

A longitudinal study of infant view-invariant face processing during the first 3–8 months of life

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ABSTRACT

View-invariant face processing emerges early in life. A previous study (Nakato et al., 2009) measured infant hemodynamic responses to faces from the frontal and profile views in the bilateral temporal areas, which have been reported to be involved in face processing using near-infrared spectroscopy. It was reported that 5-month-old infants showed increased oxyhemoglobin (oxy-Hb) responses to frontal faces, but not to profile faces. In contrast, 8-month-old infants displayed increased oxy-Hb responses to profile faces as well as to frontal faces. In this study, we used the experimental method developed in the previous study to investigate the development of view-invariant face processing, every month for 5 months (from the first 3–8 months of life). We longitudinally measured hemodynamic responses to faces from the frontal and profile views in 14 infants. The longitudinal measurements allowed us to investigate individual differences in each participant. We modeled each infant's hemodynamic oxy-Hb responses to frontal and profile faces using linear regression analysis. Processing of profile faces emerged later and underwent larger improvements than that of frontal faces. We also found an anti-correlation between the speed of improvement in face processing and the hemodynamic response to faces at the age of 3– months. Group analysis of the averaged hemodynamic data from the 14 infants using linear regression revealed that the processing of profile faces emerged between 5 and 6 months of age. Infant view-invariant face processing developed first for frontal faces. This was followed by the emergence of processing of profile faces.

1. Introduction

View-invariant face processing emerges early in life in infants. Newborn infants were reported to not recognize the identity of a face previously learned in the frontal view through the profile view. Similarly they were reported to not recognize the identity of a female face previously learned in the profile view through the frontal view (Turati et al., 2008). A previous study in older infants by Fagan (1976) reported that approximately 7-month-old infants identified profile views of male faces

that were previously learned in the frontal view. Rose, Jankowski, and Feldman (2002) reported that 12-month-old infants successfully recognized the identity of a baby face previously learned in the frontal view through the profile view, while 7-month-old infants did not have this ability. Although the above studies differed in terms of experimental procedure and the face images used, they suggest that an infant's ability to recognize facial identity irrespective of the view point gradually develops during the first year of life.

Face processing in infancy has been investigated by measuring brain

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activity (Ichikawa et al., 2010; Ichikawa et al., 2013; Kobayashi et al., 2011; Kobayashi et al., 2018; Nakato et al., 2009; Nakato et al., 2011a; Nakato et al., 2011b; Otsuka et al., 2007; Yamashita et al., 2012). The above studies used near-infrared spectroscopy (NIRS), which was used to measure cerebral hemodynamic changes while the infants were observing face images. Since infants are not able to wait patiently during the measurements, the equipment used to measure brain activity should be non-invasive, silent, and easily placed onto the infant's head. Previous studies have mainly used event-related potentials (ERPs) or NIRS to measure brain activity in infants. Previous studies using ERP have revealed developmental differences in electrocortical responses to faces in infants of different ages (de Haan et al., 2002; Halit et al., 2003). In the above studies, the images of human and monkey faces either in the upright or inverted orientation were presented to the subjects, and event-related potentials in response to the face images were compared between adults and infants. Electrocortical responses to human upright face images exhibited by 12-month-old infants were more similar to those exhibited by adults than those displayed by 3- or 6-month-old infants. The findings of the aforementioned studies indicate that cortical responses related to face processing gradually mature and specialize to human upright faces during the first year of life.

View-independent recognition of face identity has been reported to emerge during the first 8 months of life. Nakato et al. (2009) measured hemodynamic responses to faces at bilateral temporal areas around the superior temporal sulcus (STS) in 5- and 8-month-old infants using NIRS while the infants passively observed facial images from the frontal and profile views. The STS has been reported to be involved in face processing in adults (Kanwisher et al., 1997; Kanwisher and Yovel, 2006; Puce et al., 1996) and in infants in previous NIRS studies (Ichikawa et al., 2010; Ichikawa et al., 2013; Kobayashi et al., 2011; Kobayashi et al., 2018; Nakato et al., 2009; Nakato et al., 2011a; Nakato et al., 2011b; Otsuka et al., 2007; Yamashita et al., 2012). In the study by Nakato et al. (2009), 5-month-old infants displayed increased oxy-hemoglobin (oxy-Hb) responses in the right temporal area only to the frontal views. In contrast, 8-month-old infants exhibited increased oxy-Hb responses in the right temporal area to both frontal and profile views. Differences in the responses of 8-month-old and 5-month-old infants imply that face processing of profile faces gradually emerges after the first 5 months of life.

NIRS has also been utilized to investigate the development of certain brain regions (Franceschini et al., 2007; Moriguchi and Hiraki, 2011; Perlman et al., 2016). Blasi, Lloyd-Fox, Johnson, and Elwell (2014) longitudinally assessed brain development in infants as it relates to social perception at 2 time points at an interval of 8.5 months. The authors reported a tendency for consistent test-retest reliability regardless of reattachment of the NIRS probe. We are not aware of other studies using NIRS to investigate longitudinal brain development in infancy. Webb et al. (2005) assessed maturational changes in ERP responses to face and object images in the same age group, infants aged 4–12 months. The authors reported that the ERP components changed in amplitude and latency over the first year of life. These studies suggest that longitudinal measurements of hemodynamic responses to faces using NIRS can be used to investigate developmental changes in the neural basis of face processing during the first year of life. Such a longitudinal design could clarify individual differences of the developmental trajectory in face processing and extend our understanding of early face processing. Comparing the processing of profile views of faces, which emerges during the first half year of life, and that of the processing of frontal face views, which emerges earlier in the life, is a suitable subject for a longitudinal design study to elucidate the different developmental trajectories involved in face processing.

In this study, which is focused on view-invariant face processing, we aimed to study longitudinal changes in hemodynamic responses to faces early in life. We longitudinally measured hemodynamic responses to frontal and profile faces in 14 infants at 6 time points ranging from 3 to 8 months of age. Several studies indicate that face-specific brain activity

should be observed in 3-month-old infants (e.g., Halit et al., 2003; Johnson and Morton, 1991) and that 8-month-old infants display hemodynamic responses related to face processing of profile faces as well as frontal faces (Kobayashi et al., 2011a; Nakato et al., 2009). To account for individual differences in the development of view-invariant face processing in infants, we modeled hemodynamic responses to frontal and profile faces measured at each age in months using the linear regression function $y = ax + b$. We then examined the slope (a) and intercept (b) values of the individual regression models. Furthermore, to investigate the general tendency of the development of view-invariant face processing, we will discuss the distribution of individual model parameters. Since a previous study (Nakato et al., 2009) reported that 8-month-old infants displayed hemodynamic responses to profile faces while 5-month-old infants did not, we hypothesized that hemodynamic responses to frontal faces would be present at 3 months of age, while those to profile faces would emerge 5–8 months after birth. The slope (a) of the linear regression model for the profile face condition was greater than that of the model for the frontal face condition. In addition, the intercept (b) of the linear regression model for profile faces was smaller than that of the model for the frontal face condition.

2. Methods

2.1. Participants

The participants were 14 healthy infants (11 boys and 3 girls). Two infants were excluded from the final analysis due to insufficient numbers of available trials (fewer than 3 trials for either the frontal or profile condition) or motion artifacts. This study was approved by the Ethical Committee of Chuo University and that of the National Institute for Physiological Sciences. Written informed consent was obtained from the parents of the infant participants. The experiments were conducted according to the Declaration of Helsinki.

2.2. Stimuli and design

The stimuli used and the study design were identical to those of a previous study (Nakato et al., 2009). The stimulus presentation consisted of a test and baseline period. The stimuli for the test period were full-color photo images of 5 female faces either in the frontal or 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 face stimuli were $\sim 17.5^\circ \times 21^\circ$ and the vegetable stimuli were $16.8^\circ \times 16.8^\circ$ in size.

In each trial, 5 faces were presented in random order at the rate of 1 Hz under either the frontal or profile condition. The faces shown in the frontal and profile views were presented in alternating trials. 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 order of the 2 conditions was counterbalanced across infants. The total duration of each test period was fixed at 5 s.

Each test period followed a baseline period of at least 10 s. During the baseline period, 5 vegetables were shown in random order at a rate of 1 Hz. To compare the hemodynamic responses to faces (during the test period) to those to vegetables (during the baseline period), it was important to ensure that the infants continued to look at the vegetables for 3 s immediately before they observed the faces. To this end, the experimenter observed the infant's behavior 10 s after the start of the baseline period and ended the baseline period when he/she confirmed that the infant had looked at the vegetables on the monitor continuously for 3 s. The results obtained from the viewing of vegetables were used as baseline data.

In both the baseline and test periods, the stimulus duration was 800 ms, and a small red cross was presented during the 200-ms inter-stimulus interval. To attract and retain the attention of the infants, both the face and vegetable stimuli were accompanied by a beeping sound presented at 1 Hz. Two different sounds were used for the face

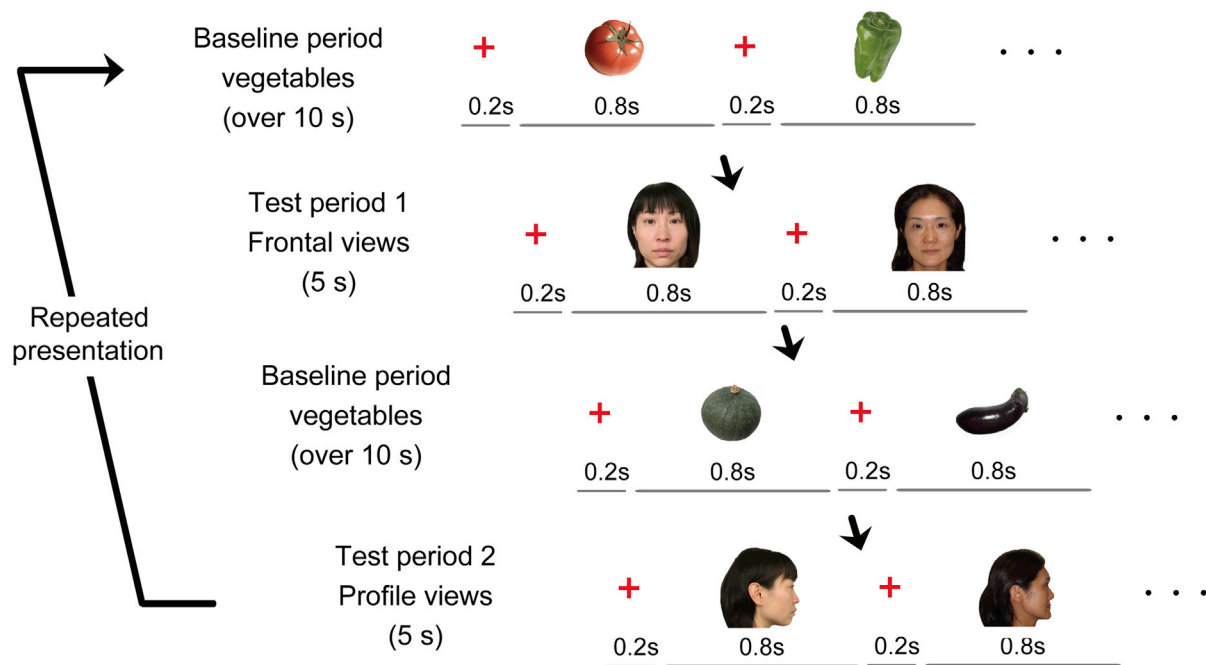


Fig. 1. Experimental procedure. In each trial, the baseline period consisted of the presentation of the images of 5 vegetables. The duration of the baseline period was at least 10 s. The test period consisted of the presentation of 5 female facial images in the frontal and profile views. The duration of the test period was 5 s. The presentation order was altered for test periods 1 and 2 for each infant.

stimuli and the vegetables, and these sounds were used in both the frontal and profile conditions. The relationship between the sounds and the visual stimuli was counterbalanced across infants.

2.3. Apparatus and procedure

The procedure and apparatus used in this study were identical to those used in a previous study (Nakato et al., 2009). Throughout the experiments, all stimuli were displayed on a 22-inch color cathode ray tube (CRT) monitor with a resolution of 1024×768 pixels controlled by a computer. The infant and the CRT monitor were located inside an enclosure made of iron poles and covered with cloth. The distance between the infant and the monitor was approximately 40 cm. There were 2 loudspeakers, one on either side of the CRT monitor. There was a charge-coupled device (CCD) camera just below the monitor screen. Throughout the experiment, the infant's behavior was videotaped using this camera. The experimenter could observe the infant's behavior via a video monitor connected to a pinhole camera.

Each infant was tested while sitting in the experimenter's lap and facing a computer screen. The infants watched the stimuli passively while their brain activity was measured, and they were allowed to watch the stimuli for as long as they were willing to.

2.4. Recording

We used a Hitachi ETG-4000 system (Hitachi Medical; Chiba, Japan) to measure hemodynamic changes in oxy-Hb, deoxyhemoglobin (deoxy-Hb), and total Hb concentrations using 24 channels with a 0.1-s time resolution. Twelve channels were assigned for measurements in the right temporal area and 12 channels were assigned for the left temporal area. Two wavelengths of near-infrared light (695 and 830 nm) were projected through the skull. The intensity of the NIR light illumination at each channel was 0.4 mW.

The NIRS probes (Hitachi Medical) contained 9 optical fibers (3×3 arrays) comprising 5 emitters and 4 detectors. The optical fibers were kept in place using a soft silicon holder. The distance between the emitters and detectors was set to 2 cm. Each pair of adjacent emitting and

detecting fibers defined a single measurement channel.

We placed the probes over the same locations on the bilateral temporal areas centered at T5 and T6 according to the International 10–20 system (Jasper, 1958; see Honda et al., 2010; Ichikawa et al., 2010; Kobayashi et al., 2011; Kobayashi et al., 2012; Nakato et al., 2011a; Nakato et al., 2011b; Yamashita et al., 2012, for other infant studies recording from the same sites).

When the probes were positioned, the experimenter ensured that the fibers were touching each infant's scalp correctly. The Hitachi ETG-4000 system automatically detects whether the contact is adequate to measure emerging photons in each channel. The channels were excluded from analysis if adequate contact between the fibers and the infant's scalp could not be achieved due to hair interference.

2.5. Data analysis

Before performing the data analysis, we monitored the videotape recording of the infant's behavior to determine the valid trials used for the statistical analysis. We excluded a trial from the analysis when any of the following occurred: when the infant looked away from the face stimuli or became fussy, when the infant looked back at the face of the experimenter during the experiment, or when movement artifacts were detected by analysis of sharp changes in the time series of the raw NIRS data.

Raw oxy-Hb, deoxy-Hb, and total-Hb data from individual channels were digitally bandpass-filtered at 0.02–2.0 Hz to remove noise due to heartbeat pulsations or longitudinal signal drift (Ichikawa et al., 2013). Raw data from each channel were averaged across the trials within a subject in a time series of 0.1-s time resolutions from 1 s before the test period onset to 1 s after the test period offset (Nakato et al., 2009). We used the time series of raw oxy-Hb, deoxy-Hb, and total-Hb data to calculate Z-scores at each time point in order to examine deviations of the hemodynamic responses to the presentation of faces from those obtained during the baseline period, when images of the vegetables were shown. Z-scores were calculated separately for oxy-Hb, deoxy-Hb, and total-Hb in the frontal and profile conditions for each channel within each subject. The Z-scores were calculated using the following formula:

$$d = (m_{test} - m_{baseline}) / sd$$

m_{test} represents the averaged raw data at each time point during the test period and $m_{baseline}$ represents the mean of the averaged raw data during the baseline period. sd represents the standard deviation of the data during the baseline period. The “baseline” used to calculate the Z-score was the period of 1 s immediately before the beginning of each test period, which reflects activation during the observation of the vegetable images. The Z-scores obtained from the 12 channels within each measurement area were averaged to increase the signal-to-noise ratio. Data for channel numbers 1–12 were obtained from the left temporal area and those for channel numbers 13–24 were obtained from the right temporal area. Although the raw NIRS data were originally relative values and could not be averaged directly across subjects or channels, normalized data, such as the Z-scores, could be averaged regardless of the unit (Schroeter et al., 2003; Matsuda and Hiraki, 2006; Shimada and Hiraki, 2006).

As in a previous study (Nakato et al., 2009), we averaged Z-scores during the period from 4 to 5 s after the face stimulus onset. A two-tailed one-sample *t*-test against a chance level of 0 (baseline) was performed on the mean Z-score from 4 to 5 s after the face stimulus onset of the test trials in both temporal areas. As the aim of the present study was to describe the developmental trajectory of each participant, we conducted linear regression analyses on each participant's Z-score with age as a dependent variable. In a previous study (Nakato et al., 2009), we observed differences between experimental conditions and between the right and left hemisphere. As such, regression analysis was conducted separately for each experimental condition and for each hemisphere. Moreover, to investigate individual differences in the linear regression graphs, we analyzed the parameters embedded in the linear regression model. Based on a previous study (Nakato et al., 2009), we concluded that this study should focus only on oxy-Hb data. Therefore, we only report our analysis of oxy-Hb hemodynamics data here.

3. Results

We analyzed hemodynamic responses obtained from 14 infants who observed the stimuli in 2 or more trials in both the frontal and profile view conditions at every measurement time point. The mean numbers of valid trials are listed in Table 1. We performed a 2-way analysis of variance (ANOVA) of the number of valid trials with condition and age as factors. We found no significant differences in the mean number of trials between the different conditions or different ages.

To account for individual differences in the development of view-invariant face processing from our longitudinal NIRS measurement, we performed linear regression analysis of the relationship between the hemodynamic responses to the face and the age at which the infants were tested. Each infants' hemodynamic response for each condition was calculated by averaging Z-scores from 4 to 5 s after stimulus onset, across trials for every month and for every condition.

We fitted a linear regression model and calculated the slope (a) and the intercept (b), for the frontal and profile conditions and the right and left temporal areas. The slope (a) of the linear regression model represents the increase in the hemodynamic response per month and the model with a greater slope predicts greater hemodynamic responses to faces than a model with a smaller slope. The intercept (b) of the linear regression model represents the hemodynamic response to a face at the age of 3 months and a model with a greater intercept thus predicted a

larger hemodynamic response at the age of 3 months when compared to a model with a smaller intercept.

Fig. 2 shows each participant's Z-score for oxy-Hb concentration in the left and right temporal areas at each age between 3 and 8 months in the frontal and profile condition. The slope a in the regression model $y = ax + b$ was greater for the profile condition than for the frontal condition.

Table 2 contains the estimated values of the slope and the intercept. The slopes in the linear regression model were larger for the profile condition than for the frontal condition in 11 of 14 infants in the right temporal area and in 12 infants in the left temporal area. A repeated-measures ANOVA of the slope was performed with 2 factors, condition (frontal versus profile view) and measurement area (right versus left). ANOVA of the slope revealed a significant main effect of condition, $F(1,13) = 9.10$, $p = .010$, partial $\eta^2 = 0.41$.

The intercept was smaller for the profile condition than for the frontal condition in 12 of 14 infants in the right temporal area and in 12 infants in the left temporal area. A repeated-measures ANOVA of the intercept with 2 factors, condition (frontal versus profile view) and measurement area (right versus left), revealed a significant main effect of condition, $F(1,13) = 6.18$, $p = .027$, partial $\eta^2 = 0.32$.

To focus on the individual difference in developmental trajectory, we further analyzed the distributions of the slope and intercept parameters of the model. We plotted the slope as y-values and the intercept as x-values, as shown in Fig. 3. As shown in each scatterplot representing the distributions of the parameters, the slope and intercept negatively correlated with each other (left temporal area in frontal condition, Pearson's $r = -0.79$, $p = .00$; right temporal area in frontal condition, $r = -0.88$, $p = .00$; left temporal area in profile condition, $r = -0.96$, $p = .00$; right temporal area in profile condition, $r = -0.54$, $p = .46$).

To show how much the correlation between the slopes and the intercepts explains the variance of individual differences, we applied Principal Component Analysis to the pairs of slopes and intercepts. The green line in Fig. 3 illustrates the first principal component, which represents the greatest variance of the data. The first principal component explained 98.3% of the variance in the distributions of the model parameters in the left temporal area in the frontal condition, 98.9% of that in the right temporal area in the frontal condition, 99.6% of that in the left temporal area in the profile condition, and 93.6% of that in the right temporal area in the profile condition.

To investigate the general tendency in the regression model used for the infants in our study, the Z-scores of all 14 subjects for oxy-Hb concentration were plotted as a function of age (Fig. 4). Consistent with the above data analysis, the regression lines for the profile view condition had larger slopes and smaller intercepts than those for the frontal view condition. We also calculated the x-intercept, which indicates the time point at which a predicted hemodynamic response was equal to the baseline value of 0. The x-intercepts in the linear regression models for the frontal condition were smaller than 3 months (model for left temporal area = -2.43 and, that for the right temporal area = -1.65), and the x-intercepts in the linear regression models for the profile condition were close to 5-months (model for the left temporal area = 5.79 , and that for the right temporal area = 5.28).

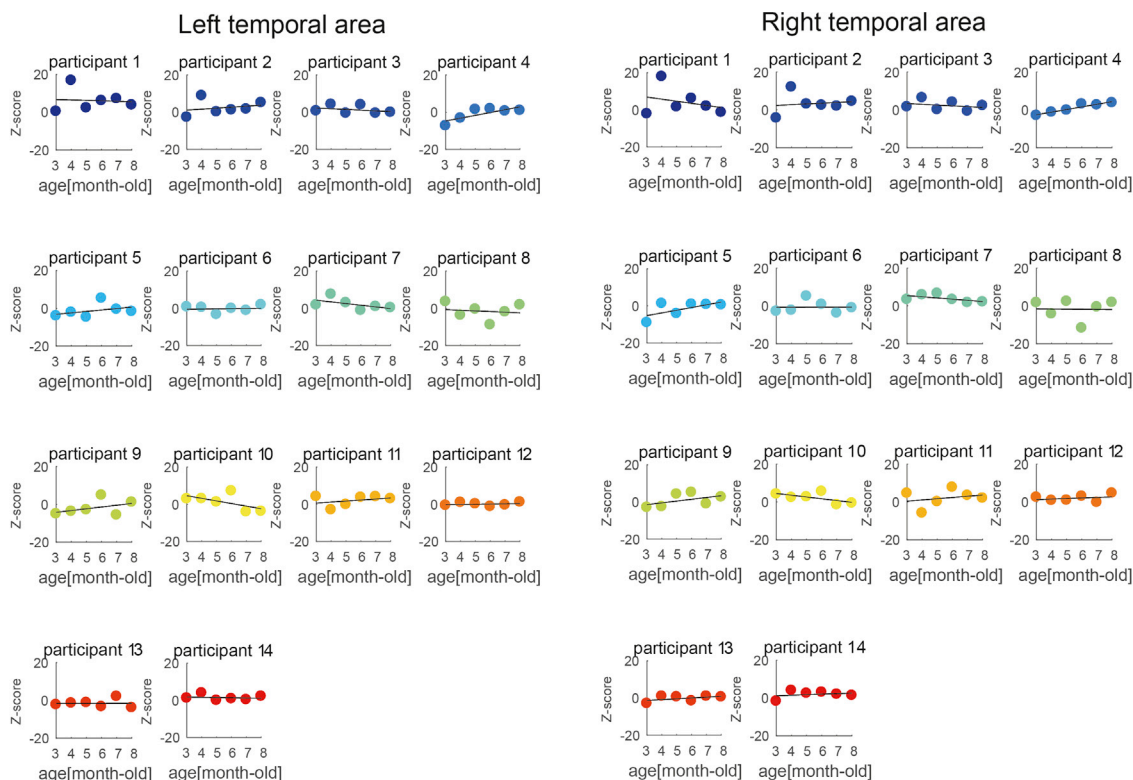
4. Discussion

In the present study, we longitudinally measured hemodynamic responses to frontal and profile faces in 14 infants every month from the age of 3 months to the age of 8 months. We investigated the individual differences in the development of view-invariant face processing. The oxy-Hb responses to frontal and profile faces for each infant at each age were modeled using a linear regression function whose parameters reflected the individual differences in the development of face processing. The slope of the linear regression model represented the increase in the hemodynamic response per month. A model with a greater slope thus predicted greater increase in the hemodynamic responses to faces than a model with a smaller slope. The intercept of the linear regression model

Table 1
Means and standard deviations of the number of valid trials.

	3 m	4 m	5 m	6 m	7 m	8 m
Frontal view	4.73	5.87	5.80	5.53	4.20	4.67
(SD)	1.79	1.88	2.34	1.96	1.57	1.76
Profile view	4.93	5.27	4.73	5.33	4.20	4.13
(SD)	1.62	1.67	2.19	2.09	1.15	1.68

Frontal condition



Profile condition

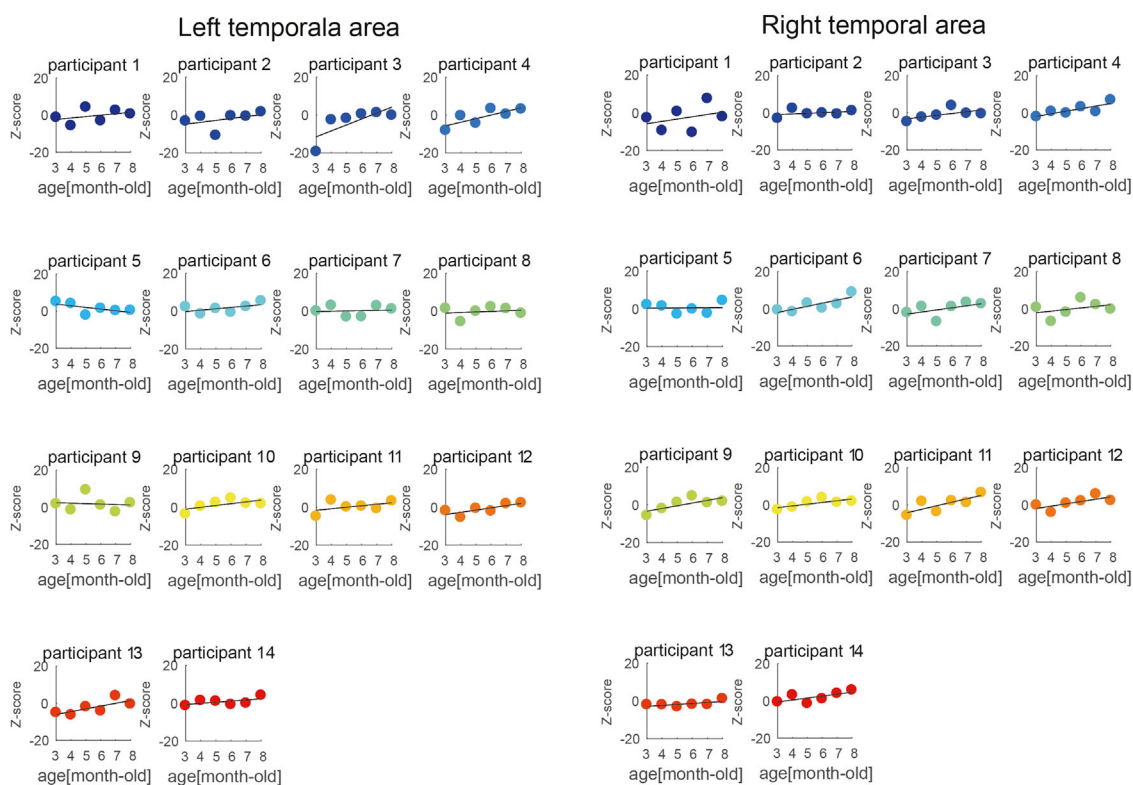


Fig. 2. Each participant's Z-score for oxy-Hb concentration at the ages of 3–8 months. Individual graphs correspond to each participant. Vertical axes indicate Z-scores and horizontal axes indicate age.

Table 2
Estimated values of the slope (*a*) and intercept (*b*) for each participant's linear regression model, $y = ax + b$. Check marks indicate that the value of the slope or intercept in the model for the frontal condition was smaller than that for the profile condition.

subject	slope (a)						intercept(b)					
	left			right			left			right		
	frontal	profile	f < p	frontal	profile	f < p	frontal	profile	f < p	frontal	profile	f < p
1	−0.23	0.76	✓	−1.13	1.21	✓	6.70	−2.33		6.87	−5.78	
2	0.53	1.00	✓	0.38	0.34		1.10	−4.82		2.35	−1.03	
3	−0.39	3.14	✓	−0.40	0.94	✓	2.27	−11.50		3.30	−3.28	
4	1.52	1.90	✓	1.38	1.38		−4.74	−5.70		−2.57	−1.96	✓
5	0.76	−0.89		1.45	0.07		−3.20	3.76	✓	−5.22	0.28	✓
6	0.11	0.72	✓	0.02	1.66	✓	−0.53	−0.23		−0.68	−1.99	
7	−0.89	0.14	✓	−0.63	1.11	✓	4.30	−0.18		5.44	−2.85	
8	−0.34	0.29	✓	−0.07	0.86	✓	−0.74	−1.03		−1.56	−2.15	
9	0.94	−0.25		0.96	1.44	✓	−4.23	2.40	✓	−1.45	−3.38	
10	−1.39	0.97	✓	−0.94	0.93	✓	4.59	−1.08		4.48	−1.52	
11	0.54	0.79	✓	0.65	1.87	✓	0.65	−1.64		0.41	−4.25	
12	0.10	1.18	✓	0.28	1.24	✓	−0.16	−3.90		1.25	−1.95	
13	0.02	1.48	✓	0.44	0.50	✓	−1.69	−6.00		−1.31	−2.90	
14	−0.14	0.61	✓	0.28	1.05	✓	1.80	−0.72		1.19	−0.58	
average	0.08	0.85		0.19	1.04		0.44	−2.36		0.89	−2.38	
s.d	0.75	0.96		0.79	0.50		3.35	3.85		3.35	1.54	

Note. Check marks indicate that the value of the slope or intercept in the model for the frontal condition was smaller than that for the profile condition.

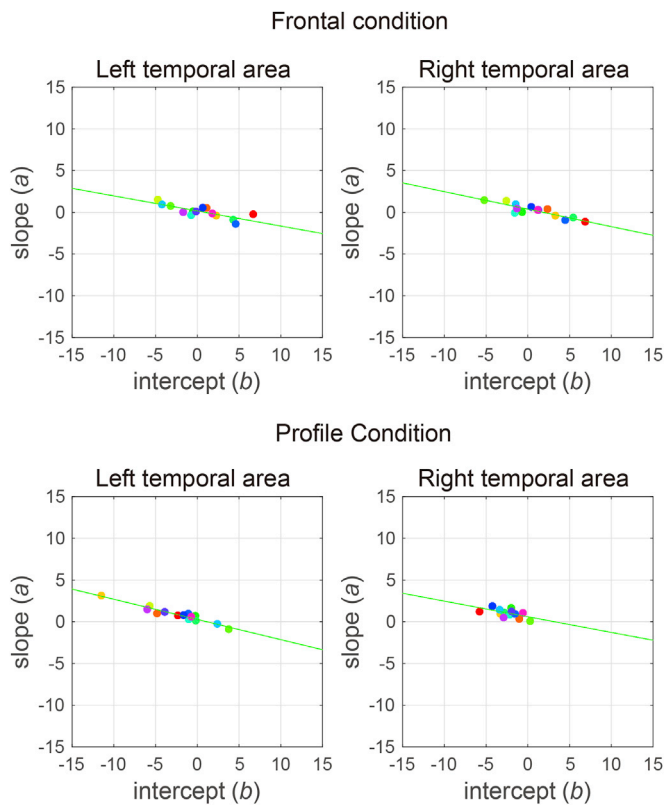


Fig. 3. Scatterplot of the slope and intercept parameters embedded in the linear regression model. In each plot, the vertical axis indicate the slope and the horizontal axis indicates the intercept. The green line illustrates the first principal component, which represented the greatest variance of the data. Each dot represent a participant.

represented the hemodynamic response to a face at the age of 3 months. A model with a greater intercept thus predicted a larger hemodynamic response at the age of 3 months when compared to a model with a smaller intercept.

Linear regression analyses of individual infants revealed that most infants had larger slopes in the model for the profile condition than for the model for the frontal condition. The averaged value of the slope for

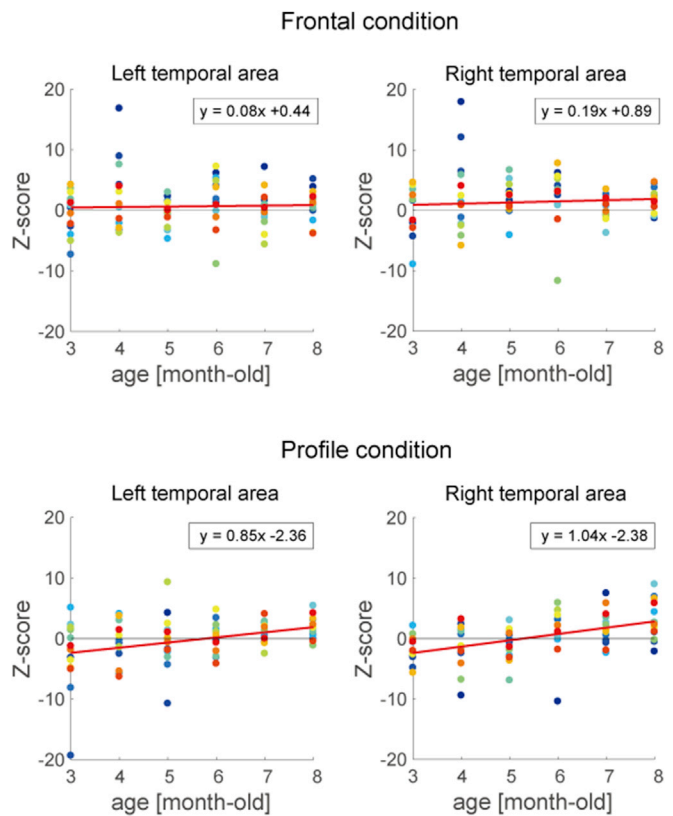


Fig. 4. Mean Z-scores for oxy-Hb concentration as a function of age. Each dot represents a subject at each age, and 14 dots were mapped. Each subject is represented by 6 points in the figure. Red lines represent the regression line for each scatterplot.

the profile condition in all infants was also larger than that for the frontal condition. These results indicate that hemodynamic responses to profile faces increased more during the period from 3 to 8 months of age than those to frontal faces. The increase in the hemodynamic response to faces with age implies that increased oxy-Hb responses correlate with cortical neuronal activation in adults, as supported by previous studies (for review, see [Lloyd-fox, Blasi and Elwell, 2010](#)). Our longitudinal

examination would allow us to expand the findings obtained in a previous study (Nakato et al., 2009), which reported that 8-month-old infants, but not 5-month-old infants, had hemodynamic responses to profile faces.

Processing of profile faces is predicted to emerge at around the age of 5 months based on our linear regression analysis. In the linear regression model, the x-intercept represented the estimated time point at which hemodynamic responses to faces were equal to the baseline value of 0. At ages older than the x-intercept, the infants' hemodynamic responses to faces were estimated to be greater than the baseline value of 0, and the infant were estimated to process profile face images differently than vegetable images. The averaged value of the x-intercept for the profile condition in all infants was larger than the 5 months. This result suggests that processing of profile faces began to emerge after the age of 5 months. This finding is consistent with those of a previous study (Nakato et al., 2009), which reported that hemodynamic responses to profile faces and frontal faces are increased in infants at an age greater than 5 months. The improvement of visual acuity could not explain the results since the visual acuity of 5-month-olds (5 cycle/degree, 0.17 in decimal visual acuity; Atkinson, 2002) and that of 8-month-olds (8 cycle/degree, 0.27 in decimal visual acuity; Atkinson, 2002) are equivalent in regards to seeing profiles of faces. We first estimated the developmental period wherein view-invariant face processing emerged using longitudinal measurements.

The y-intercepts, which indicate hemodynamic responses to profile faces at the age of 3 months, were smaller bilaterally in most infants when compared to the baseline values of 0, which was the hemodynamic response to the images of vegetables. As discussed in previous studies, greater hemodynamic responses to face images when compared to baseline indicates brain activity related to face processing. Therefore, our results suggest that most of the infants did not process the profile faces as faces at 3 months of age. About half of the infants had smaller intercepts than the baseline for the frontal face condition, while the other half had intercept values equal to or greater than the baseline. This result indicates that half of the infants already processed the frontal face images as faces at the age of 3 months. Halit et al. (2003) measured a face-responsive ERP component in infants aged 3, 6, and 12 months using upright and inverted face images of humans and monkeys. They demonstrated that even 3-month-old infants had some specialization for human upright face processing, while showing large variability in the timing of N290. Consistent with the findings of Halit et al. (2003), our findings also suggest the presence of large individual differences in face processing around the age of 3 months.

Our longitudinal measurements indicated that individual difference appeared in the parameters of the linear regression model. The individual differences affected both the slope and the intercept, which were negatively correlated. The models with smaller intercepts thus had larger slopes, and infants with smaller hemodynamic responses to faces at the age of 3 months tended have more rapid increases in the hemodynamic response during the period between 3 and 8 months of age. The individual differences converged approximately at the age of 8 months. Although our study investigated individual differences in face processing, previous behavioral studies had demonstrated individual differences in object processing and reported that such differences were related to motor ability, such as sitting or crawling. Schwarzer, Freitag, Buckel, and Lofruth (2012) demonstrated that 9-month-old infants who had crawling ability learn to recognize a three-dimensional object presented in rotational views and discriminate a mirrored object from the familiar object. In contrast, infants of the same age who did not crawl did not discriminate the two objects. Furthermore, when testing infants aged 4–8 month with face stimuli, Cashion et al. (2013) also reported that sitting ability affects infants' face processing.

The limitations of the current study are described below. We did not find differences in the hemodynamic response between the right and left hemisphere in the frontal or profile face condition. This finding was inconsistent with that in a previous study (Nakato et al., 2009). This

difference might be due to the repeated measurement of the hemodynamic response. To our knowledge, there are no reports of repeated exposure to the same experimental stimuli for 10 min per month. This may lead to memorization of the faces by the infants and should be investigated in the future. Webb et al. (2005) also reported that their longitudinal study did not fully replicate a previous short study.

In the present study, we investigated individual differences in the development of face processing during the first 3–8 months of life. To our knowledge, we are the first to longitudinally measure hemodynamic responses to human faces in infants. We used the same face stimuli and NIRS measurement procedure as those used in a previous study (Nakato et al., 2009), which reported differential responses to profile faces between 5 and 8-month-old infants. Our results indicate that the processing of profile faces emerges prior to 8 months after birth. We also investigated individual differences in the development of view-invariant face processing. The speed of the development of profile face processing was inversely correlated with the degree of hemodynamic response to faces at the age of 3 months.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Atkinson, J., 2002. *The Developing Visual Brain*. Oxford University Press, London.
- Blasi, A., Lloyd-fox, S., Johnson, M.H., Elwell, C., 2014. Test – retest reliability of functional near infrared spectroscopy in infants. *Neurophotonics* 1 (2). <https://doi.org/10.1117/1.NPh.1.2.025005>, 025005-1 – 025005-12.
- Cashion, C.H., Ha, O.R., Allen, C.L., Barna, A.C., 2013. A U-shaped relation between sitting ability and upright face processing in infants. *Child Dev.* 84, 802–809. <https://doi.org/10.1111/cdev.12024>.
- de Haan, M., Pascalis, O., Johnson, M.H., 2002. Specialization of neural mechanisms underlying face recognition in human infants. *J. Cognit. Neurosci.* 14 (2), 199–209. <https://doi.org/10.1162/089892902317236849>.
- Fagan, J.F., 1976. Infants' recognition of invariant features of faces. *Child Dev.* 47 (3), 627–638. <https://doi.org/10.2307/1128177>.
- Franceschini, M.A., Thaker, S., Themelis, G., Krishnamoorthy, K.K., Bortfeld, H., Diamond, S.G., Boas, D.A., Grant, P.E., 2007. Assessment of infant brain development with frequency-domain near-infrared spectroscopy. *Pediatr. Res.* 61 (5), 546–551. <https://doi.org/10.1203/pdr.0b013e318045be99>.
- Halit, H., de Haan, M., Johnson, M.H., 2003. Cortical specialisation for face processing?: face-sensitive event-related potential components in 3- and 12-month-old infants. *NeuroImage* 19, 1180–1193. [https://doi.org/10.1016/S1053-8119\(03\)00076-4](https://doi.org/10.1016/S1053-8119(03)00076-4).
- Honda, Y., Nakato, E., Otsuka, Y., Kanazawa, S., Kojima, S., Yamaguchi, M.K., Kakigi, R., 2010. How do infants perceive scrambled face?: a near-infrared spectroscopic study. *Brain Res.* 1308, 137–146. <https://doi.org/10.1016/j.brainres.2009.10.046>.
- Ichikawa, H., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2010. Infant brain activity while viewing facial movement of point-light displays as measured by near-infrared spectroscopy (NIRS). *Neurosci. Lett.* 482 (2), 90–94. <https://doi.org/10.1016/j.neulet.2010.06.086>.

- Ichikawa, H., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2013. Contrast reversal of the eyes impairs infants' face processing: a near-infrared spectroscopic study. *Neuropsychologia* 51 (13), 2556–2561. <https://doi.org/10.1016/j.neuropsychologia.2013.08.020>.
- Jasper, H.H., 1958. The ten twenty electrode system of the international federation. *Electroencephalogr. Clin. Neurophysiol.* 10, 371–375.
- Johnson, M.H., Morton, J., 1991. Conspect and Conlern in the human infant. In: Johnson, M.H., Morton, J. (Eds.), *Biology and Cognitive Development: the Case of Face Recognition*. Basil Blackwell, Oxford, England, pp. 104–128.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- 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 Biol. Sci.* 361 (1476), 2109–2128. <https://doi.org/10.1098/rstb.2006.1934>.
- Kobayashi, M., Macchi Cassia, V., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2018. Perceptual narrowing towards adult faces is a cross-cultural phenomenon in infancy: a behavioral and near-infrared spectroscopy study with Japanese infants. *Dev. Sci.* 21 (1) <https://doi.org/10.1111/desc.12498>.
- Kobayashi, M., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2012. Size-invariant representation of face in infant brain?: an fNIRS-adaptation study. *NeuroReport* 23 (17), 984–988. <https://doi.org/10.1097/WNR.0b013e32835a4b86>.
- Kobayashi, M., Otsuka, Y., Nakato, E., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2011. Do infants represent the face in a viewpoint-invariant manner? Neural adaptation study as measured by near-infrared spectroscopy. *Front. Hum. Neurosci.* 5, 153. <https://doi.org/10.3389/fnhum.2011.00153>.
- Lloyd-fox, S., Blasi, A., Elwell, C.E., 2010. Illuminating the developing brain?: the past, present and future of functional near infrared spectroscopy. *Neurosci. Biobehav. Rev.* 34, 269–284. <https://doi.org/10.1016/j.neubiorev.2009.07.008>.
- 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. <https://doi.org/10.1016/j.neuroimage.2005.08.019>.
- Moriguchi, Y., Hiraki, K., 2011. Longitudinal development of prefrontal function during early childhood. *Developmental Cognitive Neuroscience* 1 (2), 153–162. <https://doi.org/10.1016/j.dcn.2010.12.004>.
- Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Honda, Y., Kakigi, R., 2011a. I know this face?: neural activity during mother' face perception in 7- to 8-month-old infants as investigated by near-infrared spectroscopy. *Early Hum. Dev.* 87 (1), 1–7. <https://doi.org/10.1016/j.earlhumdev.2010.08.030>.
- Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2011b. Distinct differences in the pattern of hemodynamic response to happy and angry facial expressions in infants-a near-infrared spectroscopic study. *NeuroImage* 54 (2), 1600–1606. <https://doi.org/10.1016/j.neuroimage.2010.09.021>.
- Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Watanabe, S., Kakigi, R., 2009. When do infants differentiate profile face from frontal face? A near-infrared spectroscopic study. *Hum. Brain Mapp.* 30 (2), 462–472. <https://doi.org/10.1002/hbm.20516>.
- Otsuka, Y., Nakato, E., Kanazawa, S., Yamaguchi, M.K., Watanabe, S., Kakigi, R., 2007. Neural activation to upright and inverted faces in infants measured by near infrared spectroscopy. *NeuroImage* 34, 399–406. <https://doi.org/10.1016/j.neuroimage.2006.08.013>.
- Perlman, S.B., Huppert, T.J., Luna, B., 2016. Functional near-infrared spectroscopy evidence for development of prefrontal engagement in working memory in early through middle childhood. *Cerebr. Cortex* 26 (6), 2790–2799. <https://doi.org/10.1093/cercor/bhv139>.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J. Neurosci.* 16 (16), 5205–5215.
- Rose, S.A., Jankowski, J.J., Feldman, J.F., 2002. Speed of processing and face recognition at 7 and 12 months. *Infancy* 3 (4), 435–455. https://doi.org/10.1207/S15327078IN0304_02.
- Schroeter, M.L., Zysset, S., Kruggel, F., von Cramon, D.Y., 2003. Age dependency of the hemodynamic response as measured by functional near-infrared spectroscopy. *NeuroImage* 19, 555–564. [https://doi.org/10.1016/S1053-8119\(03\)00155-1](https://doi.org/10.1016/S1053-8119(03)00155-1).
- Schwarzer, G., Freitag, C., Buckel, R., Lofruth, A., 2012. Crawling is associated with mental rotation ability by 9-month-old infants. *Infancy* 18, 432–441. <https://doi.org/10.1111/j.1532-7078.2012.00132.x>.
- Shimada, S., Hiraki, K., 2006. Infant's brain responses to live and televised action. *NeuroImage* 32, 930–939. <https://doi.org/10.1016/j.neuroimage.2006.03.044>.
- Turati, C., Bulf, H., Simion, F., 2008. Newborns' face recognition over changes in viewpoint. *Cognition* 106 (3), 1300–1321. <https://doi.org/10.1016/j.cognition.2007.06.005>.
- Webb, S.J., Long, J.D., Nelson, C.A., 2005. A longitudinal investigation of visual event-related potentials in the first year of life. *Dev. Sci.* 8 (6), 605–616. <https://doi.org/10.1111/j.1467-7687.2005.00452.x>.
- Yamashita, W., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2012. The effect of gaze direction on three-dimensional face recognition in infant brain activity. *Neuroreport* 23 (13), 799–803. <https://doi.org/10.1097/WNR.0b013e32835734a8>.