curves that differed significantly from 0 (baseline).

Two sets of analyses were conducted. First, mean hemodynamic responses for each condition and detector were compared to zero (HbO₂ displayed in Table 1; HbR displayed in Table 2). As predicted, in the primary visual cortex (O1), a significant increase in HbO₂ was observed in response to both events at both D1 and D2. In the posterior parietal cortex (P3), a significant increase in HbO₂ was observed in response to the spatiotemporal-discontinuity event, but not the control event, at both D3 and D4. For the spatiotemporal-discontinuity condition, there was a significant increase in HbO₂ in LOC (T5) at both D5 and D6 and in inferior temporal (T3), however, only at D6, which is the most posterior detector. For the control condition, there was not a significant increase in HbO₂ in the either LOC (T5) or the inferior temporal cortex (T3).

In the second set of analyses, independent samples t-tests were conducted for each detector with condition (spatiotemporal-discontinuity vs. control) as the between-subjects factor. The purpose of this set of analyses was to test the extent to which the responses observed at each detector varied by the event seen. The outcome of this set of analyses are also displayed in Table 1 (HbO₂) and Table 2 (HbR). Two major results were obtained. 1) The only significant differences between conditions in the HbO₂ response occurred in the posterior parietal cortex (P3) at both D3 and D4. That is, in the parietal cortex, the HbO₂ response to the spatiotemporal-discontinuity event was significantly greater than the response to the control event. 2) As predicted, the HbO₂ responses in visual (O1), LOC (T5), and inferior temporal (T3) did not differ significantly by condition.

Table 1. Relative Change in [HbO₂] and Independent T-tests. Cells contain mean (standard deviation) relative optical density units in mM x cm averaged from 6 to 24 s for all detectors. Mean responses were compared to zero using t-tests. In the final column, the outcome of the independent t-tests comparing responses across condition are reported. Asterisks indicate those responses that reached two-tailed statistical significance.

HbO ₂		Condition		independent t-tests
Neural Region	Detector	Spatiotemporal- Discontinuity M (SD)	Control M (SD)	* P < .05 ** P < .025 *** P < .01
O1	D1	.0126 (.009) *** t = 5.16, df = 14	.0103 (.010) ** t = 3.85, df = 14	t = .65 df = 28
	D2	.0116 (.009) *** t = 4.72, df = 11	.0121 (.008) *** t = 5.53, df = 12	t =16, df = 23
Р3	D3	0.0053 (0.009) * t = 2.29, df = 14	0024 (.008) t = -1.09, df = 14	t = 2.41, $df = 28 **$
	D4	. 0060 (.008) ** t = 2.85, df = 14	0014 (.008) t =65, df = 13	t = 2.43, df = 27 **
	D5	.0069 (.007) *** t = 4.21, df = 15	.0026 (.006) t = 1.68, df = 14	t = 1.94, df = 29
T5	D6	.0047 (.006) ** t = 2.99, df = 15	.0042 (.008) t = 1.96, df = 13	t = .20, df = 28
	D6	.0044 (.008) * t = 2.22, df = 15	.0014 (.007) t = .73, df = 14	t = 1.11, df = 29
Т3	D7	0010 (.002) t = -1.67, df = 15	.0008 (.005) t = .69, df = 14	t = -1.37, df = 29
	D8	0.003 (0.008) t = 0.16, df = 15	.0013 (.007) t = .77, df = 14	t =38, df = 29

Table 2. Relative Change in [HbR] and Independent T-tests. Cells contain mean (standard deviation) relative optical density units in mM x cm averaged from 6 to 24 s for all detectors. Mean responses were compared to zero using t-tests. In the final column, the outcome of the independent t-tests comparing responses across condition are reported. Asterisks indicate those responses that reached two-tailed statistical significance.

HBR		Condition		independent t-tests
Neural Region	Detector	Spatiotemporal- Discontinuity M (SD)	Control M (SD)	* P < .05 ** P < .025 *** P < .01
O1	D1	0033 (.003) ** t = -3.88, df = 14	0008 (.003) t = -1.12, df = 14	t = -2.33, df = 28 *
	D2	t = -4.00, df = 11	0023 (.003) ** t = -2.58, df = 12	t = -1.32, df = 23
Р3	D3	0028 (.006) t = -1.85, df = 14	0006 (.003) t =64, df = 14	t = -1.27, df = 28
	D4	0010 (.004) t =89, df = 14	.0015 (.004) t = 1.31, df = 13	t = -1.56, df = 27
Т5	D5	0005 (.004) t =51, df = 15	0017 (.003) * t = -2.12, df = 14	t = .87, df = 29
	D6	t = -3.04, df = 15	0006 (.002) ** t = -1.08, df = 13	t = -1.47, df = 28
Т3	D6	0016 (.002) ** t = -2.59, df = 15	0011 (.003) * t = -1.34, df = 14	t =55, df = 29
	D7	.0004 (.003) t = .53, df = 15	0011 (.006) t =68, df = 14	t = .86, df = 29
	D8	.0001 (.003) t = .18, df = 15	0006 (.004) t =50, df = 14	t = .53, df = 29

The outcome of the relative change HbR (Table 2) was similar in many ways to the HbO₂ response. In response to the spatiotemporal-discontinuity event, a significant decrease in HbR was obtained in the visual cortex (O1) at both D1 and D2. This decrease also occurred in response to the control condition. However, it was only significant at D2. In the parietal cortex, there was not a significant decrease in HbR in response to either condition. In response to the spatiotemporal-discontinuity event, there was a significant decrease in HbR in LOC (T5) at D5 and D6 and in inferior temporal (T3) at D6, which is the most posterior detector. In response to the control event, there was a significant decrease HbR in LOC (T5) at D5 and D6 and in inferior temporal (T3) at D6. As with the HbO₂ response, the HbR responses obtained in LOC and in the inferior temporal cortex did not vary by condition. However, in the visual cortex, D1 varied significantly by condition due to the lack of a significant HbR response to the control condition. Additionally, the HbR response did not vary by condition in the parietal cortex.

4. DISCUSSION

Developmental psychologists have relied on behavioral measures to assess the nature and development of object representations in the first year of life. In addition, neuroscientists have identified many of the sophisticated object processing pathways in adults and non-human primates. However, due to a lack of available techniques, little is understood about the functional development of these pathways in the human infant. With the onset of the availability of techniques like NIRS, researchers are beginning to bridge the gap between the brain and cognitive development. The current study seeks to replicate and extend upon the findings in Wilcox et al. (2005, 2008) in which featural but not spatiotemporal information was mediated by areas in the ventral pathway at 6.5 months. By examining activation simultaneously in the dorsal and ventral pathways to spatiotemporal-discontinuities and to control events this study has 1) replicated that spatiotemporal information is not mediated by areas in the ventral pathway at 5.5 months and 2) determined that areas in the dorsal pathway mediate the processing of the spatiotemporal information in the discontinuity event but not in the control event. Together, these results suggest that the dorsal pathway, but not the ventral pathway, mediates the processing spatiotemporal information at 5.5 months. These findings not only have implications for how to replicate and extend upon decades of behavioral findings, but they will also provide converging evidence that NIRS is indeed a reliable source for examining neural activation in the developing brain. The remainder of this

section will further discuss these findings and what implications they have for understanding the functional development of object processing in infants.

Patterns of Activation in the Visual Cortex

A robust response was seen in O1, as evidenced by a significant increase in HbO₂ and a significant decrease in HbR, in both conditions. The increase in HbO₂ in the visual cortex in response to an event with visual objects has been consistent across several experiments (e.g. Bortfeld, Wruck, & Boas, 2007, Wilcox et al., 2005, 2008). In most studies, the visual cortex renders a robust response to visual stimuli. However, one unpredicted result was found in O1 with the HbR response to the control condition. Although there was a decrease in HbR at D1, it was not significantly different from zero, and it was significantly different from the HbR response to the spatiotemporal-discontinuity condition at D1. There are two possible explanations for this result: 1) the HbR response at D1 is less robust than the HbO₂ response, and since there is a surge in HbO₂ and HbT the HbR response is simply flushed out or 2) infants in the control condition rendered more variable data.

Patterns of Activation in the Posterior Parietal Cortex

The HbO₂ results obtained from both D3 and D4 in the parietal cortex strongly supported the predictions. In the spatiotemporal-discontinuity event, there was a significant increase in HbO₂ at both D3 and D4. In the control condition, there was not a significant change in HbO₂ for either D3 or D4. Finally, the HbO₂ response at both D3 and D4 to the spatiotemporal-discontinuity event was significantly different from the response in D3 and D4 to the control condition. These results provide evidence that the

posterior parietal cortex is responsible for processing complex spatiotemporal information (i.e. spatiotemporal discontinuities like objects jumping through space and time). Additionally, since there was no activation in P3 in response to the control condition, it can be assumed that this area does not process motion information, more generally, but rather discontinuities in motion-carried information. The HbR response to both conditions was not significantly different from zero in the parietal cortex nor was it significantly different between conditions.

Patterns of Activation in the Lateral Occipital Cortex

As predicted, the hemodynamic responses observed in both LOC (T5) and in the inferior temporal cortex (T3) did not vary by condition for either HbO₂ or HbR. This suggests that any activation occurring in the inferior temporal cortex or LOC is not due to the different spatiotemporal properties of the two events. Some significant activation was observed in LOC to both conditions. In particular, in response to the spatiotemporal discontinuity condition, D5 and D6 displayed a significant increase in HbO₂ and also a decrease in HbR, but this was significant only at D6. For the control condition, both D5 and D6 displayed an increase in HbO₂, but it was only significant at D6. Additionally, both detectors displayed a significant decrease in HbR to the control condition. Overall, then, the infants in both conditions demonstrated hemodynamic changes at T5 in response to the occlusion event. These data suggest that LOC responds to moving, occluded objects. What remains open to speculation is whether the properties of the objects involved in the event influences the hemodynamic response. For example, the object used in the present study was relatively complex in its featural composition (a

striped column). Hence, some analysis would be required to determine if the object seen to the left of the occluder was featurally identical to that seen to the right of the occluder. Perhaps when the objects are complex in their featural properties, requiring detailed featural analysis, LOC is more likely to be activated than when the objects are simple in their featural properties (e.g., a solid green ball). Further research will be needed to explore the extent to which the response at LOC depends on the complexity of the objects.

Patterns of Activation in the Inferior Temporal Cortex

In the spatiotemporal-discontinuity condition, activation was observed at D6 (the most posterior detector) as evidenced by an increase in HbO₂ and a decrease in HbR. No significant activation was seen in either D7 or D8. In the control condition, a significant decrease in HbR was obtained at D6, but no other significant results were obtained. How do we interpret the response obtained at D6? On the one hand, the infants in the spatiotemporal-discontinuity but not the control condition evidence a significant increase in HbO₂, in response to the occlusion event, suggesting that only the former group demonstrated neural activation. At the same time, the two groups did not differ statistically in their response to the event, making it difficult to draw conclusions about group differences. One possible explanation is that the neural area underlying S4-D6 plays a similar role in object processing as the area underlying S3-D6. Hence, both groups demonstrated at least some evidence of neural activation (a significant increase in HbO2 and/or a decrease in HbR). Another possibility is that this detector, which reads the signals from both S3 and S4, although frequency modulated, could be confusing the

signals. Activation in this area requires further examination utilizing alternate instrumentation (from which this detector would only be reading from one light source). Finally, no activation was observed at D7 and D8 in either condition, suggesting that these more anterior temporal areas (IT) are not involved in the processing of spatiotemporal discontinuities.

The Relationship Between HbO₂ and HbR

The relationship between the chromophores and between neighboring rCBF is not clearly defined. HbO₂ proved to be a more robust indicator of neural activation compared to HbR which replicates the findings of several other researchers (Chen et al., 2002; Hoshi &Tamura, 1993; Jasdzewski et al., 2003; Kato, Kamei, Takashima, & Ozaki, 1993; Sakatani et al., 1999; Strangman et al., 2002; Strangman, Franceschini, & Boas, 2003; Wilcox et al., 2008). Typically, in the event of neural activation and an increase in rCBF, an increase in HbO and a decrease in HbR are observed. However, the inconsistency of the HbR response could be the result of the maturing brain on the infant and blood regulation systems. Perhaps, in response to metabolic demands, infants overcompensate with higher levels of oxygenated blood than are necessary, and as a result the decrease in HbR is less detectable. This hypothesis would be consistent with neuroanatomical and metabolic data (Chugani & Phelps, 1986; Chugani, Phelps, & Massiotta, 1987; Franceschini et al., 2007; Purpura, 1975a,b).

Summary and Conclusions

The outcome of the present study demonstrates, using a non-invasive neuroimaging technique, that there are region specific differences in visual object

processing and that NIRS is sufficiently sensitive to detect these differences. It also suggests that the object processing system in the infant is organized, at least in some respects, in a way similar to that of the adult. This study extended upon previous studies to show the functional segregation of the two object processing pathways simultaneously. Results indicate that by 5.5 months, the dorsal but not the ventral route mediates the analysis of spatiotemporal information that is important for object individuation. Given the importance of object individuation and identification to human cognition, it is not surprising to find specialized object processing pathways in the infant.

The present study also builds upon a foundation for future investigation of the neural basis of object processing in infants. This study successfully assessed neural activation during an event involving a spatiotemporal-discontinuity event. Future studies could assess neural activation during a discontinuity in path to assess neural responses to other spatiotemporal discontinuities. Future studies also could assess responses to a spatiotemporal-discontinuity versus a featural-difference event, to show that the ventral route, alone, would mediate the analysis of featural-differences in occlusion events while the dorsal route mediates only the processing of spatiotemporal information.

The development of NIRS technology for use in the experimental setting offers developmental scientists, for the first time, a method by which to explore the functional development of the cortex in human infants. The ability to study functional brain activation in awake, processing infants represents a significant advancement in the field of developmental neuroscience and as investigators become more sophisticated in their ability to use this technique, we expect to see a growing body of neuroimaging results.

These results will have the potential to bridge the fields of cognitive, developmental, and neural science and inform theories which take into account brain-behavior relations.

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