



Perception of invisible masked objects in early infancy

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Recurrent loops in the visual cortex play a critical role in visual perception, which is likely not mediated by purely feed-forward pathways. However, the development of recurrent loops is poorly understood. The role of recurrent processing has been studied using visual backward masking, a perceptual phenomenon in which a visual stimulus is rendered invisible by a following mask, possibly because of the disruption of recurrent processing. Anatomical studies have reported that recurrent pathways are immature in early infancy. This raises the possibility that younger infants process visual information mainly in a feed-forward manner, and thus, they might be able to perceive visual stimuli that adults cannot see because of backward masking. Here, we show that infants under 7 mo of age are immune to visual backward masking and that masked stimuli remain visible to younger infants while older infants cannot perceive them. These results suggest that recurrent processing is immature in infants under 7 mo and that they are able to perceive objects even without recurrent processing. Our findings indicate that the algorithm for visual perception drastically changes in the second half of the first year of life.

visual development | recurrent processing | backward masking | infant

The standard view of cortical visual processing is that visual information is hierarchically processed along feed-forward pathways, with more complex representations created serially by relaying information from lower to higher visual areas (1). However, recurrent processing, which is mediated by corticocortical feedback and intra-areal horizontal pathways (2, 3), also contributes to fundamental visual functions (4–6). Although the role of recurrent processing is not yet well understood, many studies have proposed that visual perception is not mediated by a purely feed-forward system but rather by a system incorporating recurrent loops (7–12).

Anatomical studies of the infant brain have reported that feed-back and horizontal connections develop later than feed-forward connections (13–15). Anatomical data from postmortem brains of human infants have shown that the adult-like laminar termination pattern of forward connections between V1 and V2 emerges by 4 mo of age (14), but the feedback (14) and long-range horizontal (15) connections are immature at that age. These findings imply that until at least around the second half of the first year of life, recurrent processing is immature, and visual information may be processed mainly in a feed-forward manner. However, this possibility has so far not been examined. Although neuroimaging studies of human infants have revealed functional and structural brain development (16, 17), it is difficult to determine whether the observed activities or structures are derived from feed-forward or recurrent pathways using imaging techniques in human infant studies. Thus, in the present study, we examined recurrent processing in early infancy using visual backward masking.

Visual backward masking is a perceptual phenomenon in which a stimulus is rendered invisible by a mask presented after the target stimulus. We used object substitution masking (OSM) (18), a type of backward masking which is thought to arise from a disruption of recurrent processing (18–23). In OSM, target perception is impaired when a target is briefly presented with a sparse mask that surrounds the target, and the mask remains on screen after the target disappears, while target perception remains intact when the target and the mask disappear simultaneously. OSM has been proposed to

occur because the temporally trailing mask disrupts the recurrent signals related to the target (18). Although some studies have questioned the recurrent explanation (24, 25), evidence from psychophysical studies suggests that OSM can be plausibly explained by the recurrent theory rather than the feed-forward theory (18, 20, 22, 23). Indeed, a neuroimaging study has shown that recurrent activities in the early visual cortex are modulated when target perception is impaired by OSM (19).

Although an infant study has suggested that OSM occurs in 6-mo-old infants (26), its mechanism and development remain poorly understood. If visual processing is performed without recurrent processing in early infancy, as suggested by the anatomical studies (14, 15), OSM may not occur in younger infants. In other words, younger infants may be able to perceive a masked stimulus that older infants cannot.

Results

OSM Is Present in Older Infants. We first examined the development of OSM in 3- to 8-mo-old infants, applying a familiarization condition (26) and a preferential looking paradigm with face stimuli (Fig. 1A). It is known that infants show spontaneous preferences (longer looking time) for faces over nonface objects (27). Using this characteristic of infant's looking behavior, we can test whether or not they can perceive face stimuli followed by a mask. In an adult study, OSM has been shown to occur when faces are used as a target (28).

Two types of trials were presented in alternating sequence: delayed-mask offset and simultaneous-offset conditions (Fig. 1A). Visual stimuli were presented repeatedly on the central area of a screen in a trial. We measured infant's looking time at this screen area and compared the looking time during the trial between the

Significance

Recent studies in neuroscience suggest that visual perception is not processed by the purely feed-forward system but by the interaction of forward, horizontal, and feedback processing called recurrent loops. The present study examined the development of recurrent processing using visual backward masking, a perceptual phenomenon in which a visual stimulus is rendered invisible by a mask that follows the stimulus, possibly because of the disruption of recurrent processing. We showed that backward masking is ineffective for infants under 7 mo of age and that they can perceive masked objects that older infants cannot see because of masking. These results suggest that recurrent processing is immature in early infancy and that the mechanisms of visual perception drastically change around this age.

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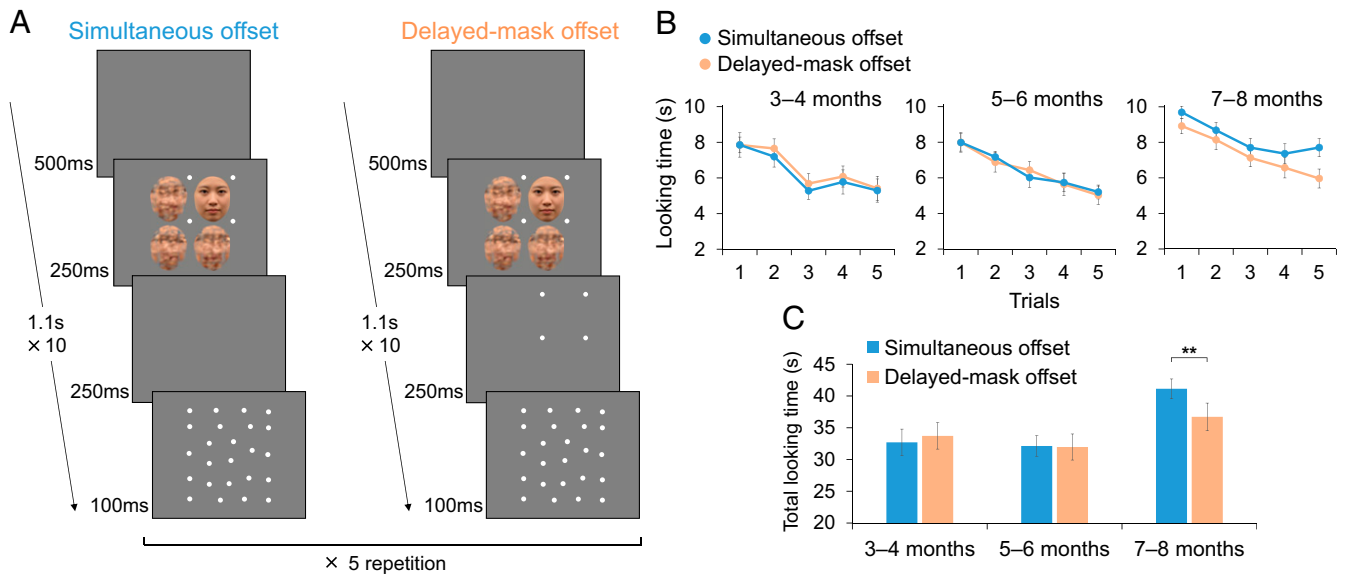


Fig. 1. OSM occurs in 7- to 8-month-old infants. (A) The two conditions in the first experiment. The trials in the two conditions were presented in alternating sequence. If OSM occurs, faces can be perceived in the simultaneous-offset condition but not in the delayed-mask offset condition. Thus, looking times should be longer in the simultaneous-offset condition. (B) Looking times for simultaneous-offset (blue) and delayed-mask offset (orange) conditions on each trial. The looking time was calculated by summing the duration in a trial during which infants looked at the central screen area. (C) Total looking times on the five trials for each condition. Refer to *SI Appendix, Fig. S1A* for individual data. All data are mean \pm SEM; $**P < 0.01$.

two conditions. Given the fact that infants prefer faces, when faces can be seen in a trial, infants would be attracted to the trial (repetition of the stimuli) and look longer at the screen area on which the stimuli were presented.

In both conditions, a face was presented with three distractors (scrambled faces) for 250 ms (Fig. 1A), during which the face was surrounded by a four-dot mask typically used in OSM (18). In the delayed-mask offset condition (masked condition), the mask remained on the screen for 250 ms after the face and distractors disappeared. In the simultaneous-offset condition (unmasked condition), the face

and mask disappeared simultaneously. To prevent the persisting four-dot mask from attracting the infants' attention, the dot array was then presented for 100 ms in both conditions. This stimulus sequence was repeated for 11 s (i.e., 10 times) on a trial. Trials in the two conditions were repeated five times. If OSM occurs, infants can perceive faces in the simultaneous-offset condition but not in the delayed-mask offset condition. Thus, the looking times should be longer in the simultaneous-offset condition.

Infants were separated into three age groups: 3 to 4 mo, 5 to 6 mo, and 7 to 8 mo of age. Looking time was different between the

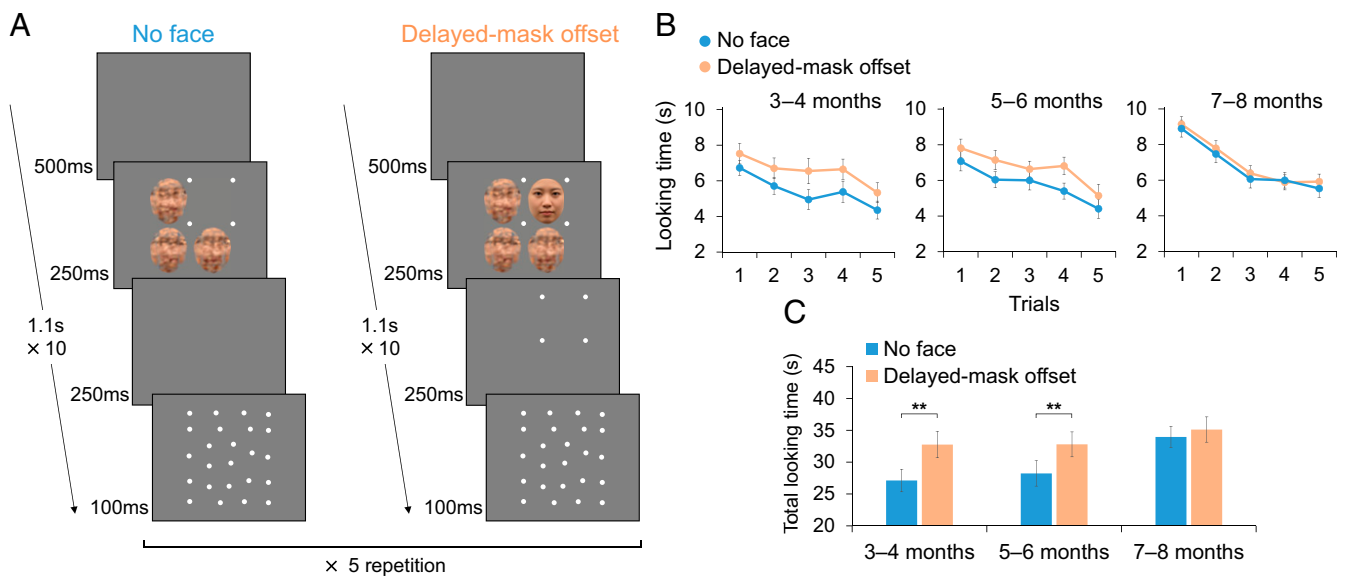


Fig. 2. Infants at 3 to 6 months are immune to OSM and can perceive faces in the masked condition. (A) The no-face and delayed-mask offset conditions in the second experiment. If OSM does not occur, looking times should be longer in the delayed-mask offset condition. (B) Looking times for the no-face (blue) and delayed-mask offset (orange) conditions on each trial. (C) Total looking times on the five trials for each condition. Refer to *SI Appendix, Fig. S1B* for individual data. All data are mean \pm SEM; $**P < 0.01$.

two conditions only in 7- to 8-mo-old infants (Fig. 1 *B* and *C*). Total looking time on the five trials was compared between the two conditions (Fig. 1*C*). Infants at 7 to 8 mo looked longer in the simultaneous-offset condition (paired Student's *t* test, $t_{19} = 3.36$, $P < 0.01$, $d = 0.52$), while infants at 3 to 4 mo and at 5 to 6 mo showed no differences between conditions (3 to 4 mo: $t_{19} = -1.12$, $P = 0.56$, $d = -0.11$; 5 to 6 mo: $t_{19} = 0.19$, $P = 0.86$, $d = 0.02$). These results indicate that only 7- to 8-mo-old infants could not perceive faces in the delayed-mask offset condition, suggesting that OSM begins to occur in 7- to 8-mo-old infants.

OSM Is Ineffective for Younger Infants. Although there was no difference between the masked and unmasked conditions in 3- to 6-mo-old infants in the first experiment, we cannot conclude that masking does not occur in younger infants based solely on nonsignificant results. To further test the absence of OSM in younger infants, we next compared delayed-mask offset and no-face conditions (Fig. 2*A*). The delayed-mask offset condition was same as that in the first experiment, and the no-face condition was the same as the simultaneous-offset condition, except that a face was not presented at the target position. If OSM does not occur, infants should perceive faces in the delayed-mask offset condition, and looking time should be longer in the delayed-mask offset condition than in the no-face condition.

In contrast to the first experiment, a difference in looking time between the two conditions was observed for infants at 3 to 4 mo and 5 to 6 mo but not at 7 to 8 mo (Fig. 2 *B* and *C*). Total looking time on the five trials was longer in the delayed-mask offset condition for infants at 3 to 4 and 5 to 6 mo (3 to 4 mo: $t_{19} = 6.15$, $P < 0.01$, $d = 0.66$; 5 to 6 mo: $t_{19} = 5.26$, $P < 0.01$, $d = 0.52$), while there was no difference for 7- to 8-mo-old infants ($t_{19} = 1.18$, $P = 0.25$, $d = 0.14$; Fig. 2*C*). These results indicate that the persisting four-dot mask was not effective for 3- to 6-mo-old infants and that they could perceive faces that the older infants could not. Taken together, these results suggest that OSM occurs in infants over 6 mo of age as it does in adults, whereas younger infants are immune to OSM.

OSM Is Ineffective for Younger Infants Even with a Contour Mask. Infants under 7 mo of age were able to perceive a face in the masked condition. However, the four-dot mask may have been insufficiently strong to cause OSM in younger infants. That is, 3- to 6-mo-old infants may have perceived the four-dot mask as four separate dots, rather than as an object (a blank square produced by four dots).

To test this possibility, we examined whether the results for younger infants could be replicated with a stronger mask, an elliptical contour, instead of four dots. The delayed-mask offset and no-face conditions were compared (similar to the second experiment) in 5- to 6-mo-old infants (Fig. 3*A*). The delayed-mask offset condition was the same as that in the previous experiments except that the mask was an elliptical ring, and the no-face condition was same as the delayed-mask offset condition except that the face was replaced by a distractor.

The results replicated those of the second experiment (Fig. 3 *B* and *C*). Infants at 5 to 6 mo looked longer in the delayed-mask offset condition ($t_{19} = 3.47$, $P < 0.01$, $d = 0.48$). Thus, infants at 5 to 6 mo could perceive faces although the mask was stronger, supporting the conclusion that OSM is ineffective for infants under 7 mo.

Validation of the Preferential Looking Paradigm. In these three experiments, it was possible that faces were presented so briefly that infants could not perceive them clearly even without masking. To confirm the validity of our paradigm, we examined whether infants preferred faces without masking. We compared looking times between face and no-face conditions without masks (*SI Appendix, Fig. S2 A and D*). The two types of comparisons were conducted in separate experiments, that is, face versus no-face with a blank in the target position (blank experiment) and face versus no-face with a distractor in the target position (distractor experiment).

In the blank experiment, infants in all age groups had longer looking times in the face condition (3 to 4 mo: $t_{15} = 3.49$, $P < 0.01$, $d = 0.58$; 5 to 6 mo: $t_{15} = 3.96$, $P < 0.01$, $d = 0.57$; 7 to 8 mo: $t_{15} = 7.49$, $P < 0.01$, $d = 0.74$; *SI Appendix, Fig. S2 B and C*). In the distractor experiment as well, infants in all age groups preferred the face condition (3 to 4 mo: $t_{15} = 3.54$, $P < 0.01$, $d = 0.52$; 5 to 6 mo: $t_{15} = 6.51$, $P < 0.01$, $d = 0.65$; 7 to 8 mo: $t_{15} = 4.94$, $P < 0.01$, $d = 0.96$; *SI Appendix, Fig. S2 E and F*). Thus, we confirmed that infants could clearly perceive faces and discriminate them from distractors.

Discussion

The present study examined OSM in infants using a preferential looking paradigm with face stimuli, taking advantage of the fact that infants prefer faces. Infants at 7 to 8 mo looked longer at the screen when unmasked faces were presented than when masked faces were presented, but infants at 3 to 6 mo did not show such difference in looking time. Moreover, when comparing the looking

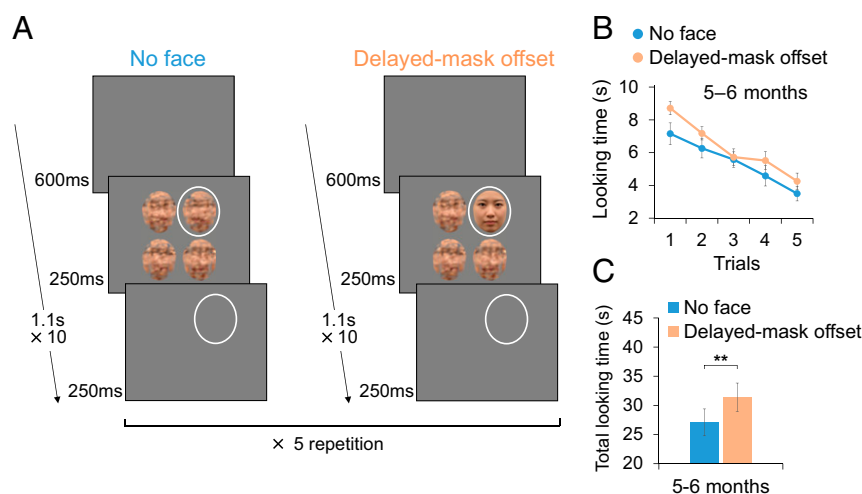


Fig. 3. Infants at 5 to 6 mo can perceive faces even with the contour mask. (*A*) In the third experiment, a stronger mask, an elliptical ring, was used in the same conditions as in the second experiment. (*B*) Looking times for the no-face (blue) and delayed-mask offset (orange) conditions on each trial. (*C*) Total looking times on the five trials for each condition. Refer to *SI Appendix, Fig. S1C* for individual data. All data are mean \pm SEM; ** $P < 0.01$.

time between the trials in which masked faces were presented and in which no face was presented, younger infants looked longer when masked faces were presented, while older infants looked equally long. These results suggest that OSM occurs in 7- to 8-mo-old infants but not in 3- to 6-mo-old infants. Importantly, the target masked by OSM, which disrupts perception in adults, remained visible to infants at 6 mo and younger. This provides evidence of distinct mechanisms of visual perception in younger infants and adults. Given the anatomical studies showing immature recurrent pathways in early infancy (14, 15), the present results could be interpreted as suggesting that recurrent processing is immature in infants at 6 mo and younger and that they can perceive visual stimuli without mature recurrent processing.

Our results demonstrate that a stimulus that can be perceived in early infancy becomes imperceptible during development. This counterintuitive result suggests that the algorithm for visual perception drastically changes in the second half of the first year. Visual processing may be performed through a feed-forward system without (or with immature) recurrent processing until around 6 mo, while it is performed through the recurrent loops in older infants and adults. Several positive functions would be acquired by incorporating recurrent processing, but it also may lead to backward masking since recurrent processing becomes critical to perceive objects.

What positive functions are acquired by maturing recurrent loops? Recurrent processing is related to the ability to integrate local information into a global context, such as figure-ground segregation (4, 6), illusory contour (29), and surround suppression (30). Thus, these functions are expected to be lacking in younger infants that do not have mature recurrent processing. Indeed, orientation-based texture segregation develops after 5 mo (31), and illusory contours can be robustly perceived after 7 mo (32, 33). Surround suppression is also immature until 6 mo (34). These complex functions develop later than processing of simple features such as orientation and motion selectivity, which develop by 3 mo (35). These facts, together with our results, imply that basic processing such as simple feature selectivity is mediated by feed-forward pathways, while more complex functions that require global integration are acquired through the development of the feedback and horizontal connectivity.

Some studies have proposed that OSM can be explained by the disruption of feed-forward processing without assuming recurrent feedback (24, 25). However, our results are somewhat difficult to reconcile with the feed-forward theory of OSM. A feed-forward account of the absence of OSM in younger infants may posit that the forward processing of a target is so fast that a masker does not catch up with it. It is unlikely, however, that forward processing is faster in younger infants than in older infants. Myelination in the occipital lobe is immature in infants (36), and the latencies of event-related potentials associated with visual perception are longer in infants than in adults (37, 38). Thus, in line with other studies suggesting that OSM is involved in recurrent processing (18–23), the recurrent account is a more plausible explanation for our results.

Another important function related to recurrent loops is predictive processing. Theoretical studies assume that the visual system constantly integrates top-down predictions with sensory inputs to resolve perceptual ambiguity (7, 11, 12). Recurrent processing has been shown to be important for robustly perceiving degraded stimuli such as occluded or unclear images (39, 40). In early infancy, such predictive mechanisms may be immature, and perception could be vulnerable to degradation and ambiguity. Perhaps, in return for susceptibility to visual masking, robustness of visual perception is acquired. On the other hand, it has been shown that visual cortical activity is modulated by top-down predictions in infants at 6 and 12 mo (41, 42). These studies used association learning tasks with visual and auditory stimuli; thus, they were related to cross-modal processing. Moreover, association learning tasks may be

related to the subcortical pathways (43). We infer that the mechanisms related to those tasks are different from those in the present study and that their developmental time course may also be different.

Materials and Methods

Participants. A total of 60 infants participated in the first experiment. The infants were divided into three age groups: 3- to 4-mo old (8 female and 12 male, age range 90 to 132 d, mean age 115.5 d), 5- to 6-mo old (9 female and 11 male, age range 148 to 191 d, mean age 170.8 d), and 7- to 8-mo old (12 female and 8 male, age range 207 to 254 d, mean age 233.2 d). An additional 17 infants were excluded from the analysis because of fussiness ($n = 10$; 3 to 4 mo: 4 infants, 5 to 6 mo: 5 infants, 7 to 8 mo: 1 infant) or insufficient looking time (the total looking time on the 10 trials was less than 30% of the entire duration of the trials, $n = 7$; 3 to 4 mo: 6 infants, 5 to 6 mo: 1 infant). An additional 24 infants were recruited for the experiment but did not agree to participate, and another 7 agreed to participate but canceled or did not show up.

A total of 60 infants participated in the second experiment and were divided into three age groups: 3- to 4-mo old (11 female and 9 male, age range 82 to 133 d, mean age 109.0 d), 5- to 6-mo old (11 female and 9 male, age range 150 to 194 d, mean age 170.5 d), and 7- to 8-mo old (10 female and 10 male, age range 204 to 254 d, mean age 227.9 d). An additional 16 infants were excluded because of fussiness ($n = 8$; 3 to 4 mo: 4 infants, 5 to 6 mo: 1 infant, 7 to 8 mo: 3 infants) or insufficient looking time ($n = 8$; 3 to 4 mo: 7 infants, 7 to 8 mo: 1 infant). An additional 25 infants were recruited but did not agree to participate, and another four agreed to participate but canceled or did not show up.

A total of 20 infants at 5 to 6 mo participated in the third experiment (7 female and 13 male, age range 136 to 190 d, mean age 162.1 d). An additional infant was excluded because of insufficient looking time. An additional five infants were recruited but did not agree to participate, and another infant agreed to participate but canceled or did not show up.

In the fourth experiment, 96 infants participated. In the blank experiment, 48 infants were divided into three age groups: 3- to 4-mo old (9 female and 7 male, age range 86 to 134 d, mean age 113.3 d), 5- to 6-mo old (9 female and 7 male, age range 142 to 194 d, mean age 171.8 d), and 7- to 8-mo old (11 female and 5 male, age range 204 to 254 d, mean age 230.8 d). An additional nine infants were excluded because of fussiness ($n = 6$; 3 to 4 mo: 4 infants, 5 to 6 mo: 2 infants) or insufficient looking time ($n = 3$; 3 to 4 mo: 2 infants, 5 to 6 mo: 1 infant). An additional 20 infants were recruited but did not agree to participate, and another 6 agreed to participate but canceled or did not show up. In the distractor experiment, 48 infants were divided into three age groups: 3- to 4-mo old (7 female and 9 male, age range 85 to 134 d, mean age 114.5 d), 5- to 6-mo old (9 female and 7 male, age range 152 to 194 d, mean age 172.8 d), and 7- to 8-mo old (11 female and 5 male, age range 200 to 253 d, mean age 230.5 d). An additional six infants were excluded because of fussiness ($n = 5$; 3 to 4 mo: 3 infants, 7 to 8 mo: 2 infants) or insufficient looking time ($n = 1$; 7 to 8 mo: 1 infant). An additional 18 infants were recruited but did not agree to participate, and another 14 agreed to participate but canceled or did not show up.

The infants were recruited through advertisements posted in local newspapers twice a month and on the laboratory website. Participants received payment for their participation in the experiment. All infants were at full term at birth and healthy at the time of the experiment. This study was conducted according to the Declaration of Helsinki and was approved by the Ethical Committee of Chuo University. Written informed consent was obtained from parents.

Apparatus and Visual Stimuli. Visual stimuli were presented on an LCD monitor (Cambridge Research Systems, Display++, 32 inch, 1920 × 1080 resolution, 120 Hz) using PsychoPy 1.90.3. An infant sat on a parent's lap in front of the display at a viewing distance of 60 cm in a dark room. A camera was set below the display to monitor and record the infant's looking behavior. An experimenter observed the infant's behavior through a monitor connected to the camera. To record the starting and end points of each trial, which are needed for the offline analysis, captions were inserted in the video through a character generator (Horita, SCT-50), which was operated by the computer controlling the stimulus presentation.

Face stimuli were created by morphing photo images of female frontal view faces. Five-face stimuli were created; four to eight different persons were morphed for each face stimulus. All face stimuli were cropped into an identical shape (5.3° in width, 6.6° in height) to remove the outer features. Distractors were created by local-phase scrambling of a face: the face image

was separated into nine square areas and phase scrambling was done in each area. The scrambled image was then cropped, and a Gaussian blur was applied. Six scrambled images were created, and three were randomly chosen as distractors for each trial. The size and contour of distractors were the same as the face stimuli. A face and three distractors were presented in the cells of a 2×2 matrix on a uniform gray background (50.2 cd/m^2). The distance between the centers of the monitor and the stimuli was 3.2° on the horizontal axis and 3.4° on the vertical axis.

The four-dot mask consisted of four white dots (0.7° in diameter, 98.8 cd/m^2) located at the corners of the face stimulus. The distance between each dot and the center of the face stimulus was 3.1° on the horizontal and vertical axes. In the third experiment, the ring mask (6.6° in width, 7.8° in height, 0.3° in line width, 98.8 cd/m^2) was presented instead of the four-dot mask. The spacing between the ring mask and the contour of the faces was at least 0.4° . The dot array presented after the four-dot mask consisted of a few dozen dots (each identical to those in the four-dot mask) and subtended 12.8° (width) by 15.5° (height).

Experimental Procedure. We applied a familiarization condition (26) and the preferential looking paradigm to test whether infants could perceive faces. Trials of two conditions were presented sequentially. Visual stimuli were presented repeatedly on the central area of a screen in a trial. We measured infants' looking time at the central screen area on which the stimuli were presented and compared the looking time during the trial between two conditions to examine which condition infants looked at longer. Infants tend to prefer faces (27). Thus, when faces can be seen in trials of one condition, the trials would be attractive to infants and the looking time would be longer.

In the first experiment, the delayed-mask offset and simultaneous-offset conditions were compared in 3- to 8-month-old infants (Fig. 1A). In both conditions, first, a face surrounded by the four-dot mask and three distractors were presented for 250 ms. In the delayed-mask offset condition, the mask remained on the screen for 250 ms after the face and distractors disappeared. In the simultaneous-offset condition, the face and mask disappeared simultaneously and were followed by a 250-ms blank. The dot array was then presented for 100 ms in both conditions to prevent the persisting four-dot mask from attracting the infants' attention. This stimulus sequence was repeated 10 times at 500-ms intervals (i.e., 11 s) in a trial. The same face stimulus was presented in a trial (the face of a person was repeated 10 times). On each repetition in a trial, the face and distractors were located at random positions in the 2×2 matrix, but a face did not appear in the same position sequentially so that infants did not see the face in central vision.

The trials in the two conditions were presented in sequence, with the order of the two conditions counterbalanced across infants. The pair of the two trials (simultaneous and delayed-mask offset conditions) were repeated five times (five trials for each condition). Five different faces were used on the five trials. The two conditions shared the same five-face stimuli, but the ordering was randomized for each condition. Each trial started when the infant looked at a cartoon presented at the center of the monitor at the same time as a short beeping sound. The cartoon was presented repeatedly for 1 s with 400-ms intervals until infants looked at it.

We measured the duration during which the infant looked at the central screen area on which the stimuli were presented in a trial from recorded videos and defined it as the looking time (*Data Coding and Analysis*). We compared the total looking time in the five trials between the two conditions (Fig. 1C). If OSM occurs, infants can perceive faces in the simultaneous-offset condition but not in the delayed-mask offset condition. Thus, the looking time would be longer in the simultaneous-offset condition.

In the second experiment, the delayed-mask offset and no-face conditions were compared in 3- to 8-month-old infants (Fig. 2A). The delayed-mask offset condition was the same as that in the first experiment. The no-face condition was the same as the simultaneous-offset condition, except that the face was replaced by a blank. If OSM does not occur, the looking time would be longer in the delayed-mask offset condition.

In the third experiment, the delayed-mask offset and no-face conditions were compared in 5- to 6-month-old infants (Fig. 3A). The same two conditions as in the second experiment were compared, but an elliptical ring was used as the mask instead of the four dots. In the no-face condition, unlike that in the second experiment in which a blank was surrounded by the mask, a distractor was surrounded by the mask. Also, unlike the previous no-face condition, the mask remained on screen after the target disappeared to exclude the possibility that infants would prefer the persisting mask. This enabled a fairer comparison of the delayed-mask offset and no-face conditions. The dot array was not presented in this experiment because the mask was presented in both conditions.

In the fourth experiments, to confirm validity of our paradigm, the face and no-face conditions were compared without the mask in 3- to 8-month-old infants (*S1 Appendix, Fig. S2 A and B*). In the face condition, the face and the four dots coterminated (as in the simultaneous-offset condition of the first experiment). The no-face conditions were same as the face condition, except that the face was replaced by either a blank or a distractor. The two experiments were conducted separately: face versus no-face (blank) and face versus no-face (distractor).

Data Coding and Analysis. Looking time was scored offline from videos of the infant's face recorded during the experiment. An observer, blind to the stimuli presented on the trials, judged whether the infant looked at the central screen area on which the stimuli were presented. The observer pressed a key whenever the infant looked at the central screen area and released the key whenever they looked away during the trial. The observer could identify when the cartoon was presented and when the trial started and ended through the captions on the video. The duration during which the key was pressed was recorded in milliseconds using our PsychoPy program. The duration in a trial was summed, and it was defined as the looking time for a trial. The data of infants whose total looking time in the 10 trials was less than 30% (33 s) of the entire duration of the 10 trials (110 s) was excluded to exclude infants that directed little attention to the stimuli presented on the monitor. To calculate an interobserver reliability, a second independent observer who was not informed of the study objectives measured the looking time from ~30% of all the data for each experiment: 18 of the 60 infants (6 infants for each age group) for the first and second experiments, 6 of the 20 infants for the third experiment, and 15 of the 48 infants (5 infants for each age group) for the fourth experiments. The interobserver reliabilities (Pearson correlation) calculated on the total looking time of the five trials were $r = 0.93, 0.95, 0.94, 0.96,$ and 0.96 in the first, second, third, and fourth (blank and distractor) experiments, respectively.

Sample size was estimated based on data of previous infant studies that measured looking time (44) and was calculated to achieve a power of 0.8 with an effect size of 0.65 in the first, second, and third experiments (masking paradigm). In the fourth experiment (nonmasking paradigm), sample size was determined to achieve a power of 0.8 with an effect size of 0.75.

Paired Student's t tests were conducted to compare the total looking times on five trials between the two conditions for each age group. All Student's t tests were two sided. The P values were adjusted using the Bonferroni–Holm method for the three comparisons of each age group in all experiments except the third. Effect size (Cohen's d) was calculated for all Student's t tests.

Data Availability. The data used to generate the findings of this study are available in Figshare with the identifier DOI: [10.6084/m9.figshare.13220873](https://doi.org/10.6084/m9.figshare.13220873).

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1. M. Riesenhuber, T. Poggio, Hierarchical models of object recognition in cortex. *Nat. Neurosci.* **2**, 1019–1025 (1999).
2. D. J. Felleman, D. C. Van Essen, Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* **1**, 1–47 (1991).
3. N. T. Markov et al., Anatomy of hierarchy: Feedforward and feedback pathways in macaque visual cortex. *J. Comp. Neurol.* **522**, 225–259 (2014).
4. J. M. Hupé et al., Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature* **394**, 784–787 (1998).
5. A. Pascual-Leone, V. Walsh, Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science* **292**, 510–512 (2001).
6. M. W. Self, T. van Kerkoerle, H. Supér, P. R. Roelfsema, Distinct roles of the cortical layers of area V1 in figure-ground segregation. *Curr. Biol.* **23**, 2121–2129 (2013).
7. K. Friston, A theory of cortical responses. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 815–836 (2005).
8. C. D. Gilbert, W. Li, Top-down influences on visual processing. *Nat. Rev. Neurosci.* **14**, 350–363 (2013).
9. S. Hochstein, M. Ahissar, View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron* **36**, 791–804 (2002).
10. V. A. F. Lamme, P. R. Roelfsema, The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* **23**, 571–579 (2000).

11. D. Mumford, On the computational architecture of the neocortex. II. The role of cortico-cortical loops. *Biol. Cybern.* **66**, 241–251 (1992).
12. R. P. N. Rao, D. H. Ballard, Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci.* **2**, 79–87 (1999).
13. A. Batardière *et al.*, Early specification of the hierarchical organization of visual cortical areas in the macaque monkey. *Cereb. Cortex* **12**, 453–465 (2002).
14. A. Burkhalter, Development of forward and feedback connections between areas V1 and V2 of human visual cortex. *Cereb. Cortex* **3**, 476–487 (1993).
15. A. Burkhalter, K. L. Bernardo, V. Charles, Development of local circuits in human visual cortex. *J. Neurosci.* **13**, 1916–1931 (1993).
16. G. Dehaene-Lambertz, E. S. Spelke, The infancy of the human brain. *Neuron* **88**, 93–109 (2015).
17. J. Dubois *et al.*, The early development of brain white matter: A review of imaging studies in fetuses, newborns and infants. *Neuroscience* **276**, 48–71 (2014).
18. V. Di Lollo, J. T. Enns, R. A. Rensink, Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *J. Exp. Psychol. Gen.* **129**, 481–507 (2000).
19. C. N. Boehler, M. A. Schoenfeld, H. J. Heinze, J. M. Hopf, Rapid recurrent processing gates awareness in primary visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 8742–8747 (2008).
20. S. Bouvier, A. Treisman, Visual feature binding requires reentry. *Psychol. Sci.* **21**, 200–204 (2010).
21. B. G. Breitmeyer, Visual masking: Past accomplishments, present status, future developments. *Adv. Cogn. Psychol.* **3**, 9–20 (2008).
22. S. C. Goodhew, P. E. Dux, O. V. Lipp, T. A. W. Visser, Understanding recovery from object substitution masking. *Cognition* **122**, 405–415 (2012).
23. A. Jannati, T. M. Spalek, V. Di Lollo, A novel paradigm reveals the role of reentrant visual processes in object substitution masking. *Atten. Percept. Psychophys.* **75**, 1118–1127 (2013).
24. S. L. Macknik, S. Martinez-Conde, The role of feedback in visual masking and visual processing. *Adv. Cogn. Psychol.* **3**, 125–152 (2008).
25. E. Pöder, Attentional gating models of object substitution masking. *J. Exp. Psychol. Gen.* **142**, 1130–1141 (2013).
26. E. Kotsoni, D. Mareschal, G. Csibra, M. H. Johnson, Common-onset visual masking in infancy: Behavioral and electrophysiological evidence. *J. Cogn. Neurosci.* **18**, 966–973 (2006).
27. C. C. Goren, M. Sarty, P. Y. Wu, Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics* **56**, 544–549 (1975).
28. J. E. Reiss, J. E. Hoffman, Disruption of early face recognition processes by object substitution masking. *Vis. Cogn.* **15**, 789–798 (2007).
29. P. Kok, L. J. Bains, T. van Mourik, D. G. Norris, F. P. de Lange, Selective activation of the deep layers of the human primary visual cortex by top-down feedback. *Curr. Biol.* **26**, 371–376 (2016).
30. J. J. Nassi, S. G. Lomber, R. T. Born, Corticocortical feedback contributes to surround suppression in V1 of the alert primate. *J. Neurosci.* **33**, 8504–8517 (2013).
31. C. Rieth, R. Sireteanu, Texture segmentation and visual search based on orientation contrast: An infant study with the familiarization-novelty preference method. *Infant Behav. Dev.* **17**, 359–369 (1994).
32. G. Csibra, Illusory contour figures are perceived as occluding surfaces by 8-month-old infants. *Dev. Sci.* **4**, F7–F11 (2001).
33. Y. Otsuka, M. K. Yamaguchi, Infants' perception of illusory contours in static and moving figures. *J. Exp. Child Psychol.* **86**, 244–251 (2003).
34. Y. Nakashima, M. K. Yamaguchi, S. Kanazawa, Development of center-surround suppression in infant motion processing. *Curr. Biol.* **29**, 3059–3064.e2 (2019).
35. O. Braddick, D. Birtles, J. Wattam-Bell, J. Atkinson, Motion- and orientation-specific cortical responses in infancy. *Vision Res.* **45**, 3169–3179 (2005).
36. H. C. Kinney, B. A. Brody, A. S. Kloman, F. H. Gilles, Sequence of central nervous system myelination in human infancy. II. Patterns of myelination in autopsied infants. *J. Neuropathol. Exp. Neurol.* **47**, 217–234 (1988).
37. M. de Haan, O. Pascalis, M. H. Johnson, Specialization of neural mechanisms underlying face recognition in human infants. *J. Cogn. Neurosci.* **14**, 199–209 (2002).
38. S. Kouider *et al.*, A neural marker of perceptual consciousness in infants. *Science* **340**, 376–380 (2013).
39. K. Kar, J. J. DiCarlo, Fast recurrent processing via ventrolateral prefrontal cortex is needed by the primate ventral stream for robust core visual object recognition. *Neuron* **109**, 164–176.e5 (2021).
40. D. Wyatte, T. Curran, R. O'Reilly, The limits of feedforward vision: Recurrent processing promotes robust object recognition when objects are degraded. *J. Cogn. Neurosci.* **24**, 2248–2261 (2012).
41. L. L. Emberson, J. E. Richards, R. N. Aslin, Top-down modulation in the infant brain: Learning-induced expectations rapidly affect the sensory cortex at 6 months. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 9585–9590 (2015).
42. S. Kouider *et al.*, Neural dynamics of prediction and surprise in infants. *Nat. Commun.* **6**, 8537 (2015).
43. H. E. M. den Ouden, K. J. Friston, N. D. Daw, A. R. McIntosh, K. E. Stephan, A dual role for prediction error in associative learning. *Cereb. Cortex* **19**, 1175–1185 (2009).
44. L. M. Oakes, Sample size, statistical power, and false conclusions in infant looking-time research. *Infancy* **22**, 436–469 (2017).