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# The face inversion effect in infants is driven by high, and not low, spatial frequencies

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**To investigate the mechanisms underlying development of upright face preferences in infants, the current study measured inversion effects for faces that were spatial frequency (SF) filtered, into low SF and high SF, with the notion that different SFs are analyzed by different visual mechanisms. For comparison to faces, we used object stimuli that consisted of pictures of strollers. In 4 month olds, 8 month olds, and adults, we measured the strength of the selective face inversion effect (sFIE), operationally defined as an upright over inverted looking preference that is greater for faces than objects. In Study 1, we employed unfiltered stimuli, and found a clear sFIE in both infants and adults. To determine what drove this sFIE, in Study 2, the sFIE was measured for low-SF and high-SF stimuli, with all stimuli being equated for visibility. For adults, the sFIE was equally strong for low-SF and high-SF stimuli. A different pattern was seen for infants. Infants exhibited a significantly greater sFIE for high-SF, than for low-SF, stimuli (and only for high SF was the sFIE significant). In fact, the strength of infants' upright face preference for high-SF stimuli was indistinguishable from that observed for unfiltered faces, indicating that in natural (unfiltered) stimuli, high SFs are sufficient to account for infants' upright face preferences.**

## Introduction

Faces belong to a privileged class of stimuli, which are biologically significant and are processed quite efficiently. Development of face processing abilities appears to start very early in infancy. For example, within the first few days of life, newborn infants display preferences for faces versus objects (e.g., Fantz, 1963; Johnson, Dziurawiec, Ellis, & Morton, 1991; de Haan & Nelson, 1999) and preferences for their mother's versus a stranger's face (e.g., Field, Cohen, Garcia, & Greenberg, 1984; Bushnell, 2001, and see de Haan & Nelson, 1997, for neural evidence). In habituation studies, it has been shown that infants can discriminate between different faces (e.g., Pascalis & de Schonen, 1994; Slater et al., 1998; Sangrigoli & De Schonen, 2004; Humphreys & Johnson, 2007; Kelly et al., 2008; Slater et al., 2010). Although face processing abilities begin to develop very early in infancy, a variety of face processing abilities continue to develop well into childhood, including face recognition (Diamond & Carey, 1997; Carey, Diamond, & Woods, 1980), configural face processing (Mondloch, Grand, & Maurer, 2002; Mondloch, Leis, & Maurer, 2006), and holistic face processing (Schwarzer, 2002; Pellicano & Rhodes, 2003). Most relevant to the *current study*, by 3 months of age, infants prefer upright to inverted faces (e.g., Turati, Sangrigoli, Ruel, & de Schonen, 2004; Turati, Valenza, Leo, & Simion, 2005, and see Otsuka et al., 2007, for neural evidence), and face inversion effects continue to develop into childhood (Carey & Diamond, 1977; Brace et al., 2001; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan & Johnson, 2003; Pellicano & Rhodes, 2003; Picozzi, Macchi Cassia, Turati, & Vescovo, 2009; de Heering, Rossion, & Maurer, 2012, and see McKone, Crookes, & Kanwisher, 2009; Pascalis et al., 2011, for reviews).

Despite a large literature on face processing in infants and children, relatively little is known about the mechanisms underlying its development. The purpose of the current study was to investigate mechanisms underlying one signature of face processing in infants, specifically, preferences for upright faces. In the adult literature, one way researchers have investigated face processing mechanisms has been to ask which spatial frequencies (SFs) are most important for processing faces, with the idea that different SFs are analyzed by different visual mechanisms. In these studies, faces are either SF-filtered or masked with SF noise, and then

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some aspect of face discrimination is tested. Although results across studies in adults are slightly different depending on whether subjects are discriminating between different facial identities or between different facial expressions of emotions (e.g., Schyns & Oliva, 1999; Vuilleumier, Armony, Driver, & Dolan, 2003; Gao & Maurer, 2011) the general consensus is that the most important SFs for face processing are in a midband, between 8 and 25 cycles/face width (Tieger & Ganz, 1979; Hayes, Morrone, & Burr, 1986; Costen, Parker, & Craw, 1994; Costen, Parker, & Craw, 1996; Näsänen, 1999; Parker & Costen, 1999; Boutet, Collin, & Faubert, 2003; Vuilleumier et al., 2003; Tanskanen, Näsänen, Montez, Päällysaho, & Hari, 2005; Willenbockel et al., 2010; Gao & Maurer, 2011). Importantly, this reliance on midband SFs for faces appears to differ from the SFs used for nonface objects, making the midband SF reliance at least somewhat selective for faces (Biederman & Kalocsai, 1997; Boutet et al., 2003; Goffaux, Gauthier, & Rossion, 2003 Collin, Liu, Troje, McMullen, & Chaudhuri, 2004).

In the child development literature, there have been a handful of studies addressing which SFs children use most for discriminating between different facial identities (Deruelle, Rondan, Gepner, & Tardif, 2004; Deruelle & Fagot, 2005; Deruelle, Rondan, Salle-Collemiche, Bastard-Rosset, & Da Fonséca, 2008; Leonard, Karmiloff-Smith, & Johnson, 2010; Gao & Maurer, 2011). In particular, Gao and Maurer (2011) used SF masking and showed that, by 10 years of age (the youngest age tested in their study), the critical band for face discrimination is similar to that of adults, with midband SFs (peak at 11 cycles/face width) being most important. In line with Gao and Maurer's finding of a midband SF bias in children and adults, Leonard et al. (2010) used SF masking and showed that, like their adult subjects, 9- and 10-year-old children rely mostly on midband SFs ($\sim$16 cycles/face width, and see their discussion for why results from Deruelle et al. (2004, 2008) also support a mid-band SF bias in childhood). Most interestingly, younger children in the Leonard et al. study, ages 7 and 8 years, showed a different pattern—roughly equal reliance on mid and high SFs (with high being roughly $\sim$32 cycles/face width). These results from younger children in the Leonard et al. study suggest that there may be a developmental change in the mechanisms underlying face processing, an idea we return to in the Discussion.

In the infant literature, it has been proposed that infants should have a low-SF bias for face processing. This low-SF hypothesis, which has been reviewed in depth previously (Johnson, 2005, 2011, and see Pessoa & Adolphs, 2010), is based on the confluence of three concepts: (a) there are two systems for face processing, one subcortical (through the superior colliculus, pulvinar, and amygdala), and the other cortical (involving the fusiform face area, FFA), (b) the subcortical system is more responsive to low SF, while the cortical system is more responsive to high SF, and (c) infants rely more on subcortical face processing mechanisms, partially because the cortical system takes longer to mature. To date, a single study in newborns has investigated which SFs infants use most for discriminating between different facial identities (de Heering et al., 2007). In this study that employed SF-filtered faces, the habituation method was used to compare face discrimination abilities for low- versus high-SF faces, where SF was described in cycles/degree, not cycles/face width (although the latter is easily calculable based on knowing viewing distance, and we return to the issue of using cycles/degree vs. cycles/face-width in the Discussion). (Note that in this infant study, only low and high SF were tested, rather than three different SF bands, as in many adult studies [see above], most likely because [a] infants cannot tolerate many different conditions, and [b] their range of visible SFs is limited, and thus dividing this limited range into smaller divisions becomes unfeasible.)

In the first experiment of de Heering et al. (2007), where the low-SF faces were below 1 cycle/° (24 cycles/face width) and the high-SF faces were above 1 cycle/°, infants revealed better performance for the low-SF stimuli. However, the authors acknowledged that this result was likely due to newborn infants, with their very poor acuity (e.g., Atkinson, Braddick, & Braddick, 1974; Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978; Atkinson & Braddick, 1983), not being able to detect the high-SF stimuli. To address this, in a second experiment, they used a cutoff of 0.5 cycles/° (12 cycles/face width), with the notion that the high-SF stimuli in this experiment should be detectable to infants (based on newborn acuity being about 1 cycle/° and previous data from their laboratory showing that newborns can discriminate other nonface stimuli when filtered from 0.5 to 1 cycles/°: Macchi Cassia, Simion, Milani, & Umiltà, 2002). Mirroring the results of their first experiment, in this second experiment, infants showed better performance for the low-SF, than the high-SF, stimuli. Based on these findings, the authors concluded that newborn infants rely more on low-SF, than high-SF, for face processing.

We believe, however, that there is a limitation to this conclusion. Despite the fact that infants in the second study of de Heering et al. (2012) could probably detect both the low- and high-SF stimuli, it is highly unlikely that the two stimulus types were equally visible for them (i.e., that they were of the same "perceived contrast"). Given newborn infants' very poor acuity and low contrast sensitivity, the low-SF stimulus was likely far more visible than the high-SF stimulus. If this were the case, it would not be surprising to find better discrimination performance for the low-SF stimulus.

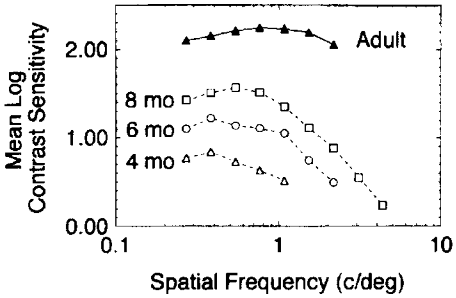

Figure 1. Contrast sensitivity functions (CSFs). Plotted is mean log contrast sensitivity as a function of spatial frequency for 4-, 6- and 8-month-old infants and adults. Reproduced from Peterzell and Teller (1996, p. 3082).

In the current study, we employed SF-filtered stimuli to investigate face processing in infants, while attempting to equate the visibility (i.e., the perceived contrast) of the different SF-band stimuli. To this end, we first determined contrast detection thresholds for low- and high-SF stimuli, and then presented them at equal multiples of contrast threshold.[1] Our low-SF and high-SF stimuli were selected by using a SF cutoff that was close to the peak SF of the contrast sensitivity function for the ages tested (based on data from Peterzell, Werner, & Kaplan, 1995, Figure 1, and see Methods), which were 4 months olds, 8 month olds, and adults in the current study. Our measure was preference for upright over inverted faces, which we chose because such preferences are thought to be a signature of special processing of faces in infants, and because these preferences are quite robust and easy to measure in infants. We refer to this preference as a face inversion effect (FIE). In children and adults, FIEs are typically demonstrated in the form of faster and/or superior detection and/or discrimination for upright than inverted faces (see references, above). Because these inversion effects are not typically seen for nonface stimuli (with the exception being objects for which a person has expertise, such as birds to a bird expert, e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000), they are thought to provide evidence that faces engage special processing mechanisms.

In the current study, we created a measure of the selectivity of inversion effects for faces by adding control stimuli that consisted of pictures of strollers. Face and stroller stimuli were equated in terms of low-level visual characteristics (luminance, contrast, size, and SF) to ensure that any differences in results between faces and strollers could not be due to these factors. A *selective face inversion effect* (sFIE) was defined as a greater inversion effect for faces than objects. In Study 1, we employed unfiltered stimuli, and found that both infants and adults exhibited a clear sFIE. To investigate which SFs underlie the sFIE revealed in Study 1, Study 2 used spatial frequency (SF)-filtered stimuli, and asked whether the sFIE is driven more by low-SF versus high-SF stimuli.

# Methods

## Subjects

Typically developing 4- and 8-month-old infants were recruited from the San Diego area via letters sent to parents. All infants were screened through parent report questionnaires for any abnormal medical conditions. Adult subjects were recruited from the student population at UC San Diego and from our laboratory. In accordance with the guidelines of the Internal Review Committee at UC San Diego, all adult subjects signed a consent form and the parent of each infant signed a consent form for their infant to participate.

In total, 56 4 month olds (mean age = 4.03 + 0.15 months), 32 8 month olds (mean age = 8.01 + 0.14 months), and 18 adults (mean age = 22 + 0.94 years) participated in and contributed to the data in these studies. A different set of 4 month olds contributed to the data in Study 1 ($n = 14$, seven female) and Study 2 ($n = 24$, eight female), because we found that 4 month olds could not tolerate being in more than one study. By contrast, the same set of 8 month olds contributed to the data in Studies 1 and 2 ($n = 14$, 11 female). Note that in Study 2, there were more 4 month olds tested than 8 month olds because the data from the former group were noisier and therefore needed more subjects to obtain clear results. Prior to conducting Study 2, we obtained contrast detection thresholds (see Contrast detection thresholds, explained further below) to make the stimuli in Study 2 all equally visible. To this end, we tested a different set of 18 4 month olds ($n = 9$ for face contrast thresholds and $n = 9$ for object contrast thresholds) and 18 8 month olds ($n = 9$ for face contrast thresholds and $n = 9$ for object contrast thresholds). Fourteen adult subjects (11 female) participated in Study 1. Ten adult subjects (nine female) participated in Study 2, six from Study 1 plus an additional four. Prior to conducting Study 2, contrast thresholds were obtained for each of the 10 adult subjects.

## Apparatus

Stimuli were generated on a Dell Dimension computer with a VSG graphics card and were displayed on an Iiyama Vision Master Pro 510 monitor (40 × 32 cm). At a viewing distance of 39 cm, the viewable portion of the monitor took up 54.3° × 43.5°. The stimulus monitor had a refresh rate of 100 Hz. Stimuli were created with Matlab (6.0) and presented using the

CRS toolbox (Cambridge Research Systems Ltd.). The voltage/luminance relationship was linearized (i.e., calibrated) (Cowan, 1983) with a PR-650 Spectra Colorimeter (Photoresearch).

## Image preparation

In both Studies 1 and 2, the first step was to linearize the luminance values of all images. The reason for this is that on video monitors, there is a nonlinear relationship between gun values and the luminances, referred to as "gamma" function, which is a power function that usually has an exponent of 2.2 on monitors. Because digital images are intended to be displayed on monitors, the luminance values of the original image are compressed (in JPEG, BITMAP, etc) with an inverse-gamma function (~1/2.2). As a consequence, when the compressed image is presented on a video monitor, the original luminance values of images are recreated (thereby making a person's face look like the actual, original face). Because we wanted complete control over the mean luminances, contrasts, sizes, and SF content of all of our stimuli (equating these parameters across images), our first step was to convert the digital images (which were in JPEG or BITMAP) back to their original luminance values by passing them through an inverse-gamma function. After standardizing all of our images (luminance, contrast, size, SF content, described below) in this "true" luminance space, we then presented these values on a gamma-corrected (i.e., calibrated) video monitor.

There were several aspects of the low-level image characteristics that were manipulated:

1) The mean size of the images was manipulated in Adobe Photoshop.
2) All images were converted to gray scale in Adobe Photoshop.
3) The mean luminance of the images was manipulated by determining the mean luminance of the original image and multiplying each point by a value that would make the mean luminance the desired value.
4) The root-mean-squared (RMS) contrast of the images was manipulated, where RMS contrast is described as follows, which is equivalent to the standard deviation of the pixel intensities:

$$C_{\mathrm{RMS}} = \sqrt{\left\{\sum L_{x,y}^{2} - \left[\left(\sum L_{x,y}\right)^{2}/\mathrm{N}\right]\right\}/\mathrm{N}}, \qquad (1)$$

where $C_{\mathrm{RMS}}$ is RMS contrast, $L$ is the luminance of a given pixel, $N$ is the total number of pixels, and $x$ and $y$ represent the position (row and column) of each particular pixel. RMS contrast for an image was manipulated by, first, determining the RMS contrast of the luminance-adjusted image, and then dividing each image-pixel value by a ratio (RMS contrast of the luminance-adjusted image / desired RMS contrast) to make the total RMS contrast of the image the desired value.

5) The spatial frequency (SF) of images (i.e., cycles per image width) was measured and manipulated using fast Fourier transform (FFT) (see Bosworth, Bartlett, & Dobkins, 2006). In FFT, images are described by a linear function in log-SF versus log-energy space, where the height of this function (i.e., its vertical position) reflects the total contrast in the image, and the slope reflects the relative contrast at different SFs. In Study 2, the stimuli were filtered to create low-SF and high-SF images using Matlab code that was adapted from Dr. Paul Van Diepen's "Paul van Diepen - Matlab Filter Program for Full Color Images" available online at http://psy.van-diepen.com/pvdmatl.html. This filtering can be conceptualized as changing the slope of the linear function describing the stimuli in log-SF versus log-energy space. For low-SF stimuli, the slope is steeper than in the original unfiltered image. Conversely, for high-SF stimuli, the slope is shallower than in the original unfiltered image. The filtering was done around a specified SF cutoff (which varied for the different ages, see below). For example, for a frequency cutoff of 0.5 cycles/° (7.8 cycles/face width), the low-SF images were processed so that they contained frequencies primarily below 0.5 cycles/°. Likewise, the high-SF images contained frequencies primarily greater than 0.5 cycles/°.

## Stimuli in Study 1: Upright preferences for unfiltered stimuli

This study measured preferences for upright pictures of faces and objects, which were not SF filtered. Face stimuli consisted of six faces with neutral expression and no hair (three male, three female) obtained by permission from Dr. Kang Lee's database. The images were cropped so that they fit into an oval (with the ears removed), aspect ratio = 15.61° (horizontal) × 21.23° (vertical), which is 5776° squared. Object stimuli were pictures of strollers, taken with a Canon 5.0 megapixel digital color camera against a gray background. The reason for using strollers (rather than something like toys) is because strollers have a clear upright and inverted position. The stroller images were cropped so they fit into a rectangle, with a mean area of 4254° squared ±191.2° squared (on average, aspect ratio = 11.48° [horizontal] × 21.23° [vertical]). The reason the

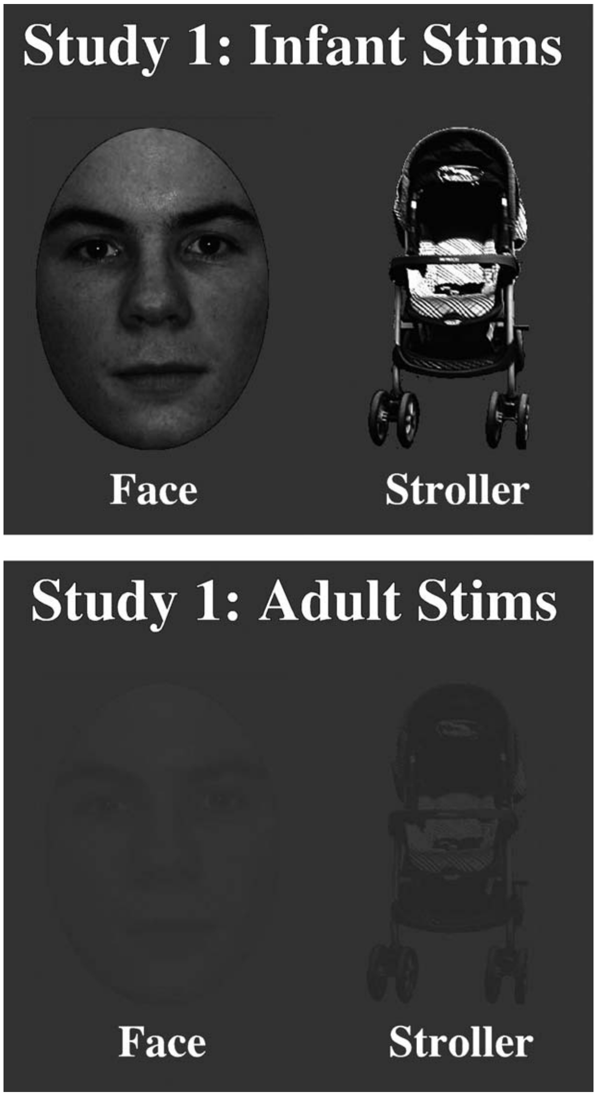

Figure 2. Unfiltered faces and objects from Study 1. Example stimuli shown to Infants (top panel) and Adults (bottom panel). There were six different female faces and six different strollers. Shown are example images of one upright face and one upright stroller. In the actual experiment, the display consisted of an upright image on one side and its inverted image on the other side. The stimuli for adults were higher contrast than those for infants in order to roughly equate the "perceived contrast" (i.e., visibility) for infants and adults (see text for details).

strollers were slightly smaller in area than the faces (and the reason there was variation in the area of strollers) was because we thought it best to keep the vertical dimension the same for the faces and strollers. Since strollers have a higher aspect ratio than faces (and their aspect ratio is variable), this made the strollers take up a smaller area on the monitor, and made their area variable.

The luminance of all images was 13.5 cd/m$^2$, presented on a gray background of the same mean luminance. The mean root-mean-squared (RMS) contrast of the images was 11.43 for infants and 0.87 for adults. Note that the images shown to adults were ~ 13 times lower in RMS contrast compared to those shown to infants with the goal of making the images be roughly the same "perceived contrast" (i.e., visibility) for infants and adults. This 13-fold value was based on pilot studies showing that contrast thresholds for these unfiltered stimuli were roughly 13-fold greater in infants than adults, which is consistent with previous findings from our and other laboratories showing that adults are about an order of magnitude more sensitive than infants (e.g., Dobkins, Anderson, & Lia, 1999; Dobkins, Anderson, & Kelly, 2001). FFT analysis confirmed that the SF content, as reflected in slopes of log contrast by log SF, were nearly identical between unfiltered faces and objects (faces $= -1.41 \pm 0.12$, strollers $= -1.48 \pm 0.06$. $p = 0.18$) and that both the face and object slope values were very close to those observed in our and other previous studies of faces (e.g., Bosworth et al., 2006). Upright and inverted versions of the same stimulus were presented simultaneously on the left and right sides of the video monitor. Example stimuli are presented in Figure 2.

## Contrast detection thresholds for Study 2

As a direct way of attempting to equate the visibility of all stimuli in Study 2 (see below), each of the four stimuli (2 Stimulus Types: Faces vs. Objects × 2 SFs: Low SF vs. High SF) was presented at 3.3 times the contrast detection threshold for that stimulus. These contrast detection thresholds were obtained before beginning Study 2, by presenting these four stimuli at five different RMS contrast levels. This contrast manipulation can be conceptualized as changing the height of the linear function describing the stimuli in log-SF versus log-energy space. Note that the slope (reflecting the relative energy of different SFs, see above) remained the same across different contrasts. The five RMS contrasts varied in log base 2 (i.e., a doubling), ranging from 1.5–24 in infants and 0.01–0.16 in adults. On each trial, either a low- or high-SF stimulus appeared, at one of the five contrasts, on the left or right side of the video monitor. For infants, contrast detection thresholds were measured with forced-choice preferential looking (see Dobkins & Teller, 1996, for details). Contrast thresholds data were obtained from a different set of infants (ages 4 and 8 months old) than the infants that participated in the actual study, and each infant provided contrast thresholds for either faces or objects, but not both (due to limited number of trials we can obtain from infants). Each infant provided 100 trials for each of the two SF conditions. For adults, detection thresholds were measured with self-report and standard two alternative forced-choice (2-AFC) techniques, and each adult provided 150 trials for each condition.

Contrast detection thresholds were determined for each subject by fitting psychometric functions to the data using Weibull functions and maximum likelihood analysis (Weibull, 1951; Watson, 1979). Threshold was defined as the contrast yielding 75% correct performance. For infants, contrast detection thresholds were averaged across infants for each of the four stimuli (2 Stimulus Types: Faces vs. Objects × 2 SFs: Low SF vs. High SF), separately for each age group, and then multiplied by 3.3 times to set the contrast of the stimuli in Study 2. For adults, each subject provided 12 thresholds (2 Stimulus Types: Faces vs. Objects × 2 SFs: Low SF vs. High SF × 3 SF Cutoffs: 0.5, 1, and 2 Cycles/°), which were then used to individually set the contrast of the stimuli (3.3 times threshold) in Study 2.

## Stimuli in Study 2: Upright preferences for low-SF and high-SF stimuli

This study measured preferences for the same upright pictures of faces and objects as employed in Study 1, except that the stimuli were SF filtered in Matlab into low SF and high SF and presented at 3.3 times contrast threshold (see above). Only two different SFs (low and high SF) were tested, rather than three different bands (as is often the case in the adult literature, see Introduction), because (a) infants cannot tolerate many different conditions, and (b) their range of visible SFs is limited. As a reasonable starting point, with the goal of roughly equating the "perceived contrast" (i.e., visibility) of low- and high-SF stimuli, we used a cutoff filter that was at the peak of spatial contrast sensitivity functions obtained from previous reports (see Peterzell et al., 1995, Peterzell & Teller, 1996, and Figure 1). Although we necessarily had to use cycles/degree for this, we present the SF cutoffs in both cycles/degree and cycles/face width, as the latter may be a better description of the stimulus (as studies in adults suggest that the best SF band for face processing is largely independent of viewing distance, e.g., Hayes et al., 1986; Näsänen, 1999; Ojanpää & Näsänen, 2003; Gao & Maurer, 2011). For 4 month olds, the cutoff was 0.4 cycles/°, with low SF $<$ 0.3 cycles/° (4.68 cycles/face width) and high SF $>$ 0.5 cycles/° (7.81 cycles/face width), resulting in mean (averaged across the six faces and six strollers) log-log slopes of $-3.35 + 0.10$ and $-1.08 + 0.12$ for low-SF and high-SF stimuli, respectively. For 8 month olds, the cutoff was 0.5 cycles/°, with low SF $<$ 0.4 cycles/° (6.24 cycles/face width) and high-SF $>$ 0.6 cycles/° (9.37 cycles/face width), resulting in mean log-log slopes (averaged across the six faces and six strollers) of $-3.44 + 0.10$ and $-0.87 + 0.12$ for low-SF and high-SF stimuli, respectively. Upright and inverted versions of the same stimulus were presented simultaneously on the left and right sides of the video monitor. Example stimuli are shown in Figure 3.

For adults, we used three different cutoffs in order to ensure that different results between infants and adults were not driven by having not used the appropriate cutoff in adults. To this end, we tested: (a) 0.5 cycles/°, with low SF $<$ 0.4 cycles/° (6.24 cycles/face width, mean log-log slope $= -3.44 + 0.10$) and high SF $>$ 0.6 cycles/° (9.37 cycles/face width, mean log-log slope $= -0.87 + 0.12$). This was chosen because it matched what was used for infants. (b) 2 cycles/°, with low SF $<$ 1.6 cycles/° (25.0 cycles/face width, mean log-log slope $= -4.26 + 0.11$) and high SF $>$ 2.4 cycles/° (37.5 cycles/face width, mean log-log slope $= 1.05 + 0.10$). This was chosen because it coincides with the peak of adults' contrast sensitivity function (e.g., Peterzell et al., 1995, Peterzell & Teller, 1996). (c) 1 cycle/°, with low SF $<$ 0.8 cycles/° (12.5 cycles/face width, mean log-log slope $= -3.67 + 0.10$) and high SF $>$ 1.2 cycles/° (18.7 cycles/face width, mean log-log slope $= 0.18 + 0.10$). This SF of 1 cycle/° was chosen to be in the middle of the two extremes. In sum, for each age group, there were four stimulus types: low-SF faces, high-SF faces, low-SF objects, and high-SF objects. For adults, there were three sets of the four stimulus types (one for each SF cutoff condition).

## Procedure

In both Study 1 and Study 2, we used looking preferences, which were measured using the FPL technique (Teller, 1967), as described in detail previously (Dobkins & Teller, 1996). A picture of the FPL setup is presented in Figure 4. For infants, the subject was held by the parent 39 cm from the monitor, and the experimenter (highly trained in the FPL method) viewed the infant's face via a camera monitor aimed at his/her face. Each trial began with a small orienting stimulus (consisting of a rotating figure) presented in the center of the display to get the infant centrally focused. When the infant was deemed to be looking at this orienting stimulus, the experimenter pressed a key to begin the trial. At that point, an upright stimulus was presented on one side of the display and the inverted version of that stimulus was presented on the other side of the display (both centered at 14.7° from the middle of the monitor), with the side containing the upright stimulus (left or right) randomized and counterbalanced across trials. On each trial, the experimenter used the infant's head turning and eye gaze behavior to judge the (left vs. right) preference. The stimuli remained present until a decision was made, which typically took between 2 and 4 s. Adults

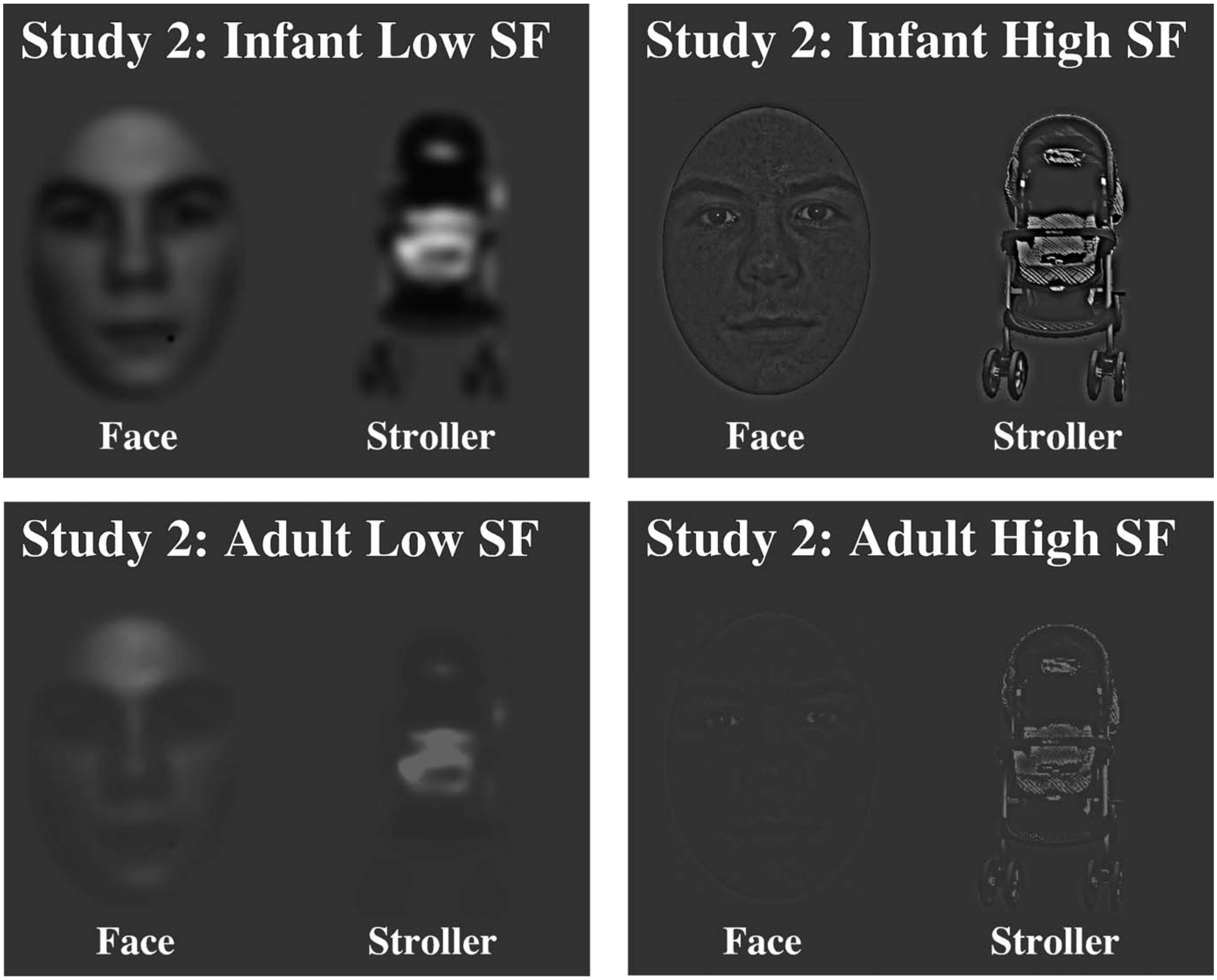

Figure 3. Low-SF (left panels) and high-SF (right panels) faces and objects from Study 2. Example stimuli shown to infants (top panels) and adults (bottom panels). Each panel shows an image of one upright face and one upright stroller. In the actual experiment, the display consisted of an upright image on one side and its inverted image on the other side. Stimuli were presented at 3.3 times subjects' contrast threshold. Because thresholds are much higher in infants, the stimuli shown to infants were higher contrast (upper panels) than those shown to adults (lower panels, see text for explanation). The cutoff frequency shown here is 0.5 cycles/° at a viewing distance of 39 cm (used for 8 month olds and for one condition in adults, see text).

were also tested with FPL, which we believe is a fairer way to compare adult and infant data. Although somewhat unconventional, we and others have previously tested adults in this fashion (McDonough, Choi, & Mandler, 2003, Wagner & Dobkins, 2011). Adults were requested to simply watch the video monitor and were free to look anywhere they wanted. And, like infants, the stimuli remained present until a decision was made by the experimenter.

In Study 1, there were two stimulus conditions: unfiltered faces and unfiltered objects. In Study 2, there were four stimulus conditions (2 Stimulus Types: Faces vs. Objects × 2 SFs: Low SF vs. High SF), all presented at 3.3 times contrast threshold (see contrast thresholds for Study 2, above). The stimulus conditions were identical for infants and adults, with the exception that, in Study 2, adults were tested at three different SF cutoffs (see above), in separate blocks. Each infant was tested with 24 trials per condition. Each adult was tested with 100 trials per condition.

## Data analyses

In both Studies 1 and 2, the measure of performance was the percentage of trials where the subject preferred the upright over the inverted image, with a value greater than 50% representing a preference for upright images. In Study 1, this was calculated for (a) unfiltered faces and (b) unfiltered objects. In Study 2, this was

Figure 4. Forced-choice preferential looking (FPL) technique used in the current study. On each trial, an upright and inverted stimulus appeared on the left and right side of the monitor, respectively, and an experimenter used the subject's head turning and eye gaze behavior (viewed with a video camera aimed at the infant's face, projected onto the camera monitor above) to judge which side the subject preferred. (In this example, an infant is being tested. However, adults were also tested using FPL.) Note that the experimenter was blind to the stimulus locations because a piece of cardboard blocked her view of the video monitor. Above chance (i.e., > 50% correct) scores indicate a preference for the upright over the inverted stimulus.

calculated for (a) low-SF faces, (b) low-SF objects, (c) high-SF faces, and (d) high-SF objects. Effects of stimulus type: faces versus objects (within subjects factor), SF: low SF versus high SF (within subjects factor), and age: 4 months, 8 months and adults (between subjects factor) were investigated using analysis of variances (ANOVAs) and two-tailed post hoc *t* tests. For each analysis, the data satisfied Kolmogorov-Smirnov tests for normality.

## Results

### Study 1: Upright preferences for unfiltered stimuli

Group mean preferences for upright unfiltered stimuli (face and objects) are presented in Figure 5, for the three different age groups (4 month olds, 8 month olds, and adults), with values significantly greater than 50% indicating an upright preference. The results of a two-factor mixed-design ANOVA (2 Stimulus Types: Faces vs. Objects × 3 Age Groups: 4 Month Olds, 8

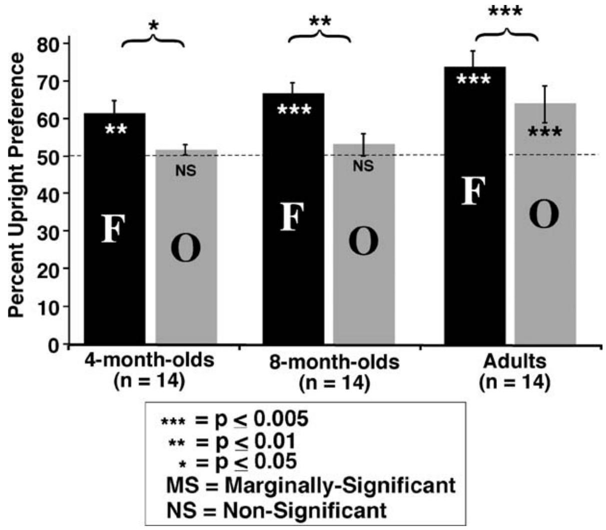

Figure 5. Study 1: Group mean percent upright preferences for unfiltered faces (F) and unfiltered objects (O), for 4 month olds, 8 month olds, and adults. Error bars denote standard errors of the means. All three age groups showed a significant sFIE, defined as a greater upright preference for faces than objects, depicted with symbols above brackets. Symbols on the data bars themselves depict whether each upright preference (separately for faces and objects) was significantly above 50%.

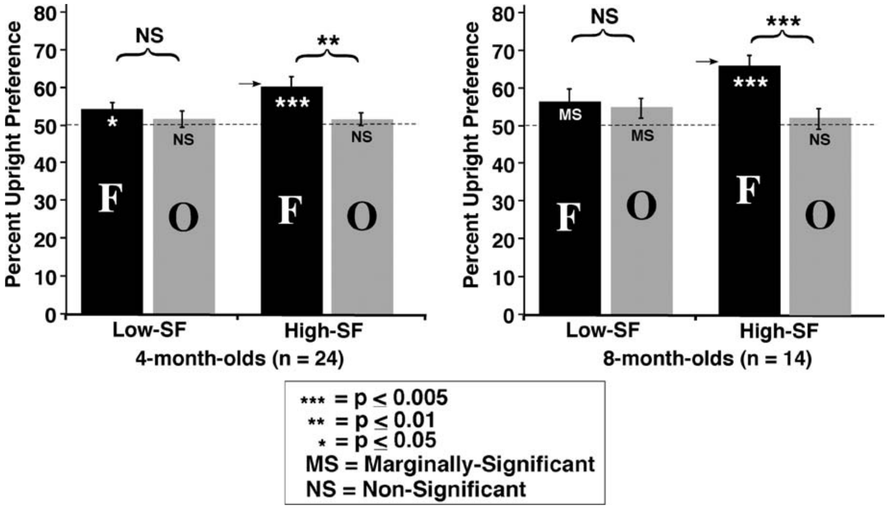

Figure 6. Study 2 infants: Group mean percent upright preferences for low- and high-SF faces (F) and objects (O), for 4 month olds (left) and 8 month olds (right). Error bars denote standard errors of the means. Both infant ages showed a significant sFIE, i.e., a greater upright preference for faces than objects, but only for high-SF stimuli, depicted with symbols above brackets. And, for both ages, the upright face preference was greater for high-SF than for low-SF faces (comparison not shown in figure). Symbols on the data bars themselves depict whether each upright preference (separately for faces and objects, and for low-SF vs. high-SF stimuli) was significantly above 50%. Arrows show the amount of upright preference for unfiltered faces in Study 1, which is about the same as the amount of upright preference for high-SF faces in Study 2.

Month Olds, and Adults) revealed a main effect of age, ($F(2, 39) = 4.67$, $p = 0.015$), which was driven by upright preferences (collapsed across faces and objects) being larger in adults than in 4 month olds ($p = 0.013$, two-tailed $t$ test) and marginally larger in adults than in 8 month olds ($p = 0.077$, two-tailed $t$ test). There was also a main effect of stimulus type, ($F(1, 39) = 27.3$, $p < 0.005$), which was driven by greater upright preferences for faces than for objects. By our definition, this stimulus effect indicates a selective face inversion effect (sFIE). There was no interaction between stimulus type and age, ($F(2, 39) = 0.41$, $p = 0.66$), indicating that the strength of the sFIE did not vary significantly between 4 months of age and adulthood. Note that even though the magnitude of the sFIE (which takes the upright preference for objects into account) did not increase with age, the inversion effect for just faces alone, i.e., the FIE, did (going from 61.7% to 67.3% to 74.1% in 4 month olds, 8 month olds, and adults, respectively), which is consistent with studies showing that FIEs get stronger with age (see Introduction).

In infants, post hoc analyses conducted for each age separately revealed that, for both 4 and 8 month olds, there was a significant sFIE, i.e., the upright preference for faces was significantly greater than for objects (4 month olds: $p = 0.026$, 8 month olds: $p = 0.006$, two-tailed $t$ test). And, the upright preference for faces was significantly above chance (4 month olds: 61.7%, $p = 0.007$, 8 month olds: 67.3%, $p = 0.0001$, two-tailed $t$ test), while the upright preference for objects was not (4 month olds: 51.4%, $p = 0.31$, 8 month olds: 53.27%, $p = 0.30$, two-tailed $t$ test). For adults, there was a significant sFIE, ($p = 0.004$, two-tailed $t$ test). And the upright preference for both faces and objects was significantly above chance (faces: 74.1%, $p < 0.001$, objects: 64.6%, $p < 0.001$, two-tailed $t$ test). Note that the greater upright preferences for faces versus objects (seen in all three age groups) cannot be accounted for by low-level stimulus differences between the two image types because the stimuli were manipulated to be of the same luminance, contrast same SF makeup (see Methods).

In sum, the results from Study 1 show a significant sFIE in all age groups. Our results in infants are in line with previous studies showing that infants as young as 3 months of age show upright preferences for (unfiltered) faces (e.g., Turati et al., 2004; Turati et al., 2005, and see Otsuka et al., 2007, for neural evidence), however, here we show that the inversion effect in infants is *selective* for faces (for evidence of face selectivity in older children, ages 3 to 5 years old, see Picozzi et al., 2009, and see Rossion, 2009, for a review of adult data).

## Study 2: Upright preferences for low- and high-SF stimuli

To investigate which SFs underlie the sFIE revealed in Study 1, Study 2 used spatial frequency (SF)-filtered stimuli, and asked whether the sFIE is driven more by

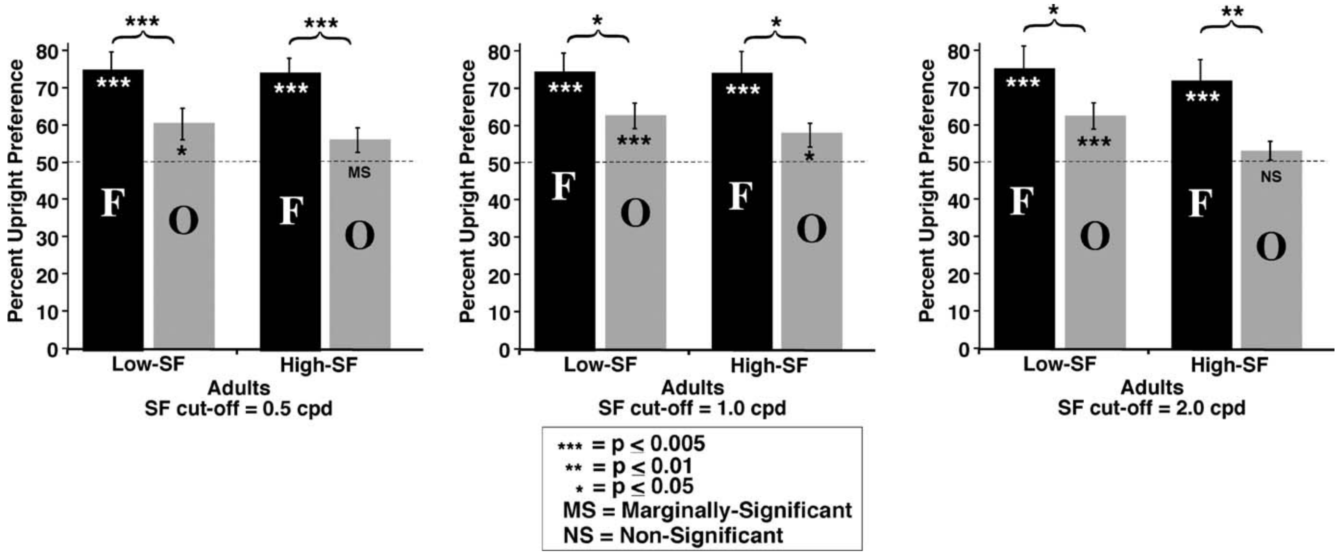

Figure 7. Study 2 adults: Group mean percent upright preferences for low- and high-SF faces (F) and objects (O), at three different cutoff SFs: 0.5 cycles/° (left), 1.0 cycles/° (middle), and 2.0 cycles/° (right). Error bars denote standard errors of the means. Adults showed significant sFIE, i.e., greater upright preferences for faces than objects, but unlike infants, this effect was seen for both low- and high-SF stimuli, depicted with symbols above brackets. Symbols on the data bars themselves depict whether each upright preference (separately for faces and objects, and for low-SF vs. high-SF stimuli) was significantly above 50%. These results show that unlike infants, adults do not show a greater sFIE at high SFs versus low SFs. This effect is robust in that it is seen at all of the different SF cutoffs.

low-SF versus high-SF stimuli. Group mean upright preferences for low- and high-SF faces and objects are presented in Figure 6 for infants (4 and 8 month olds) and in Figure 7 for adults. Data were analyzed separately for infants and adults, since adults were tested at three different SF cutoffs (0.5, 1, and 2 cycles/°). For infants, the results of a three-factor mixed-design ANOVA (2 Stimulus Types: Faces and Objects × 2 SFs: Low and High SF × 2 Age Groups: 4 Month Olds and 8 Month Olds) revealed a main effect of stimulus type, i.e., faces versus objects, ($F(1, 36) = 12.9$, $p = 0.001$), as was the case in Study 1 that presented unfiltered images. However the interpretation of this main effect of stimulus type needs to be reexamined, since there was a significant interaction between stimulus type: faces versus objects and SF: low-SF versus high-SF, ($F(1, 36) = 7.49$, $p = 0.01$). This interaction was driven by the fact that the sFIE, (i.e., greater upright preference for faces vs. objects) was greater for high-, than low-, SF images. Because the ANOVA revealed no three-way interaction between stimulus type, SF, and age, ($F(1, 36) = 1.05$, $p = 0.31$), this suggests that the greater sFIE for high SF than low SF did not vary between 4 and 8 months olds. (Other results of the ANOVA that are less relevant are presented in Footnote 2.[2]

Post hoc analyses revealed that, for both infant ages, at high SFs, there was a significant sFIE, i.e., the upright preference for faces was significantly greater than that for objects (4 month olds: $p = 0.010$, 8 month olds: $p = 0.002$, two-tailed $t$ test). And, the upright preference for high-SF faces was significantly above chance (4 month olds: 60.9%, $p < 0.01$, 8 month olds: 66.4%, $p < 0.01$, two-tailed $t$ test), while the upright preference for high-SF objects was not (4 month olds: 52.0%, $p = 0.26$, 8 month olds: 52.4%, $p = 0.39$). In contrast to the results at high SFs, at low SFs, the sFIE was *not* significant, i.e., the upright preference for faces was not significantly greater than that for objects at either infant age (4 month olds: $p = 0.21$, 8 month olds: $p = 0.78$, two-tailed $t$ test). (For low-SF images, whether upright preferences were significantly above chance varied a bit across age and stimulus type. For 4 month olds, it was above chance for low-SF faces, 54.57%, $p = 0.016$, but not low-SF objects, 51.4%, $p = 0.54$. For 8 month olds, it was marginally above chance for both low-SF faces, 56.6%, $p = 0.089$, and low-SF objects, 55.1%, $p = 0.069$.) With respect to comparisons between high- and low-SF faces (comparison not shown in Figure 6), 4 month olds showed a significantly greater upright preference for high-SF versus low-SF faces ($p = 0.036$, two-tailed $t$ test) while 8 month olds showed a marginally significant effect ($p = 0.055$, two-tailed $t$ test). It is important to emphasize that these differences between results for high- and low-SF stimuli are not likely accounted for by differences in visibility, since all stimuli were presented at 3.3 times contrast threshold.

It is also interesting to point out that the strength of the upright preferences for high-SF faces was almost identical and statistically indistinguishable from that observed for the unfiltered faces employed in Study 1, as depicted by arrows in Figure 6 (4 month olds: $p = 0.86$, two-tailed $t$ test, 8 month olds: $p = 0.79$, two-tailed $t$ test). (This effect cannot be accounted for by the high-SF stimuli in Study 2 having unnaturally high contrast, because they did not. Because we carefully manipulated the makeup of all our stimuli, we were able to verify that the high-SF stimulus we presented in Study 2 had less, not more, contrast than that existing in the high-SF portion of the unfiltered stimuli of Study 1.) By comparison, for low SFs, the strength of the upright preferences for faces was significantly different or marginally significantly different from that observed for the unfiltered faces employed in Study 1 (4 month olds: $p = 0.057$, two-tailed $t$ test, 8 month olds: $p = 0.043$, two-tailed $t$ test). In sum, this secondary analysis suggests that in the unfiltered images (Study 1), the high-SF information was sufficient to drive infants' upright face preferences.

For adults, upright preferences for faces and objects are presented in Figure 7, separately for low- and high-SF images, and for all three cutoff SFs. The results of a within-subjects three-factor ANOVA (2 Stimulus Types: Faces and Objects × 2 SFs: Low and High SF ×3 cutoff SFs: 0.5, 1, and 2 cycles/°) revealed a main effect of stimulus type, i.e., faces versus objects, ($F(1, 9) = 27.7$, $p = 0.001$), which was driven by greater upright preferences for faces than for objects. This was further supported by post hoc analyses showing that for all conditions (both low and high SFs, and for all three SF cutoffs) the preference for upright faces was significantly greater than the preference for upright objects, i.e., in all cases, there was a significant sFIE (all $p$ values $< 0.04$, two-tailed $t$ tests). In almost all cases, upright preferences were significantly above chance (all $p$ values $< 0.03$ two-tailed $t$ tests), except for two object conditions; 0.5 cycles/° cutoff, high-SF objects (where the effect was marginally significant, $p = 0.09$) and 1.0 cycles/° cutoff, high-SF objects ($p = 0.22$, where there was a trend towards an inversion effect). (Other results of the ANOVA that are less relevant are presented in Footnote 3.[3]

Unlike infants in Study 2 who showed a significant interaction between stimulus type and SF (see above), for adults, there was no interaction, ($F(1, 9) = 0.99$, $p = 0.34$), indicating that, for adults, the sFIE (i.e., greater upright preference for faces than objects) did not differ between low and high SFs. There was also no three way interaction, ($F(2, 18) = 0.079$, $p = 0.92$), indicating that the lack of an interaction between stimulus type and SF was not due to there being an interaction at some, but not all, SF cutoff conditions. In fact, overall effects look extremely similar for all three SF cutoffs (0.5, 1, or 2 cycles/°). In addition, the strength of the upright preferences for both low- and high-SF faces did not differ from that observed for the unfiltered faces employed in Study 1 (all $p$ values $> 0.5$). This suggests that, for adults, either low- or high-SF information is sufficient to drive adults' upright face preferences in unfiltered stimuli. In total, the results from adults suggest that the sFIE is robust to effects of SF manipulation, which is quite different from the results in infants who show a significant sFIE only for the high-SF stimuli.

## Discussion

The results of the current study show that the selective face inversion effect (sFIE) in infants is driven by SFs that are relatively high for infants. At first glance, this may seem surprising, since it has been proposed that infants ought to have a low-SF bias for face processing. In addition to the mechanistic reasons for this notion laid out in the Introduction, another (more obvious) reason why one might predict that infants rely more on low SFs for face processing rests on thinking of low SF as an *absolute* property rather than *relative* to the age being tested. Infants clearly have much lower peak SFs and lower spatial acuities than adults (e.g., Atkinson, Braddick, & Braddick, 1974; Atkinson, Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978; Atkinson & Braddick, 1983). If we think of low SF in absolute terms, it is obvious that infants will rely on low SFs in faces, simply because they cannot detect the high-SF components of the face. However, if we think of low SF as a relative term, then the question becomes whether infants rely on SFs that are low *for them*. It is for this reason that the current study used low and high SFs that were tailored for each age, using a cutoff near the peak SF in the contrast sensitivity function.

In addition to using appropriate cutoffs, we believe that studies testing different SF-band stimuli should attempt to equate the "perceived contrast" (i.e., visibility) of the different stimuli, especially in infants, for whom contrast sensitivity is very poor. This is the main difference between the current study and the only other study that tested effects of low versus high SF on face processing in infants. In this study by de Heering et al. (2007), which measured newborn face discrimination (using habituation), they reported that infant performance was better for (and thus relied more on) low SFs than high SFs, a conclusion opposite to that of the current study. As we mention in the Introduction, we believe that one possible reason for de Heering et al.'s finding is that—because they did not attempt to equate visibility—the low-SF faces may have simply been of higher visibility for the infants, therefore leading to better performance. There are, however, other possible reasons that could account for the differences in results between our study and that of de Heering et al's. First, it could be that infants rely more on low SFs for face discrimination in a habituation study (de Heering et al.'s study), yet rely more on high SFs for upright face preferences (current study). Second, the two studies tested different ages, and thus it could be that newborns rely more on low SFs (de Heering et al's study), yet by 4 months of age, they rely more on high SFs (current study). Finally, the results of the two studies may be reconciled if we consider SF in terms of cycles/face width (which is object based) rather than cycles/degree (which is retinally based), the former perhaps being the more relevant measure (as studies in adults suggest that the best SF band for face processing is largely independent of viewing distance, Hayes et al., 1986; Näsänen, 1999; Ojanpää & Näsänen, 2003; Gao & Maurer, 2011). Specifically, while the low and high SF of both the current and de Heering et al. study were similar in terms of cycles/degree (cutoff of about 0.5 cycles/°), in terms of cycles/face width, the two studies had different low-SF stimuli (current study: <5.5 cycles/face width,[4] de Heering et al. study: <12 cycles/face width) and high-SF stimuli (current study: >8.6 cycles/face-width, de Heering et al. study: >12 cycles/face width). (This difference between studies is due to the faces in their study being nearly twice as large as ours, 25° vs. 15° wide, respectively.) Thus, by the object-based measure, if we imagine that infants rely on SFs in the range between 8.6 to 12 cycles/face width for face processing, this could explain what looked like a high-SF bias in the current study, yet a low-SF bias in the de Heering et al. study (and see Leonard et al., 2010, for discussion of how differences in what is considered low SF vs. high SF might account for different results across studies). Future studies in infants, which vary the viewing distance, will be required to determine whether face processing in infants is more tied to cycles/degree versus cycles/face width.

On a final note, we discuss the finding in the current study of differences between infants and adults; in contrast to infants for whom the sFIE was driven by high SF, the sFIE in adults was equally driven by low and high SF, and was robust to the effects of different SF cutoffs. Although our findings in adults may seem contradictory to results from previous adult studies, where the general consensus is that adults possess a midband SF bias (see Introduction), the comparison between studies is not quite fair since previous studies have tested three bands (low, medium, and high), while the use of two bands in the current study did not allow us to selectively capture the midband SF range (~8–25 cycles/face width, see Introduction). Still, some of our conditions had more midband SF energy than others (see Methods), so it is somewhat surprising that the strength of the sFIE was so robust to manipulations of SF. Most likely, the difference in results between adults of the current study and those of previous studies is due to different methodologies, i.e., looking preferences in the current study and face discrimination in previous studies.

Regardless of the extent to which our results in adults are in line with the previous literature, we believe it is of interest to discuss the fact that, in the current paradigm measuring upright face preferences, adults responded differently than did infants. Given this difference, we suggest that—at least for upright face preferences, there is a shift from reliance on high-SF mechanisms in infancy to relatively lower SF mechanisms by adulthood. One possibility is that when infants are first learning about faces, they pay more attention to high-SF information, perhaps because high SFs contain the most relevant information for early stages of learning. To be more specific, it is generally believed that the featural properties of faces (i.e., eyes, nose, mouth) are carried by high-SF mechanisms while configural properties of faces (i.e., the spatial relationship between parts of the face) are carried by low-SF mechanisms (which is based on data showing that people rely on high SFs for featural tasks and low SFs for configural tasks, e.g., Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux & Rossion, 2006, but see Boutet et al., 2003; Watier, Collin, & Boutet, 2010). As such, our finding that infant upright face preferences rely more on high SFs than low SFs is consistent with the proposal in the literature that featural processing of faces develops earlier than configural processing of faces. Although controversial (Rakover, 2002; McKone et al., 2009; McKone et al., 2012), this notion comes from studies reporting that school-aged children succeed on tasks that require them to process featural changes at earlier ages than when they succeed on tasks that require them to process configural/holistic changes (e.g., Carey & Diamond, 1977; Campbell & Tuck, 1995; Campbell, Walker, & Baron-Cohen, 1995; Schwarzer, 2002), and studies from infants have also been interpreted this way (e.g., see Younger & Cohen, 1986; Kestenbaum & Nelson, 1990; Schwarzer, Zauner, & Jovanovic, 2007). In particular, one study that measured both featural and configural face processing (using the same stimuli and task) at different ages showed that featural, but not configural, face processing is adult-like by 10 years (e.g., Mondloch et al., 2002). In sum, it may be that young infants first focus on the features of a face (carried by high-SF mechanisms) and later start to add on the use of more configural information (carried by low-SF mechanisms). Future infant studies that test the effects of both featural/configural information and SF content on face processing abilities will be required to determine whether there is, in fact, a link between the two.

*Keywords: infants, spatial frequency, face inversion effect, face processing, adults, development, preference, objects*

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## Footnotes

[1] As one reviewer pointed out to us, our assumption that equal multiples of threshold are equally visible may not be true, because of the nonlinearity of the contrast response function (often termed the "transducer function," e.g., Legge & Foley, 1980; Ross & Speed, 1991). However, we argue that if the shape of the transducer function is roughly constant across different stimulus conditions (e.g., low vs. high SFs), equal multiples of threshold should be roughly equally visible. There is clearly no perfect solution to this issue; however, we feel our method is the best effort to equalize visibility.

[2] With regard to the three-factor ANOVA in infants (2 Stimulus Types: Faces and Objects × 2 SFs: Low SF and High SF × 2 Age Groups: 4 Months and 8 Months), there was a marginally significant main effect of SF, ($F(1, 36) = 3.49$, $p = 0.07$), but this effect is reinterpreted in light of the interaction between stimulus type and SF (see main text). There was also a marginally significant main effect of age, ($F(1, 36) = 3.14$, $p = 0.085$), which was driven by upright preferences being overall slightly larger in 8 month olds. There were no two-way interactions between stimulus type and age, ($F(1, 36) = 0.20$, $p = 0.659$), nor between SF and age, ($F(1, 36) = 0.0$, $p = 0.98$).

[3] With regard to the three-factor ANOVA in adults (2 Stimulus Types: Faces and Objects × 2 SFs: Low SF and High SF × 3 cutoff SFs: 0.5, 1, and 2 cycles/°), there was a significant main effect of SFs, ($F(1, 9) = 7.301$, $p = 0.024$), which was driven by overall greater upright preferences (combined across faces and objects) for low SFs. As stated in the text, this effect of SF did not interact with stimulus type. There was no main effect of cutoff SF, ($F(2, 18) = 0.44$, $p = 0.65$), no other two-way interactions, Stimulus Type × Cutoff SF: ($F(2, 18) = 0.25$, $p = 0.78$), SF and cutoff SF: ($F(2, 18) = 0.33$, $p = 0.73$), and, as stated in the text, no three-way interaction, ($F(2, 18) = 0.079$, $p = 0.92$).

[4] This value is based on averaging across 4 and 8 month olds.

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