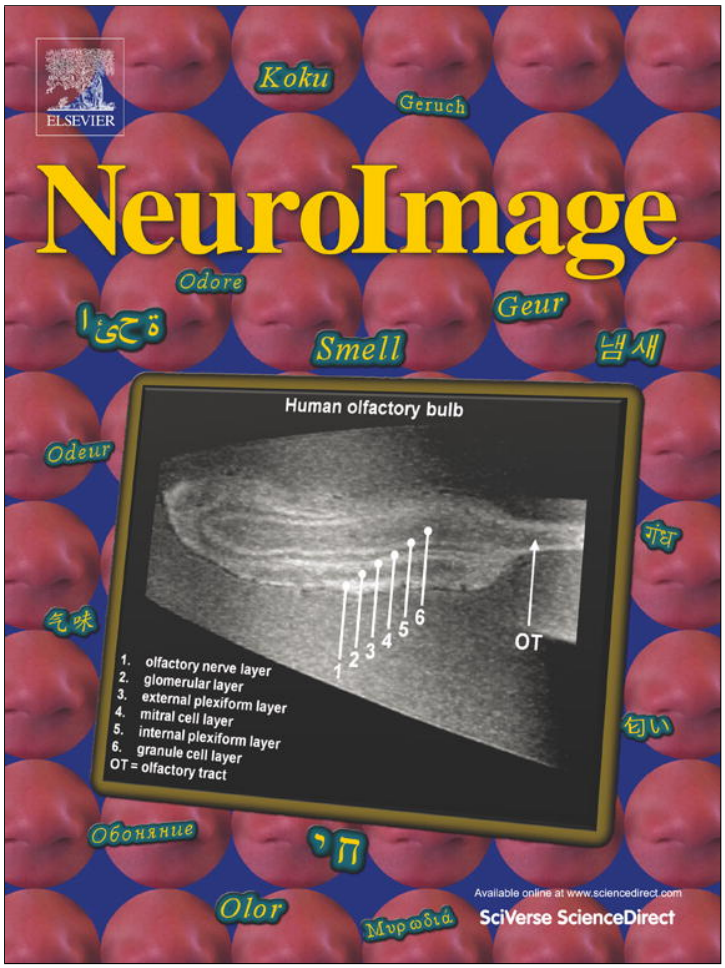

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Functional activation of the infant cortex during object processing

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ABSTRACT

A great deal is known about the functional organization of the neural structures that mediate visual object processing in the adult observer. These findings have contributed significantly to our conceptual models of object recognition and identification and provided unique insight into the nature of object representations extracted from visual input. In contrast, little is known about the neural basis of object processing in the infant. The current research used near-infrared spectroscopy (NIRS) as a neuroimaging tool to investigate functional activation of the infant cortex during an object processing task that has been used extensively with infants. The neuroimaging data revealed that the infant cortex is functionally specialized for object processing (i.e., individuation-by-feature) early in the first year but that patterns of activation also change between 3 and 12 months. These changes may reflect functional reorganization of the immature cortex or age-related differences in the cognitive processes engaged during the task.

Introduction

The ability to track the identity of objects as they move through time and space is a fundamental capacity that underlies most of human cognition. We engage in object recognition and identification in our everyday experiences with apparently little effort, which belies the complex set of perceptual and cognitive processes that are involved. A great deal has been learned about these processes through the use of behavioral methods (Biederman, 1987; Riesenhuber and Poggio, 2000). With the advent of human neuroimaging techniques, scientists have had the opportunity to investigate functional organization of the neural pathways that mediate object processing in the adult (Grill-Spector, 2003; Kanwisher, 2003). This approach has provided unique insight into the nature of object representations extracted from visual input and the conditions under which these representations are formed.

Brain imaging studies conducted with adults have revealed ventral and dorsal object processing systems similar to those first identified in the non-human primate (Ungerleider and Mishkin, 1982). For example, areas in the primary visual cortex respond to specific features, such as lines, orientation, or color, (Bartles and Zeki, 2000; Orban et al., 2004; Tootell et al., 2003) whereas areas in the occipito-temporal cortex integrate these features and code (represent) objects as wholes, independent of visual perspective (Grill-Spector, 2003; Kanwisher, 2003). Finally, more anterior areas in temporal cortex are important for higher level object processing, such as object recognition, identification, and naming (Devlin et al., 2002; Humphreys et al., 1999; Malach et al., 1995). One intriguing characteristic of this system that functional neuroimaging has revealed is that behavioral outcomes – such as object recognition and identification – can be accomplished in different (and not always obvious) ways. For example, areas in the occipito-temporal region, such as the lateral occipital complex (LOC), mediate shape representations formed on the basis of static contour cues (Kourtzi and Kanwisher, 2001; Murray et al., 2004; Peuskens, et al., 2004). In contrast, areas in the posterior parietal cortex, such as the angular gyrus, mediate shape representations formed on the basis of motion-carried information (Murray et al., 2004; Peuskens et al., 2004). Identification of the neural underpinnings of behavior can yield a more detailed picture of the processes involved and the way in which these processes give rise to object representations.

Despite significant advances in our understanding of the neural basis of object processing in the adult, we are limited in our knowledge of these brain-behavior relations in infants. One reason for this gap in knowledge is that neuroimaging techniques typically used with adults (e.g., fMRI or PET) are not well suited for use with infants. Introduction of near-infrared spectroscopy (NIRS) into the experimental setting has now given psychological scientists the opportunity to investigate functional organization of the infant cortex (Lloyd-Fox et al., 2010). Initial studies suggest that object processing areas in the infant cortex share at least two characteristics with those in the adult cortex. First, the infant brain is functionally specialized (Honda et al., 2010; Lloyd-Fox et al., 2009; Watanabe et al., 2008; Wilcox et al., 2008, 2009, 2010). For example, parietal areas mediate the processing of the spatiotemporal but not the featural properties of objects. Second, functional units are hierarchically organized (Watanabe et al., 2008; Wilcox et al., 2010). For example, posterior areas of temporal cortex respond to events involving moving

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occluded objects, whereas anterior areas respond only to events in which the objects are individuated. However, the extent to which these functional properties change with time and experience as object processing capacities become more sophisticated is unclear. Identifying the neural correlates of object processing can significantly enhance our understanding of developmental mechanisms.

The purpose of the present experiments was to assess functional organization of visual object processing areas during the first year, a time when significant changes in object individuation capacities occur. Infants aged 3 to 5 months and 11 to 12 months were shown a shape-difference, color-difference, or control event (Fig. 1). Behavioral studies have demonstrated that by at least 4.5 months (and probably before) infants interpret the shape-difference event as involving two distinct objects, and the color-difference and control event as involving a single object. By 11.5 months, infants interpret both the shape- and the color-difference event (but not the control event) as involving two distinct objects (Wilcox, 1999; Wilcox and Baillargeon, 1998). These studies indicate that early in the first year infants use shape information, but it is not until the end of the first year that they use color information, as the basis for individuating objects (Wilcox and Woods, 2009). Two predictions were made. First, infants would show different patterns of neural activation to events involving features they use, than features they do not use, to individuate objects. In addition, these patterns of neural activation would change during the first year in a way that is consistent with infants' emerging capacity to individuate objects. For example, younger infants who use shape but not color differences to individuate objects should evidence activation in anterior temporal cortex, an area implicated in object identification, in response to the shape-difference but not the color-difference event. Older infants who use shape and color differences to individuate objects should evidence activation in the anterior temporal cortex in response to both events. In contrast, posterior temporal cortex, which includes lower level object processing areas, should be activated in response to all of the events at each age. Second, patterns of neural activation should be consistent with maturation of the perceptual capacities that support individuation-by-feature. For example, young infants who have an immature visual system and, hence, are more likely to draw on motion-carried information to extract object shape than older infants (Kellman and Arterberry, 2006) should be more likely to show neural activation in posterior parietal areas in response to the shape-difference event.

Materials and methods

Participants

Infants aged 3 to 5 months participated in Experiment 1 ($N=56$; 35 males, M age = 5 months, 8 days, range = 3 months, 8 days to 5 months, 29 days) and aged 11 to 12 months participated in Experiment 2 ($N=55$; 33 males, M age = 11 months, 21 day, range = 11 months, 6 days to 12 months, 26 days). In Experiment 1, fourteen additional infants were eliminated because of procedural problems ($N=6$), difficulty in obtaining an optical signal ($N=7$), or failure to look at least 10 s on two or more test trials (N = 1). In Experiment 2, twenty-three additional infants were tested but excluded from analysis because of procedural problems ($N=3$), difficulty in obtaining an optical signal ($N=14$), motion artifacts ($N=2$), crying ($N=2$) or failure to look at least 10 s on two or more test trials (N = 2). Parents received reimbursement for travel expenses and/or a lab t-shirt for their infant.

Task and procedure

The same task and procedure were used for both experiments. Infants sat in a Bumbo® seat in a quiet and darkened room and watched the presented event (randomized by condition) in a puppet-stage apparatus. Trained experimenters produced the test events live following a precise script.

Infants were presented with four trials of one of three events (Fig. 1). In Experiment 1, shape difference ($N=19$), color difference ($N=19$), and control ($N=18$). In Experiment 2, shape difference ($N=18$), color difference ($N=19$), and 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). 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. This interval was necessary because analysis of the optical imaging data requires baseline recordings of the measured intensity of refracted light. Previous studies indicate that 10 s is sufficient for blood volume to return to baseline levels (Wilcox et al., 2008, 2009). The curtain was raised to begin each test trial.

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 four fiber optic cables that delivered near-infrared light to the scalp of the participant (emitters), eight fiber optic cables that detected the diffusely reflected light at the scalp (detectors), and 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 wavelengths of 690 nm, which is more sensitive to deoxygenated blood, and 830 nm, which is more sensitive to oxygenated blood, with two laser-emitting diodes (TechEn Inc). Laser power emitted from the end of the diode was 4 mW. Light was square wave modulated at audio frequencies of

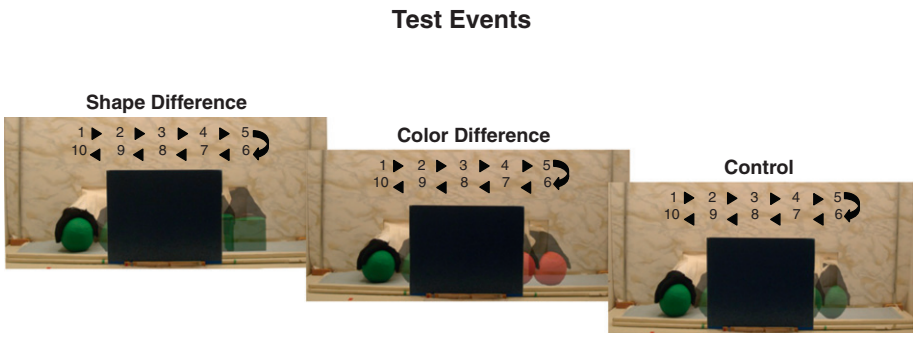


Fig. 1. Test events for Experiments 1 and 2. Each cycle of the test event was 10 s and infants saw 2 complete cycles during each test trial. Infants saw the following objects to the left and right sides of the screen, respectively: green ball–green box (shape difference); green ball–red ball (color difference); and green ball–green ball (control). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 did not interfere with the laser signals because environmental light sources modulate at a different frequency. Fiber optic cables were 2.5 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 a custom-made headgear that secured the fiber optics to the scalp. Configuration of the sources and detectors within the headgear, placement of the sources and detectors on the infant's head, and location of the nine corresponding channels are displayed in Fig. 2. Source-detector separation was 2 cm. The headgear was not elastic so the distance between sources and detectors and between the four source-detector groups (O1, P3, T5, T3) remained fixed. The headgear was placed on the infant's head using O1 as the primary anchor and T3 and P3 as secondary anchors. The mean head circumference for the younger and older groups was 42.6 cm (SD = 1.31) and 46.6 cm (SD = 1.72), respectively. Hence, for the two age groups the mean difference in the distance between 01 and T3 (1/4 of the head circumference) was 1 cm. The mean A1 to A2 measurement for the younger and older infants was 26.38 cm (SD = 2.01) and 29.25 cm (SD = 1.51), respectively. The mean nasion to inion measurement for the younger and older infants was 26.20 cm (SD = 2.06) and 28.65 cm (SD = 1.83), respectively. Hence, for the two age groups the mean difference in distance between the headgear's base to P3 (1/3 of each of these measurements) was 0.96 cm to 0.82 cm. Although the mean head size between the two age groups varied, the area of the skull (and underlying neural structures) affected was relatively small and, importantly, was smaller than the separation between each source and detector.

Processing of the NIRS data

The NIRS data were processed, for each detector separately, using a procedure identical 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 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. Additionally, trials in which the infant cumulated less than 10 s looking time were eliminated from the analysis because neural activation depends on visual attention to the events. These criteria eliminated thirty-eight (of 224 possible) trials in Experiment 1 and fifty-six (of 220 possible) trials in Experiment 2.

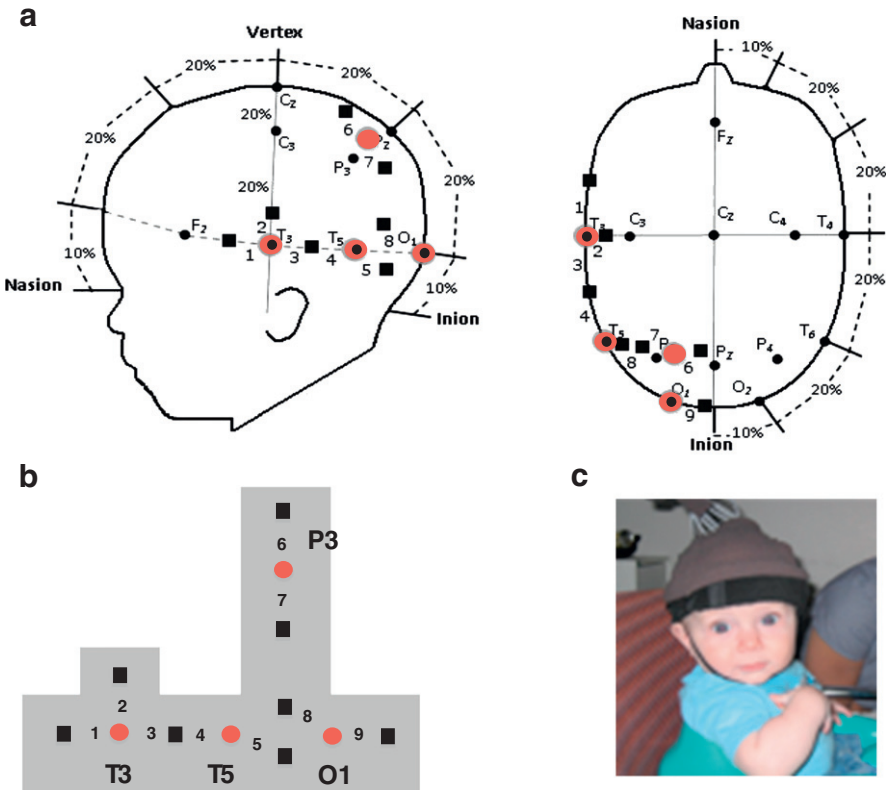
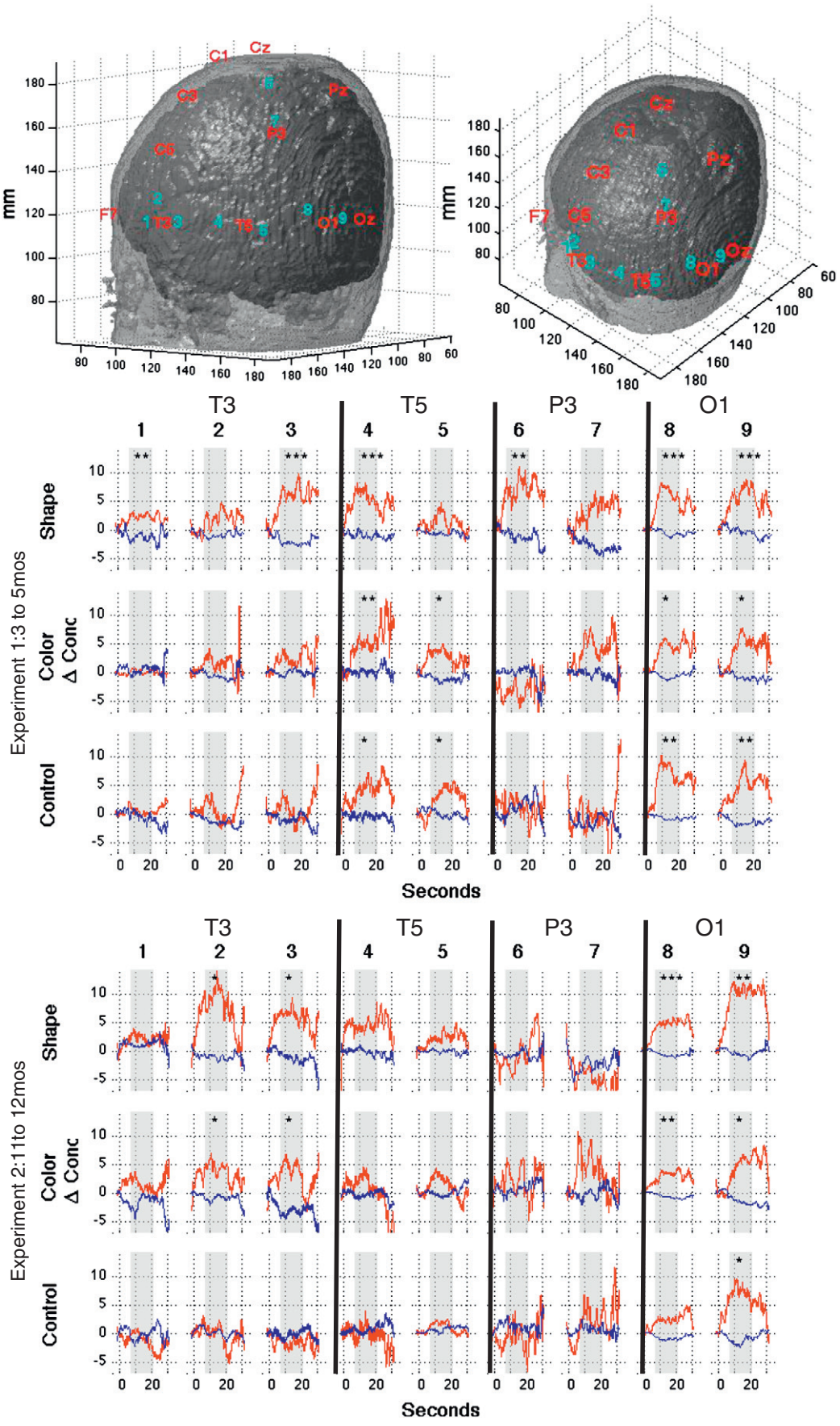


Fig. 2. Configuration and placement of optodes. (a) Location of emitters (large red circles) and detectors (black squares) on the infant's head in relation to the 10–20 International EEG system (small black circles). Note that an emitter was placed directly over O1, T5, and T3 and one emitter lay near P3. Also represented are the nine corresponding channels from which data were collected. 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) Configuration of the emitters (red circles) and detectors (black squares), and the nine channels, in the headgear. Emitter–detector distances were all 2 cm. (c) Infants sat in a supportive seat to restrain excess movement. An elasticized headband was slid onto the infant's head and secured by a chinstrap.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Results

Looking time data

Looking time data were averaged across trials and infants for each event condition to ensure that visual attention did not vary by condition, which could lead to different patterns of neural activity. In Experiment 1 (shape-difference, $M = 15.85$, $SD = 2.95$; color-difference, $M = 15.38$, $SD = 3.59$; and control, $M = 15.21$, $SD = 3.30$, $F\ (2, 53) < 1$) and Experiment 2 (shape-difference, $M = 17.54$, $SD = 1.91$; color-difference, $M = 17.58$, $SD = 3.89$; and control, $M = 16.31$, $SD = 2.82$, $F\ (2, 52) < 1$) infants' looking times did not differ significantly by condition.

Neural responses: Experiment 1 (3 to 5 months)

Hemodynamic response curves for each channel and event are presented in Fig. 3. Two analyses were conducted. First, relative changes in HbO and HbR were averaged over 6 to 20 s for each channel separately and compared to 0 (Table 1). These intervals were chosen because the first emergence of the object to the right of the screen began 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 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 move posterior to anterior in presentation of the results. A significant increase in HbO relative to baseline was obtained at channels 9 and 8 (visual cortex) in response to all events. A significant increase in HbO was obtained at channel 6 (posterior parietal cortex) in response to the shape-difference but not the color-difference or control event. An increase in HbO was obtained at channels 5 and 4 (posterior temporal cortex) in response to all of the events. Although the response to the shape-difference event at channel 5 did not reach significance, it also did not vary reliably from responses obtained to the other two events at channel 5. A significant increase in HbO was obtained at channels 3 and 1 (anterior temporal cortex) in response to the shape-difference but not the color-difference or control event.

In summary, three main findings emerged (Fig. 4). First, neural activation was obtained in visual cortex and posterior temporal cortex in response to all test events, and the magnitude of the hemodynamic responses did not vary significantly by test event. Second, activation was obtained in the parietal cortex in response to the shape-difference but not the color-difference or control event, suggesting that the younger infants used motion-carried information to extract object shape (i.e., the response could not have been to motion, per se, as all events involved object motion). Third, activation was obtained in more anterior areas of the temporal cortex in response to the event that young infants interpret as involving two objects (shape-difference) but not in response to the events that young infants interpret as involving a single object (color-difference and control). These findings suggest hierarchical organization of object processing in temporal cortex early in the first year, with posterior areas (e.g., inferior temporal gyrus and/or LOC) responding to events involving moving objects, more generally, and anterior areas (e.g., middle and/or superior temporal gyrus) responding when featural differences signal the presence of numerically distinct objects.

Neural responses: Experiment 2 (11 to 12 months)

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 and are presented in Table 1.

An increase in HbO relative to baseline was obtained at channels 9 and 8 (visual cortex) in response to all test events. Although the response to the control event in channel 8 did not reach significance, it also did not vary reliably from responses obtained to the other test events in channel 8. Unexpectedly, HbO did not increase significantly, relative to baseline, at channels 5 and 4 (posterior temporal cortex) to any of the events. A significant increase in HbO was obtained at channels 3 and 2 (anterior temporal cortex) in response to the shape- and the color-difference but not control event.

In summary, three main findings emerged (Fig. 4). First, neural activation was not obtained in parietal cortex in response to the shape-difference event, suggesting that the older (in contrast to the younger) infants did not rely on motion-carried information to extract object shape. Second, neural activation was not obtained in the posterior temporal cortex to any of the events. Third, neural activation was obtained in anterior temporal cortex in response to events that older infants interpret as involving two objects (shape- and color-difference) but not in response to an event they interpret as involving a single object (control).

Discussion

Until recently, relatively little has been known about the functional organization of the infant brain. The outcome of these studies revealed novel information about the cortical structures that mediate object processing during the first year of life and the extent to which patterns of neural activation change with infants' emerging object processing capacities.

Age-related changes in parietal activation to object shape

In the present experiment shape could be extracted from contour alone (the objects sat stationary for 1 s after each emergence from behind the screen) or from motion-carried information (change in optic flow as the objects moved along the horizontal plane). Activation was obtained in the parietal cortex in response to the shape-difference event in the 3- to 5-month-olds but not the 11- to 12-month-olds, suggesting that the younger but not the older infants drew on motion-carried information to extract object shape. (Both groups individuated-by-shape, as evidenced by responses obtained in anterior temporal cortex and as supported by previous behavioral work.) This interpretation is consistent with fMRI studies conducted with adults that have shown that posterior parietal areas are activated when motion-carried information defines object shape but not when shape is extracted from static contour alone (Murray et al., 2004; Peuskens et al., 2004). This interpretation is also consistent with the fact that the visual system, and visual acuity in particular, matures significantly between 3 and 11 months of age, making older infants less dependent on motion-carried information for object recognition and identification than younger infants (Kellman and Arterberry, 2006). Recent research using a similar protocol (Wilcox

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. 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 both experiments, 1 to 20 s was the test event and 21 to 30 s was the silent pause (baseline). The hemodynamic response was averaged over 6 to 20 s, indicated by gray shading. Asterisks indicate M (SD) responses that differed significantly from baseline ($^{*}p < .05$, $^{**}p < .01$, and $^{***}p < .001$ two-tailed). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mean (SD) HbO and HbR responses during the test events for Experiment 1 and Experiment 2. For both experiments, one sample t-tests compared HbO and HbR responses (averaged over 6 to 20 s) to zero at each channel. One-way ANOVAs tested for differences between groups at each channel. 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: 3–5 months		One sample t-tests M (SD)			One-way ANOVA (DF = 53)
Neural region	Channel	Shape difference	Color difference	Control	Between subjects effects
		N = 19	N = 19	N = 18	
HBO					
T3	1	.0023 (.003)**	.00008 (.002)	.0003 (.003)	$F=4.10^{*}$ $\eta^2=.134$ Shape vs. control $t=2.02^{*}$, $df=35$ Color vs. control $t<1$, $df=35$
	2	.0020 (.008)	.0017 (.008)	.0004 (.007)	$F<1$
	3	.0064 (.007)***	.0020 (.005)	.0004 (.008)	$F=3.70^{*}$ $\eta^2=.123$ Shape vs. control $t=2.35^{*}$, $df=35$ Color vs. control $t<1$, $df=35$
T5	4	.0059 (.007)***	.0048 (.006)**	.0043 (.006)*	$F<1$
	5	.0017 (.007)	.0033 (.006)*	.0034 (.004)*	$F<1$
P3	6	.0069 (.007)**	−.0056 (.015)	−.0008 (.011)	$F=5.89^{**}$ $\eta^2=.182$ Shape vs. control $t=2.52^{*}$, $df=35$ Color vs. control $t<1$, $df=35$
	7	.0034 (.010)	.0045 (.013)	−.0008 (.014)	$F<1$
01	8	.0063 (.006)***	.0043 (.008)*	.0074 (.011)**	$F<1$
	9	.0065 (.006)***	.0052 (.009)*	.0061 (.011)**	$F<1$
HBR					
T3	1	−.0015 (.004)	.0001 (.003)	−.0005 (.003)	$F=1.10$
	2	−.0013 (.002)*	−.0008 (.003)	−.0015 (.003)*	$F<1$
	3	−.0025 (.003)**	−.0001 (.003)	−.0011 (.002)	$F=3.90^{*}$, $\eta^2=.128$ Shape vs. control $t=1.62$, $df=35$ Color vs. control $t=1.18$, $df=35$
T5	4	−.0011 (.003)	−.0002 (.003)	−.0005 (.003)	$F<1$
	5	−.0008 (.002)	−.0014 (.004)	−.0002 (.003)	$F<1$
P3	6	−.0013 (.003)	.0002 (.005)	.0013 (.004)	$F=1.79$
	7	−.0031 (.003)***	−.0002 (.006)	−.0014 (.006)	$F=1.37$
O1	8	−.0007 (.002)	−.0010 (.002)	−.0009 (.002)	$F<1$
	9	−.0003 (.003)	−.0010 (.003)	−.0018 (.004)*	$F=1.04$

Experiment 2: 11–12 months		One sample t-tests M (SD)			One-way ANOVA (DF = 52)
Neural region	Channel	Shape difference	Color difference	Control	Between subjects effects
		N = 19	N = 18	N = 18	
HBO					
T3	1	.0022 (.007)	.0011 (.005)	−.0007 (.004)	$F=1.23$
	2	.0093 (.017)*	.0038 (.007)*	−.0007 (.005)	$F=3.60^{*}$ $\eta^2=.121$ Shape vs. control $t=2.33^{*}$, $df=35$ Color vs. control $t=2.17^{*}$, $df=34$
	3	.0063 (.013)*	.0039 (.006)*	−.0015 (.005)	$F=3.84^{*}$ $\eta^2=.129$ Shape vs. control $t=2.48^{*}$, $df=35$ Color vs. control $t=2.85^{**}$, $df=34$
T5	4	.0042 (.016)	.0018 (.006)	−.0002 (.007)	$F<1$
	5	.0023 (.006)	.0020 (.007)	.0015 (.006)	$F<1$
P3	6	−.0018 (.015)	.0044 (.010)	−.0008 (.009)	$F=1.56$
	7	−.0044 (.016)	.0041 (.013)	.0022 (.010)	$F=2.14$
01	8	.0046 (.007)***	.0034 (.004)**	.0021 (.007)	$F<1$
	9	.0105 (.012)**	.0042 (.007)*	.0069 (.012)*	$F=1.69$
HBR					
T3	1	.0009 (.004)	−.0014 (.005)	−.0008 (.005)	F = 1.25
	2	−.0013 (.004)	−.0009 (.003)	−.0002 (.003)	F < 1
	3	−.0013 (.004)	−.0029 (.005)*	−.0004 (.004)	F = 1.43
T5	4	−.0001 (.005)	−.0003 (.003)	.0006 (.003)	F < 1
	5	−.0001 (.002)	−.0004 (.002)	.0005 (.002)	F < 1
P3	6	−.0006 (.005)	−.0006 (.004)	.0012 (.005)	F < 1
	7	−.0024 (.007)	−.0002 (.005)	.0009 (.004)	F = 1.85
O1	8	−.0008 (.002)*	−.0007 (.002)	−.0010 (.002)*	F < 1
	9	−.0008 (.002)	−.0019 (.004)	−.0014 (.003)	F < 1

et al., 2010) suggests that parietal cortex is not significantly activated to a shape-difference event in infants aged 5 to 7 months (mean age = 6 months 27 days), suggesting that infants' use of motion-carried information in this situation declines between 3 and 7 months. Further research will be needed to identify the specific motion cues younger infants use to extract object shape in these types of displays.

There is an alternative (albeit unlikely) interpretation of these data to consider. It is possible that early in the first year posterior parietal areas, in addition to anterior temporal areas, mediate processing of events that infants interpret as involving two objects. In Experiment 1 these two cortical areas were activated under the same condition (shape-difference), and because a dissociation was not obtained we cannot conclude unequivocally that the two areas

were activated for different reasons (i.e., parietal mediated shape processing whereas anterior temporal mediated individuation-by-shape). Given what we currently know about the neural basis of object processing in infants and adults (Murray et al., 2004; Peuskens et al., 2004; Wilcox et al., 2010), the most probable explanation is that these two areas mediated different functions, but we cannot currently rule out the alternative interpretation.

Age-related changes in posterior temporal activation to the test events

In the younger infants, activation was obtained in posterior temporal areas in response to all test events and the magnitude of the response did not vary by event condition. What aspect (or component) of the event structure drove the neural response in the younger infants? One possibility is that posterior temporal cortex mediates processing of events involving moving occluded objects (Wilcox et al., 2010). However, given evidence that posterior temporal regions (near the occipito-temporal border) also respond to moving objects that are not occluded (Watanabe et al., 2008), we suspect this response is not specific to occlusion. Current data support that this response is (a) specific to objects, and not non-object visual stimuli such as reversing checkerboard patterns or faces (Honda et al., 2010; Lloyd-Fox et al., 2009; Watanabe et al., 2008) but (b) independent of the properties of the objects involved (Watanabe et al., 2008; Wilcox et al., 2010). These characteristics lead us to suspect that this area in the young infant serves a function similar to that of occipital–temporal area LOC identified in the adult (Grill-Spector, 2003; Kanwisher, 2003).

In contrast to the younger infants, the older infants did not evidence a significant increase in neural activation in posterior temporal areas in response to the test events. One possible explanation for this developmental pattern is that early in the first year multiple structures (or pathways) mediate processing of moving objects, but with time and experience some pathways are pared down. For example, there is evidence from nonhuman primate studies (Bachevalier and Mishkin, 1994) that in early infancy recognition of familiar objects is mediated by two pathways that project from the inferior temporal cortex to the medial temporal cortex: TEO ⇒ H and TE ⇒ H. By the end of infancy only the latter pathway remains. However, if area TE is ablated before the TEO ⇒ H pathway is eliminated, then TEO ⇒ H remains functional and object recognition abilities are spared. Perhaps in the human infant there are multiple cortical structures involved in the processing of moving objects — the area we have identified in the posterior temporal cortex and another as yet unidentified area. With the paring down of object processing pathways, the former is no longer involved. In other words, there is functional reorganization of the neural structures that mediate processing of events involving moving occluded objects between 3 and 12 months. Although speculative, this hypothesis is consistent with evidence that the infant brain undergoes functional re-organization with time and experience (Born et al., 1998) and that patterns of connectivity within and between cortical areas (i.e., the organization of brain networks) change during the first year of life (Homae et al., 2010).

Another possibility is that the cognitive processes involved in interpretation of the test events change over the course of the first year. For example, perhaps prior to the time that infants recognize that surface features, such as color, can be used to individuate objects, object features are sorted on the basis of whether infants perceive them as applicable to the individuation problem (form features = "yes" and surface features = "no"). Once infants have identified surface features as relevant to object individuation, the sorting process is no longer needed and, hence, posterior temporal areas are not activated. Although currently there are no data that speak directly to this possibility, we are confident that current behavioral models of object representation (e.g., Baillargeon, 2012) in conjunction with newly emerging functional imaging data will help establish the viability of this explanation.

Anterior temporal cortex and object individuation

In both age groups activation was obtained in anterior temporal areas when infants viewed an event they interpret, on the basis of featural information, as involving two objects. Activation was not obtained in anterior temporal areas when infants viewed an event they interpret as involving a single object. These data suggest that functional activation in response to individuation-by-feature remains stable during the first year of life. This effect may not be limited to individuation-by-feature, however. According to recent reports (Wilcox et al., 2010) neural activation is obtained in anterior temporal cortex when spatiotemporal information, such as path or speed of motion, signals the presence of distinct objects but not when it signals the presence a single object. Collectively, these results suggest that anterior temporal cortex mediates object individuation regardless of age (young or old infants) or how the objects were individuated (on the basis of featural or spatiotemporal information).

Conclusion

The present research revealed function-specific activation in the cortex during the first year of life. In addition, hierarchical processing with localized functional areas was observed in temporal and parietal areas during an object-processing task and this organization appears, at least in some respects, to be similar to that observed in the adult brain. At the same time, the present research also revealed functional

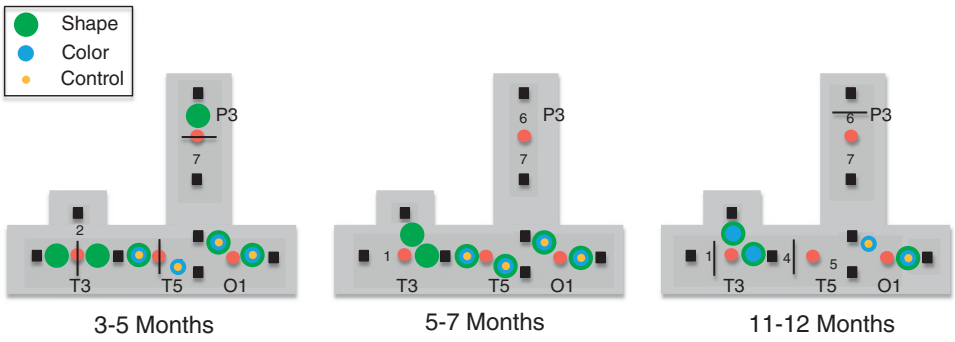


Fig. 4. Patterns of neural activation obtained for the 3- to 5-month-olds and 11- to 12-month-olds in the present experiments and for the 5- to 7-month-olds of Wilcox et al. (2010). The colored dots (large green = shape difference, medium blue = color difference, small yellow = control) indicate that neural activation was obtained during that test event at that channel. The distance between sources and detectors remained fixed but mean head size varied by age (see text). The black lines indicate the actual location of T3, T5, and P3 (based on mean head measurements) for the younger and older infants. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

re-organization of some object processing areas between 3 and 11 months of age. Given evidence that infants' object processing capacities change a great deal during the first year of life it is not surprising that the function of localized units, within a larger stream of processing, also change during this time.

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