When Do Infants Differentiate Profile Face From Frontal Face? A Near-Infrared Spectroscopic Study

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Abstract: The objective of the present study was to determine whether a developmental difference occurs in brain activity when infants look at frontal and profile views using near-infrared spectroscopy (NIRS), which is an optical imaging technique used to measure changes in the concentrations of oxyhemoglobin (oxy-Hb), deoxyhemoglobin (deoxy-Hb), and total hemoglobin (total-Hb). For this objective, we compared NIRS results in two age groups, 5- and 8-month-old infants, while they were looking at frontal views, profile views, and objects. We found that the concentration of oxy-Hb and total-Hb in the 5-month-old group increased for only frontal views in the right temporal regions. In contrast, the concentration of oxy-Hb and total-Hb in the 8-month-old group increased for both frontal and profile views in the right temporal regions. Therefore, the present study indicated that the right hemisphere was dominant for the perception of profile views as well as frontal views. In addition, the most important and interesting finding was that the infants' brain activity of the face area would become view-invariant at the age of 8 months but not at 5 months. The developmental period for view-invariant face recognition has been discussed in previous psychological studies, but this is the first objective study to confirm that the period is between 5- and 8-months by measuring the blood flow in the brain using NIRS. *Hum Brain Mapp* 30:462–472, 2009. © 2007 Wiley-Liss, Inc.

Key words: face perception; developmental changes; infants; near infrared spectroscopy; right hemisphere

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INTRODUCTION

Recently, near-infrared spectroscopy (NIRS) has been used to reveal the brain activity that underlies cognitive processing in human infants [Aslin and Mehler, 2005]. NIRS is an optical imaging technique that can measure changes in the concentrations of oxyhemoglobin (oxy-Hb), deoxyhemoglobin (deoxy-Hb), and total hemoglobin (total-Hb). The advantages of NIRS over functional magnetic resonance imaging (fMRI) and positron emission tomography

(PET) are: (1) it can measure both oxy-Hb and deoxy-Hb; (2) the measurement can be made safely and noninvasively; and (3) the measurement can be made without fixing the subject's body and brain in the apparatus. Since it is almost impossible to keep awake infants motionless, NIRS is very suitable for measuring neural activity in awake infants.

Previous developmental studies using NIRS revealed that NIRS can measure the neural activity of infants while they were exposed to a simple visual patterns [Taga et al., 2003] and hearing speech [Bortfeld et al., 2006; Minagawa-Kawai et al., 2007; Pena et al., 2003]. Moreover, there are some studies reporting successful measurement of the neural activity that underlies cognitive function of infants, such as object [Wilcox et al., 2005] and face processing [Csibra et al., 2004; Otsuka et al., 2007].

In our previous study, we revealed the inter-hemispheric difference in infants' face processing, which is similar to that in adults [Otsuka et al., 2007]. We measured changes in cerebral oxygenation in ten 5- to 8-month-olds' left and right lateral areas while they looked at upright and inverted faces, and objects. We found that the concentration of oxy-Hb and total-Hb significantly increased in the right lateral area during the presentation of upright faces compared to the presentation of inverted faces or objects. Our results suggest that face sensitive neural mechanisms become functional by 5–8 months of age, and that it is lateralized in the right hemisphere of the infant's brain.

In the present study, we further investigated the neural mechanisms underlying face processing in infants using NIRS. Although we found that the processing of upright faces differs from that of inverted faces and objects in 5- to 8-month-olds, we used only frontal faces in our previous study [Otsuka et al., 2007]. Therefore, we have not yet determined how different face views are processed in infants' brains. Since a face consists of three-dimensional objects, changes in the viewpoint cause a change in the visual information about the face that is presented. Human face processing studies on different view faces suggested that the frontal and the profile views contain different information of the face. The frontal faces convey the internal feature information; such as eyes, nose, and mouth, on the contrary the profile view face convey three-dimensional shape information; such as the nose height and shape of the chin [Valentin et al., 1999]. These two types of information are independent, and each of these is important for face processing. Nevertheless, adults can recognize the identity of a face across changes in viewpoints [Bruce et al., 1987; Valentin et al., 1997]. Previous developmental studies have examined when this ability develops during infancy. Infants' face recognition across views was first reported by Fagan [1976]. He found that 7-month-old infants could recognize a learned face across different views. In addition, infants' performance was constant across different views. Similarly, Cohen and Strauss [1979] found that at the age of 7 months, but not at 4–5 months, infants could recognize a learned face shown in different

views. These behavioral studies suggest that infants can recognize the identity of a face seen in different views by 6 months of age. However, there have been no objective studies, for example, studies that record changes in blood flow or metabolic changes by measuring fMRI/NIRS or PET, respectively.

Therefore, the aims of the present study were to examine: (1) face processing for the frontal view and profile view; and (2) developmental changes in face processing during infancy. For these objectives, we measured infants' brain activity using NIRS while they were looking at faces in a frontal view and in a profile view. To investigate whether there is a developmental change during infancy, we recorded NIRS in two different age groups: 5 months and 8 months of age.

METHODS

Participants

Twenty healthy infants, ten 5-month-olds (seven boys and three girls, mean age 151.6 days) and ten 8-month-olds (five boys and five girls, mean age 241 days), participated in this study. Fifteen additional infants were excluded because of an insufficient number of available trials (less than 4 trials for either the frontal or the profile condition) due to crying, not looking at the stimuli, or motion artifacts. This study was approved by the Ethical Committee of the National Institute for Physiological Sciences, and written informed consent was obtained from the parents of the infant participants. The experiments were conducted according to the Declaration of Helsinki.

Stimuli and Design

The stimuli for the baseline period consisted of full-color photo images of 5 vegetables, and those for the test period consisted of full-color photo images of 5 female faces either in the frontal or the profile view (Fig. 1). The profile view was right-sided for half of the infants and left-sided for the rest of the infants. The sizes of the stimuli were $\sim 17.5^\circ \times 21^\circ$ for the faces and $16.8^\circ \times 16.8^\circ$ for the vegetables.

In each trial, 5 faces were shown in random order at the rate of 1 Hz. Faces in the frontal view were shown in half of the trials, and those in the profile view were shown in the other half of the trials. The faces shown in the frontal and profile views were presented at alternating trials. The order of the presentation was counterbalanced across infants. The duration of the trials was fixed for 5 s. During the inter-trial intervals, 5 objects were shown in random order at a rate of 1 Hz. The inter-trial interval was controlled by the experimenter, and its duration was at least 10 s. The results obtained from viewing the objects were used as a control (baseline).

For both the baseline and test stimuli, the stimulus duration was 800 ms, and the 200 ms inter-stimulus interval

Figure 1.

Experimental procedure. In each trial, the baseline phase consisted of stimuli of images of 5 vegetables, and its duration was at least 10 s. The test phase consisted of five female facial images in frontal and profile views. The duration of the test phase was 5 s. The presentation order of test phases 1 and 2 was changed alternately for each infant.

was filled by the presentation of a small red cross. To draw and keep the attention of the infants, both the face stimuli and object stimuli were accompanied by a beeping sound presented at 1 Hz. Two different sounds were used for the face stimuli and object stimuli, but they were the same between the frontal and profile views. The relationship between the sounds and visual stimuli were counter-balanced across infants.

Procedure

Each infant was tested while sitting in the experimenter's lap and facing a computer screen ~40 cm away. The infants watched the stimuli passively while the brain activity was measured, and they were allowed to watch the stimuli as long as they were willing to. Their behavior was recorded on videotape during the experiment.

Recording

We used a Hitachi ETG-100 device system (Hitachi Medical, Chiba, Japan), which can record NIRS from 24 channels simultaneously, with 12 channels for the right, and 12 for the left temporal area. This instrument generated two wavelengths of NIR (780 and 830 nm) and measured the time-courses of the levels of oxy-Hb, deoxy-Hb, and their sum, total-Hb, with 0.1-s time resolution. Since we used newly developed sensor probes for NIRS (Hitachi Medical, infant probe 3×3 mode) for recording in infants, which had a lower weight than the previous probe and made softer contact with the skin, it was observed that most of the infants appeared to enjoy the experiments, and were not reluctant to participate. We used a pair of probes, each containing nine optical fibers (3×3 arrays). Of the nine fibers, five were emitters, and four were detectors. The optical fibers of each probe were kept in place with a soft silicon holder. The distance between the emitters and detectors was set at 2 cm. Each pair of adjacent emitting and

detecting fibers defined a single measurement channel, which allowed for the measurement of oxy-Hb and deoxy-Hb changes in 12 channels for each hemisphere.

On each hemisphere, the placement of the probes covered the temporal area centering at T5 and T6 according to the International 10–20 system [Jasper, 1958]. This was a more posterior region compared to that in our previous study [Otsuka et al., 2007], since the posterior region of the temporal lobe is thought to be more important for face perception than the anterior and middle regions [Halgren et al., 1999; Kanwisher and Yovel, 2006; Kanwisher et al., 1997; Puce et al., 1998] (see Fig. 2).

When the probes were positioned, the experimenter checked to see if the fibers were touching each infant's scalp correctly. The Hitachi ETG-100 system automatically detects whether the contact is adequate to measure emerging photons for each channel. The channels were rejected from the analysis if adequate contact between the fibers and each infant's scalp could not be achieved because of interference by hair.

Figure 2.

(a) The location of the measurement channels. The fibers were placed on the left and right temporal areas centering at T5 and T6 of the International 10–20 system. The distance between the fibers was set at 2 cm. (b) Location of the probe over left temporal area on an infant.

Data Analysis

Throughout the experiment, the infants' behavior was recorded on videotape. We removed the trials from analysis when the infants did not look at the test stimuli for 5 s or became fussy. In addition, we removed the trial if infants looked back at the face of the experimenter during the preceding baseline period. Further, we removed the trials that included movement artifacts, which were detected by the analysis of sharp changes in the time series of the raw data of the NIRS.

On the basis of the wavelengths of the ETG-100 model (780 and 830 nm), the estimations of oxy-Hb and total-Hb concentrations are more precise than that of deoxy-Hb concentration [Otsuka et al., 2007; Pena et al., 2003]. Since one of the advantages for NIRS as compared with fMRI is to be able to measure the concentration of both oxy- and deoxy-Hb, the data of oxy-Hb, deoxy-Hb, and total-Hb concentrations in the right and left temporal area were used for the analysis in the present study.

The raw data of oxy-Hb, deoxy-Hb, and total-Hb from individual channels were digitally high-pass-filtered at 0.02 Hz to remove any longitudinal signal drift [Taga et al., 2003]. Then the mean concentration of each channel within a subject was calculated by averaging data across the trials in a time series of 0.1 s time resolution from 1 s before trial onset to 1 s after trial offset.

On the basis of the mean concentrations in the time series, we calculated the Z-scores of oxy-Hb, deoxy-Hb, and total-Hb in the frontal and profile face conditions for each channel within a subject. The Z-scores were calculated as the difference between the means of the baseline and trial divided by the standard deviation of the baseline:

$$d = (m_1 - m_2)/s$$

Accordingly, " m_1 " and " m_2 " represent the mean concentration values during the baseline and trial, respectively, and " s " represents the standard deviation of the baseline. The mean concentration value at 1 s immediately before the trial was used as a baseline. Then the Z-scores obtained from 12 channels within each measurement area were averaged in order to increase the signal-to-noise ratio. Although the raw data of NIRS were originally relative values, and could not be averaged directly across subjects or channels, the normalized data such as the Z-scores could be averaged regardless of the unit [Matsuda and Hiraki, 2006; Schroeter et al., 2003; Shimada and Hiraki, 2006].

Previous studies showed that the hemodynamic response typically lags a few seconds behind the stimulation, and peaks around 8–10 s after stimulus presentation in infants [Bartocci et al., 2000; Csibra et al., 2004; Meek et al., 1998; Taga et al., 2003]. Therefore, the hemodynamic response would reach a peak after the end of the 5-s-long trials. However, when we measured the hemodynamic response for a longer period in a pilot study, the data obtained subsequent to the trial period were very noisy

due to head movements of the infants, and were thus not suitable for analysis. In fact, we observed that many infants in many trials looked away from the CRT monitor immediately after trial offset, and then within a few seconds looked at the monitor again. On the basis of this observation, we determined to perform statistical analyses against the mean Z-scores of the last 1 s of the trials in order to avoid data that included motion artifacts.

Statistical analysis was carried out by using a multiple analysis of variance (MANOVA): age (5 and 8 months) $\times$ view (frontal and profile) $\times$ channels (24 channels) for the mean Z-score on the data of oxy-, deoxy-, and total-Hb. Then we conducted a Tukey post hoc test on factors where we found a significant effect.

To analyze the inter-hemispheric difference, an additional ANOVA was conducted by two-way repeated-measures ANOVA view (frontal and profile) $\times$ measurement area (right and left hemisphere) for the mean Z-score on each age.

For all 24 channels, each channels' activation was tested by a t test against the baseline. To eliminate the risk of a Type I error, we performed the corrections using the false discovery rate (FDR) [Singh and Dan, 2006].

Finally, the analysis of Channels-of-interest (COI) was conducted for channels (ch.18, 21, 22, 23, and 24) in the right hemisphere of 8-month-olds. We selected these five channels as COI, which indicated high activation compared with the other channels in the right hemisphere. Also, we conducted a 2 (view) $\times$ 2 (age) ANOVA both in the COI region and outside the COI region that included seven other non-COI channels, respectively.

RESULTS

We obtained neural data from ten 5-month-olds and ten 8-month-olds who looked at the stimuli over more than 3 trials both in the frontal and profile view conditions. The mean numbers of trials were 6.65 for the frontal view condition and 5.8 for the profile view condition. The mean numbers of trials were 6.35 for 5-month-olds and 6.1 for 8-month-olds. The mean number of excluded trials from the analysis was 2.9 for the frontal condition and 4.5 for the profile condition in 5-month-olds. And the mean number of trials was 3.5 for the frontal condition and 3.2 for the profile condition in 8-month-olds. We found that there were no significant differences on the mean number of trials as well as excluded trials between views and ages.

Figure 3 shows the time-course of the average change of the oxy-, deoxy-, and total-Hb concentrations in the 5- and 8-month-old groups while the infants looked at either frontal or profile views. Zero on the horizontal axis represents the beginning of the test period and five on the horizontal axis represents the end of the test period.

At 5 months, the concentrations of oxy-, deoxy-, and total-Hb in the right hemisphere increased only when infants looked at the faces in the frontal view condition.

Figure 3.

The time-course of the average change in oxyhemoglobin (oxy-Hb), deoxyhemoglobin (deoxy-Hb), and total hemoglobin (total-Hb) in 5- and 8-month-old infants during the conditions of frontal views and profile views. In both age groups, the four graphs on the top part indicate the data for oxy-Hb in the frontal and profile view conditions, the four graphs on the middle part for deoxy-Hb, and the four graphs on the bottom part for total-Hb in both views

conditions. The data for the left temporal area are shown in the left column and those for the right temporal area are shown in the right column. On each graph, the thick line represents the mean Z-score, and the thin line represents 1 standard error (SE). Zero in the horizontal axis represents the beginning of the test period and five in the horizontal axis represents the end of the test period.

On the other hand, at 8 months, the concentrations of oxy-, deoxy-, and total-Hb in the right hemisphere increased not only for the frontal view condition but also for the profile view condition.

To examine the developmental changes, a 2 (age; 5 and 8 months) $\times$ 2 (view; frontal and profile) $\times$ 24 (channels) MANOVA for the mean Z-score on the data of oxy-Hb, deoxy-Hb, and total-Hb was conducted. On the concentration of oxy-Hb, deoxy-Hb, and total-Hb, the main effect of channels was significant (oxy-Hb: $F(23, 391) = 2.747, P < 0.01$; deoxy-Hb: $F(23, 391) = 3.427, P < 0.01$; total-Hb: $F(23, 391) = 2.967, P < 0.01$). A post hoc analysis showed that channel 24 (ch. 24) located in the right temporal area was activated greater than the other channels, which were mainly located in the left temporal area, on all the concentrations of oxy-Hb, deoxy-Hb, and total-Hb (Table I). Moreover, the data of oxy-Hb and total-Hb revealed a significant interaction between age and view (oxy-Hb: $F(1, 17) = 9.524, P < 0.01$; total-Hb: $F(1, 17) = 5.034, P < 0.05$). A simple main effect analysis showed a decrease in oxy-Hb and total-Hb on profile views for 5 months of age, whereas an increase in oxy-Hb and total-Hb was observed on profile view for 8 months of age. No significant difference of activation was found on frontal view conditions for between 5- and 8-month-olds.

To analyze the inter-hemispheric difference on each age group, a 2 (view) $\times$ 2 (measurement area) repeated-measures ANOVA was performed for the mean Z-score for each age. First, for 5-month-olds, the main effect of measurement area showed a marginal tendency for the concentration of oxy-Hb ($F(1, 9) = 4.626, P < 0.060$), and was significant for deoxy-Hb ($F(1, 9) = 7.186, P < 0.05$) and total-Hb ($F(1, 9) = 6.119, P < 0.05$). Second, for 8-month-olds, the main effect of view was significant in oxy-Hb ($F(1, 9) = 5.191, P < 0.05$), showing that profile views elicited higher Z-scores than the frontal view did. In addition, the main effect of measurement area showed

a marginal tendency in oxy-, deoxy-, and total-Hb (oxy-Hb: $F(1, 9) = 4.418, P < 0.065$; deoxy-Hb: $F(1, 9) = 4.788, P < 0.056$; total-Hb: $F(1, 9) = 4.248, P < 0.069$). On both 5- and 8-month-olds, oxy-, deoxy-, and total-Hb were increased only in the right hemisphere.

For each age group, we conducted a two-tailed one-sample t test versus a chance level of 0 for the concentrations of oxy-, deoxy-, and total-Hb within the area in each condition. In 5-month-olds, the concentrations of both oxy-Hb and total-Hb were significantly increased in the right temporal area during the frontal view condition (oxy-Hb: $t(9) = 3.124, P < 0.01$; total-Hb: $t(9) = 2.79, P < 0.05$). In 8-month-olds, the concentrations of both oxy-Hb and total-Hb were significantly increased in the right temporal area in the profile view condition (oxy-Hb: $t(9) = 4.316, P < 0.01$; total-Hb: $t(9) = 4.173, P < 0.01$) as well as in the frontal view condition (oxy-Hb: $t(9) = 3.432, P < 0.01$; total-Hb: $t(9) = 4.292, P < 0.01$). For the concentration of deoxy-Hb, the activation was increased in the right temporal area only in the frontal view condition ($t(9) = 3.894, P < 0.01$). Figure 4 clearly indicates that significant increases of oxy-Hb and total-Hb occurred in both the frontal and profile views at 8 months.

As for the effect of view, in 5-month-olds, a two-tailed paired t test revealed that the concentrations of oxy-Hb were greater for the frontal view than the profile view, but this difference was not significant (oxy-Hb: $t(9) = 2.198, P < 0.06$). In contrast, at 8 months of age, a two-tailed paired t test showed that the concentrations of oxy-Hb and total-Hb were significantly greater for the profile view than for the frontal view (oxy-Hb: $t(9) = -2.976, P < 0.05$; total-Hb: $t(9) = -2.308, P < 0.05$).

Table II shows the channels activated in the profile view conditions compared to the baseline on 8-month-old.

To exclude the possibility that the observed activations were not due to the face processing but to the artifacts by change in the arousal level or by body movement, we analyzed COI in the right hemisphere of 8-month-old infants.

Table III indicates the channels activated in right hemisphere of 8-month-old in the frontal and profile view conditions compared to the baseline. Five channels, ch. 18, 21, 22, 23, and 24, were selected as COI (Table III). We conducted a t test to compare the activations of these five channels with those of the other seven channels. The results showed a marginal tendency for the concentration of oxy-Hb in both the frontal and the profile views (frontal view: $t(118) = 1.777, P < 0.060$; profile view: $t(118) = 1.880, P < 0.065$) and was significant for total-Hb (frontal view: $t(118) = 2.258, P < 0.05$; profile view: $t(118) = 2.667, P < 0.01$).

To confirm the activated areas in both frontal and profile views in 8-month-olds, a 2 (view) $\times$ 2 (age) ANOVA was performed for five channels selected as COI (COI region) and seven other non-COI channels (outside the COI region). We found that the interaction effect of age $\times$ view was significant on the COI region for oxy-($F(1, 98) = 7.681, P < 0.01$) and total-Hb ($F(1, 98) = 4.265, P < 0.05$). However, no interaction was revealed outside the COI

TABLE I. The results of a post hoc test on between channels (ch.)

	oxy-Hb		deoxy-Hb		total-Hb	
	ch.	ch.	ch.	ch.	ch.	ch.
Left	11	12**			5	12*
Right	24				11	12**
		1*	18	8*	18	12**
		2*		12*	19	12**
		3	24	1**	21	12**
		3**		2*	23	12*
		6**		3**	24	3*
		8**		4**		6**
		10*		6**		8*
		12**		7*		12**
				8**		
				10**		
				12*		
				13*		

* $p < 0.05$, ** $p < 0.01$, Tukey (HSD).

Figure 4.

Mean Z-score during the last 1 second of the trials in the left and right temporal areas. The vertical line in the graphs represents one standard error (SE). Two graphs on the top part indicate the data from 5-month-old infants and the other two graphs on the bottom part indicate the data from 8-month-old infants. In the frontal view condition (black bars), the concentrations of both oxy-Hb and total-Hb in the right temporal area were significantly greater than the chance level of 0 in 5-month-

olds ($P < 0.05$). In 8-month-olds, the concentrations of oxy-, deoxy-, and total-Hb in the right temporal area were significantly activated greater than the chance level of 0 ($P < 0.01$). Moreover, in the profile view condition (white bars), the concentrations of both oxy-Hb and total-Hb in the right temporal area were significantly greater than the chance level of 0 only in 8-month-olds ($P < 0.01$).

region. These results indicated that ch. 18, 21, 22, 23, 24 were the activated area for both frontal and profile views in 8-month-olds.

The important finding of this study was the presence of the developmental differences in neural activation on face perception during infancy. At 5 months, the increased oxy-Hb and total-Hb concentration was observed only in the frontal view condition. In contrast, at 8-month-olds, the he-

modynamic response on the concentration of oxy-Hb and total-Hb increased for both frontal and profile views presentations.

DISCUSSION

In the present study with NIRS, we recorded the brain activity in awake infants while they looked at faces either

TABLE II. Channels activated in the profile view conditions compared to the baseline on 8-month-old

	Profile view			
	oxy-Hb		total-Hb	
	ch	Z-score	ch	Z-score
Left	5	2.88*		
Right	13	3.08*	18	3.48*
	15	3.30*	22	3.10*
	16	3.00*	23	3.06*
	18	2.64*		
	21	2.87*		
	22	3.72*		
	23	2.72*		

ch., channel.

* $P < 0.05$: one-tailed one sample t test versus chance level of 0. The significant P -value was determined by the false discovery rate (FDR).

in frontal or profile views. To examine the developmental differences, we conducted the experiment on two age groups: 5- and 8-month-olds. The results for the 5-month-olds showed that the concentrations of oxy-Hb and total-Hb significantly increased in the right hemisphere during the presentation of the frontal view but not the profile view. In contrast to 5-month-olds, the results for the 8-month-olds showed that the concentrations of oxy-Hb and total-Hb in the right hemisphere increased both in the frontal and profile view conditions. These results suggest that (1) there is a right-hemisphere dominance in perceiving faces not only in the frontal view but also in the profile view in infants, and (2) the processing of faces in profile view is established between 5- and 8-months of age.

In our previous study, we found that the right lateral area in 5- to 8-month-old infants showed an increased activation in response to the presentation of upright faces compared to the presentation of inverted faces and objects [Otsuka et al., 2007]. Similarly, we found a significant increment in the concentration of oxy-Hb and total-Hb only in the right hemisphere. These observations are consistent with the previous behavioral [de Schonen and Mathivet, 1990] and event-related potentials (ERPs) [de Haan and Nelson, 1997, 1999] studies which showed that the right hemisphere is more involved in recognition of faces in infants. Further, this is consistent with the hemispheric differences observed in neuroimaging [Puce et al., 1996; Kanwisher et al., 1997] and electrophysiological [Watanabe et al., 1999] studies on adults. Taken together, all these findings suggest that specific face-processing mechanisms may have developed in the right hemisphere by the age of 5 months.

With regard to the effect of viewpoint on facial recognition, previous behavioral studies showed that infants over 6 months of age but not younger could identify the same

person across a change in facial angles [Cohen and Strauss, 1979; Fagan, 1976; Pascalis et al., 1998]. These behavioral studies suggest that there is a developmental change in the ability to process faces in the profile view at around 6 months of age. Consistent with the findings from behavioral studies, our results clearly showed that there is a developmental change in the processing of profile view faces before and after 6 months; that is, the profile views evoked significantly increased brain activation in the right hemisphere in 8-month-olds, but not in 5-month-olds. No such age-related difference was found for the frontal face condition. That is, presentation of a frontal face elicited increased activity in the right hemisphere for both 5- and 8-month-olds. Our results suggest that 8-month-olds can process faces in both frontal and profile views differently from nonface objects.

A neuroimaging study using fMRI reported a similar finding with adult participants [Tong et al., 2000]. Tong et al., [2000] showed that faces in profile view elicited the same level of activation as faces in frontal view did in the fusiform face area (FFA), and that the responses on FFA were stronger than those induced by half-back head or back of the head views. Considering that NIRS can detect activities only in a very superficial layer of the cortex, it is less likely that our results reflect activity in the inferior temporal lobe such as the fusiform gyrus. However, our results at least showed that 8-month-olds as well as adults process faces in profile similarly to faces in the frontal view. Since the spatial resolution of NIRS is not as high as that of fMRI, the activated region cannot be determined. However, considering the regions covered by the NIRS probes [Homan et al., 1987] and the results reported by previous studies [Andrews and Ewbank, 2004; Perrett et al., 1985; Yovel and Kanwisher, 2005], we speculate that the superior temporal sulcus (STS) is the most likely responsible region.

TABLE III. Channels activated in right hemisphere of 8-month-old in the frontal and profile view conditions compared to the baseline

Frontal view				Profile view			
oxy-Hb		total-Hb		oxy-Hb		total-Hb	
ch.	Z-score	ch.	Z-score	ch.	Z-score	ch.	Z-score
21	2.94*			13	3.08*	13	2.40*
24	2.94**			15	3.30*	16	2.47**
				16	3.00*	18	3.48*
				18	2.64*	21	2.32*
				21	2.87*	22	3.10*
				22	3.72*	23	3.06*
				23	2.72*	24	2.31*
				24	2.32*		

ch., channel.

* $P < 0.05$, ** $P < 0.06$: one-tailed one sample t -test versus chance level of 0. The significant P -value was determined by the false discovery rate (FDR).

In addition to FFA, face sensitive region is often found in STS which shows greater neural response to face than nonface objects. Although recent studies have emphasized the role of STS in representing changeable aspect of the face (e.g., eye gaze, facial expression, and facial orientation) rather than invariant aspects of facial structure (facial identity) [Allison et al., 2000], some findings shed some light on the role of STS for face recognition.

Hoffman and Haxby [2000] examined the role of FFA and STS in the perception of face identity and eye gaze. FFA in both left and right hemisphere showed a greater activity while attending to identity compared while attending to gaze direction. By contrast, the left STS showed an opposite pattern of response to FFA, with greater activity to gaze direction compared to identity. Different from the left STS, however, the responses in the right STS did not differ between the two conditions, suggesting that right STS play some role in perception of face identity as well as eye gaze direction.

More interestingly, Andrew and Ewank [2004] suggest that STS plays some role in recognizing face from varying views. By using fMRI adaptation, Andrew and Ewank [2004] examined the effect of change in facial size and view-point. In their study, FFA showed a decrease in activity in response to the face when the same identity was shown repeatedly compared when the multiple different identity were shown. Further, this response pattern in FFA was preserved even when the size of face image was changed, suggesting that representation of face in FFA is size invariant. In contrast to FFA, face sensitive region in the right STS did not show the different pattern of response between the same identity condition and different identity condition if only frontal face were used. However, the right STS showed different response between the two conditions when viewpoint of the face was varied, with greater response to the same identity than different identity. Although this pattern of response is not consistent with the notion of identity specific adaptation, difference in response between the same and different identity conditions suggest that the right STS plays some role in representing face from varying views. Consistent with these findings, our finding suggests the important role of STS in recognizing face from different view-point.

One counterintuitive finding in our study would be that based on the concentration of oxy-Hb, the profile view elicited greater activation at 8 months than the frontal view. Several behavioral studies in adults indicated that on recognition tasks, profile views led to a slower reaction time and lower accuracy than did three-quarter views [Bruce et al. 1987; Hill et al. 1997]. Similarly, a recent infants' study by Rose et al. [2002] found poor performance for the profile view in 7-month-olds. Previous studies consistently showed that face recognition performance for the profile view was lower than that for the frontal view in both infants and adults [Bruce et al., 1987; Hill et al., 1997; Rose et al., 2002]. Our finding of greater activation in response to the profile view than to the frontal view might be

related to the repetition of stimuli across the trials. In the present study, 5 faces were shown in frontal and profile views repeatedly across the trials. Repetition of the same stimuli is known to reduce the activation to the stimuli [e.g., Noguchi et al., 2004]. Given the better recognition of faces in the frontal view than in the profile view, the effect of repetition of the stimuli would be greater for the frontal view than for the profile view. As the trial proceeded, activation to the frontal view became reduced in comparison to activation to the profile view, because the faces in the frontal view would be easily recognized as previously seen faces; in other words, profile view faces may be more novel for infants, though they were shown repeatedly. In any case, our results showed that 8-month-olds process faces both in the frontal view and profile view differently from nonface objects.

The advantage of NIRS is to measure both oxy-Hb and deoxy-Hb concentrations. Typically, neural activation in adults showed an increase in oxy-Hb and a simultaneous decrease in deoxy-Hb. For infants, the discrepant neural activation between oxy- and deoxy-Hb was observed as being the same as in adults [Bortfeld et al., 2006; Karen et al., in press]. On the other hand, for the nondiscrepant neural activation, an increase in both oxy- and deoxy-Hb, was observed in NIRS [Csibra et al., 2004; Sakatani et al., 1999; Wilcox et al., 2005] and in fMRI data [Yamada et al., 1997]. A recent NIRS study [Karen et al., in press] suggests that various factors, such as age group, behavioral state, and the type of stimuli, should be related to these different activation changes in between oxy- and deoxy-Hb in infants.

Although it is unclear why the deoxy-Hb concentration increased in some of the infants' data, it is assumedly because of immature hemodynamic response or the immaturity of the brain. Since we took great care to eliminate body movements and other factors which might cause artifact, we assume that the increase of deoxy-Hb activation in 8-month-olds is not due to artifact.

In conclusion, our findings demonstrated that the hemodynamic activity increased in both 5- and 8-month-olds while they were perceiving frontal views, but increased while perceiving profile views at 8 months only. This study provides the first objective evidence of developmental changes in recognizing faces in profile view in infants. The present results suggest that some developmental changes in the cortical functioning for face processing occur between 5 and 8 months of age, and that the right hemisphere is dominant for recognizing faces in profile view as well as faces in frontal view even in infants.

There has been a great interest in the neural basis of face processing mechanisms, and multiple neuroimaging techniques such as fMRI [e.g., McKone et al., 2007], ERPs [e.g., Itier and Taylor, 2004], and MEG [e.g., Xu et al., 2005] have been used to examine this problem with adult participants. Because of methodological and ethical reasons, however, ERPs has been the only way to examine this problem in healthy human infants. As we showed in

the present study and in our previous study [Otsuka et al., 2007], NIRS can effectively detect the hemodynamic responses involved in neural response to faces. Thus, NIRS can be an alternative way to examine the neural responses to face during infancy. Further studies using NIRS will contribute to understand the development of the neural basis for face processing during infancy.

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REFERENCES

- Allison T, Puce A, McCarthy G (2000): Social perception from visual cues: Role of the STS region. *Cognit Sci* 4:267–278.
- Andrews TJ, Ewbank MP (2004): Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage* 23:905–913.
- Aslin RN, Mehler J (2005): Near-infrared spectroscopy (NIRS) for functional studies of brain activity in human infants: Promise, prospects, and challenges. *J Biomed Opt* 10:011009.
- Bartocci M, Winberg J, Ruggiero C, Bergqvist L, Serra G, Lagercrantz H (2000): Activation of olfactory cortex in newborn infants after odor stimulation: A functional near-infrared spectroscopy study. *Pediatr Res* 48:18–23.
- Bortfeld H, Wruck E, Boas DA (2006): Assessing infants' cortical response to speech using near-infrared spectroscopy. *Neuroimage* 34:407–415.
- Bruce V, Valentine T, Baddeley A (1987): The basis of the 3/4 view advantage in face recognition. *Appl Cogn Psychol* 1:109–120.
- Cohen LB, Strauss MS (1979): Concept acquisition in the human infant. *Child Dev* 50:419–424.
- Csibra G, Henty J, Volein A, Elwell C, Tucker L, Meek J, Johnson MH (2004): Near infrared spectroscopy reveals neural activation during face perception in infants and adults. *J Pediatr Neurol* 2:85–89.
- de Haan M, Nelson CA (1997): Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Dev* 68:187–210.
- de Haan M, Nelson CA (1999): Brain activity differentiates face and object processing in 6-month-old infants. *Dev Psychol* 35:1113–1121.
- de Schonen S, Mathivet E (1990): Hemispheric asymmetry in a face discrimination task in infants. *Child Dev* 61:1192–1205.
- Fagan JF (1976): Infants' recognition of invariant features of faces. *Child Dev* 47:627–638.
- Halgren E, Dale AM, Sereno MI, Tootell RB, Marinkovic K, Rosen BR (1999): Location of human face-selective cortex with respect to retinotopic areas. *Hum Brain Mapp* 7:29–37.
- Hill H, Schyns PG, Akamatsu S (1997): Information and viewpoint dependence in face recognition. *Cognition* 62:201–222.
- Hoffman E, Haxby J (2000): Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat Neurosci* 3:80–84.
- Homan RW, Herman J, Purdy P (1987): Cerebral location of international 10–20 system electrode placement. *Electroencephalogr Clin Neurophysiol* 66:376–382.
- Itier RJ, Taylor MJ (2004): Source analysis of the N170 to faces and objects. *Neuroreport* 15:1261–1265.
- Jasper HH (1958): The ten-twenty electrode system of the International Federation. *Electroencephalogr Clin Neurophysiol* 10:371–375.
- Kanwisher N, Yovel G (2006): The fusiform face area: A cortical region specialized for the perception of faces. *Philos trans R Soc Lond Ser B* 361:2109–2128.
- Kanwisher N, McDermott J, Chun MM (1997): The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J Neurosci* 17:4302–4311.
- Karen T, Morren G, Haensse D, Bauschatz AS, Bucher HU, Wolf M: Hemodynamic response to visual stimulation in newborn infants using functional near-infrared spectroscopy. *Hum Brain Mapp* (in press).
- Matsuda G, Hiraki K (2006): Sustained decrease in oxygenated hemoglobin during video games in the dorsal prefrontal cortex: A NIRS study of children. *NeuroImage* 29:706–711.
- McKone E, Kanwisher N, Duchaine BC (2007): Can generic expertise explain special processing for faces? *Cognit Sci* 11:8–15.
- Meek JH, Firbank M, Elwell CE, Atkinson J, Braddick O, Wyatt JS (1998): Regional hemodynamic responses to visual stimulation in awake infants. *Pediatr Res* 43:840–843.
- Minagawa-Kawai Y, Mori K, Naoi N, Kojima S (2007): Neural attunement processes in infants during the acquisition of a language-specific phonemic contrast. *J Neurosci* 27:315–321.
- Noguchi Y, Inui K, Kakigi R (2004): Temporal dynamics of neural adaptation effect in the human visual ventral stream. *J Neurosci* 24:6283–6290.
- Otsuka Y, Nakato E, Kanazawa S, Yamaguchi MK, Watanabe S, Kakigi R (2007): Neural activation to upright and inverted faces in infants measured by near infrared spectroscopy. *NeuroImage* 34:399–406.
- Pascalis O, de Haan M, Nelson CA, de Schonen S (1998): Long-term recognition memory for faces assessed by visual paired comparison in 3- and 6-month-old infants. *J Exper Psychol Learn Mem Cogn* 24:249–260.
- Pena M, Maki A, Kovacic V, Dehaene-Lambertz G, Koizumi H, Bouquet F, Mehler J (2003): Sounds and silence: an optical topography study of language recognition at birth. *Proc Natl Acad Sci USA* 100:10702–10705.
- Perrett DI, Smith PA, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985): Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc R Soc Lond B Biol Sci* 223:293–317.
- Puce A, Allison T, Asgari M, Gore JC, McCarthy G (1996): Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *J Neurosci* 16:5205–5215.
- Puce A, Allison T, Bentin S, Gore JC, McCarthy G (1998): Temporal cortex activation in humans viewing eye and mouth movements. *J Neurosci* 18:2188–2199.
- Rose SA, Jankowski JJ, Feldman JF (2002): Speed of processing and face recognition at 7 and 12 months. *Infancy* 3:435–455.
- Sakatani K, Chen S, Lichty W, Zuo H, Wang YP (1999): Cerebral blood oxygenation changes induced by auditory stimulation in newborn infants measured by near infrared spectroscopy. *Early Hum Dev* 55:229–236.
- Schroeter ML, Zysset S, Kruggel F, von Cramon DY (2003): Age dependency of the hemodynamic response as measured

- by functional near-infrared spectroscopy. *NeuroImage* 19:555–564.
- Shimada S, Hiraki K (2006): Infant's brain responses to live and televised action. *NeuroImage* 32:930–939.
- Singh AK, Dan I (2006): Exploring the false discovery rate in multichannel NIRS. *NeuroImage* 33:542–549.
- Taga G, Asakawa K, Maki A, Konishi Y, Koizumi H (2003): Brain imaging in awake infants by near-infrared optical topography. *Proc Natl Acad Sci USA* 100:10722–10727.
- Tong F, Nakayama K, Moscovitch M, Weinrib O, Kanwisher N (2000): Response properties of the human fusiform face area. *Cognit Neuropsychol* 17:257–279.
- Valentin D, Abdi H, Edelman B (1997): What represents a face? A computational approach for the integration of physiological and psychological data. *Perception* 26:1271–1288.
- Valentin D, Abdi H, Edelman B (1999): From rotation to disfiguration: Testing a dual-strategy model for recognition of faces across view angles. *Perception* 28:817–824.
- Watanabe S, Kakigi R, Koyama S, Kirino E (1999): Human face perception traced by magneto- and electro-encephalography. *Brain Res Cogn Brain Res* 16:125–142.
- Wilcox T, Bortfeld H, Woods R, Wruck E, Boas DA (2005): Using near-infrared spectroscopy to assess neural activation during object processing in infants. *J Biomed Opt* 10:011010.
- Xu Y, Liu J, Kanwisher N (2005): The M170 is selective for faces, not for expertise. *Neuropsychologia* 43:588–597.
- Yamada H, Sadato N, Konishi Y, Kimura K, Tanaka M, Yonekura Y, Ishii Y (1997): A rapid brain metabolic change in infants detected by fMRI. *Neuroreport* 8:3775–3778.
- Yovel G, Kanwisher N (2005): The neural basis of the behavioral. Face-inversion effect. *Curr biol* 15:2256–2262.