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Bandwidths for the perception of head orientation decrease during childhood

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ABSTRACT

Adults use the orientation of people's heads as a cue to the focus of their attention. We examined developmental changes in mechanisms underlying sensitivity to head orientation during childhood. Eight-, 10-, 12-year-olds, and adults were adapted to a frontal face view or a 20° left or right side view before judging the orientation of a face at or near frontal. After frontal adaptation, there were no age differences in judgments of head orientation. However, after adaptation to a 20° left or right side view, aftereffects were larger and sensitivity to head orientation was lower in 8- and 10-year-olds than in adults, with no difference between 12-year-olds and adults. A computational model indicates that these results can be modeled as a consequence of decreasing neural tuning bandwidths and decreasing additive internal noise during childhood, and/or as a consequence of increasing inhibition during childhood. These results provide the first evidence that neural mechanisms underlying sensitivity to head orientation undergo considerable refinement during childhood.

1. Introduction

The orientation of people's heads provides a useful cue to the focus of their attention, and may thereby allow inferences about their intentions. Sensitivity to head orientation (i.e., precision in discriminating differences in head orientation) may also contribute to humans' ability to recognize faces across changes in head orientation (see Habak et al., 2008; Wilson et al., 2011). Evidence from behavioral experiments and computational modeling suggests that neural mechanisms underlying sensitivity to head orientation degrade in healthy aging (Wilson, Mei, Habak, & Wilkinson, 2011). Here, we used visual adaptation and computational modeling to investigate whether developmental changes in children's judgments of head orientation are the mirror image of the declines observed in healthy aging.

1.1. Adults' sensitivity to head orientation

Adults are highly sensitive to head orientation: they require a deviation of around 1–2° from frontal to reach 75% accuracy in detecting the deviation in a single face (e.g., Wilson et al., 2011) or between sequentially presented faces (Chen et al., 2010; Wilson et al., 2000). Prolonged exposure (adaptation) to a particular head orientation leads to repulsive aftereffects in which perceived head orientation is shifted in a direction opposite to that of the adapting orientation (Bi et al., 2009; Chen et al., 2010; Fang and He, 2005; Fang et al., 2007; Ryu and Chaudhuri, 2006; Wilson et al., 2011). Aftereffect size and sensitivity to head orientation appear to vary with adapting orientation. In one study, participants judged the orientation of heads at or near frontal, with no adaptation (baseline) or following adaptation to heads varying in orientation (0–90°, in increments of 15°) (Chen et al., 2010). The size of aftereffects increased gradually as the adapting orientation varied from 0° to 15–30°, with a gradual decrease beyond 30° (Chen et al., 2010). Relative to baseline, sensitivity was higher following adaptation to a frontal face view, and was lower for adapting orientations 15–60° to either side of frontal (Chen et al., 2010). A computational model indicated that the effects of adapting orientation on aftereffect size and sensitivity could be modeled as a consequence of reductions in response magnitude in neurons selective for head orientation, with a preferred orientation at or near the adapting orientation (Chen et al., 2010).

Aging appears to influence mechanisms underlying sensitivity to head orientation. In one study, younger (*M* age = 26 years) and older (*M* age = 67 years) adults were adapted to a frontal face view or a 20° left or right side view before judging the orientation of a head oriented toward or near frontal (Wilson et al., 2011). Following frontal adaptation, there were no age differences in judgments of

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head orientation. Following adaptation to a 20° side view, sensitivity was 2.0 times lower and aftereffects were 2.4 times larger in older adults. A computational model indicated that the effects of aging could be modeled as a consequence of increasing additive internal noise (i.e., more random fluctuation in neural responses) by a factor of 1.7, and increasing bandwidths (i.e., less selectivity for a particular head orientation) in neurons selective for head orientation, by a factor of 2.5. The authors suggested that degradation of mechanisms underlying sensitivity to head orientation could be related to findings that the ability to match facial identities across changes in head orientation declines in healthy aging, whereas the ability to match identities within the same head orientation does not (Habak, Wilkinson & Wilson, 2008).

1.2. Children's sensitivity to head orientation

Coarse sensitivity to head orientation may be present from birth. After habituation to a photograph of a person's face with a particular viewpoint (e.g., frontal), newborns look longer at the same person's face viewed from a different angle (e.g., 45° side view) than at the image viewed during habituation, a result suggesting that newborns can discriminate large differences in head orientation (Turati, Bulf, & Simion, 2008). At 3 months of age, infants orient in the direction of an adult's head turn (D'Entremont, Hains, & Muir, 1997; Scaife & Bruner, 1975). At 2–3 years of age, children exceed chance in using large head turns to make explicit judgments about which of two heads is oriented toward the child, or which of several widely spaced objects an adult's head is oriented toward (Doherty & Anderson, 1999). Previous studies have not investigated children's ability to discriminate small differences in head orientation. However, previous research indicates that until at least age 10 (oldest age tested) children make more errors than adults in recognizing faces across changes in head orientation, but not across changes in facial expression or eye gaze (Mondloch et al., 2003, but also see Jeffery et al., 2013), a pattern that could reflect immature sensitivity to head orientation.

In sum, previous studies suggest that adults are highly sensitive to head orientation (Wilson, Wilkinson, Lin, & Castillo, 2000), but that neural mechanisms underlying the perception of head orientation may degrade in healthy aging, as indicated by larger aftereffects and decreasing sensitivity following adaptation to a 20° side view (Wilson et al., 2011). Previous studies have not investigated the development of these mechanisms during childhood. The purpose of the current study was to investigate this question by comparing sensitivity to head orientation and head orientation aftereffects between children and adults. Using the same stimuli as a previous study of healthy aging (Wilson et al., 2011), and a procedure similar to that of the previous study, we adapted 8-, 10-, 12-year-olds, and adults to a frontal face view or a 20° left or right side view before participants judged the orientation of a face at or near the frontal orientation. For each adapting orientation, we measured sensitivity to head orientation. For the left and right adaptation conditions, we measured the size of head orientation aftereffects. We expected that if developmental changes in children's judgments of head orientation are the mirror image of the declines observed in healthy aging (Wilson et al., 2011), adaptation to a side view would produce larger aftereffects in young children than in adults, and would lead to lower sensitivity to head orientation in young children than in adults. We used a computational model to investigate whether our data could be modeled as a consequence of changes during childhood in neural bandwidths and additive internal noise, and/or as a consequence of changes in inhibition.

2. Method

2.1. Participants

Participants were 8-year-olds (8.5 ± 0.25 years, *M* = 8.38 years, 9 female), 10-year-olds (10.5 ± 0.25 years, *M* = 10.33 years, 10 female), 12-year-olds (12.5 ± 0.25 years, *M* = 12.58 years, 7 female) and adults (18–24 years, *M* = 18.77 years, 17 female) (*n* = 20/group). Adult participants were undergraduate students who received course credit for participation. Child participants were recruited from a database of children whose parents volunteered to participate in research at the time of their child's birth. All participants were visually screened and had normal or corrected-to-normal vision. All participants were required to have at least 20/20 letter acuity on the Lighthouse eye chart and normal stereoacuity as measured by the Randot test. Five additional participants were tested, but were excluded and replaced because they were obviously inattentive during the procedure (one 8-year-old), because they failed visual screening (one 8-year-old, one 10-year-old), or because they had a σ or aftereffect value (see Sections 3.2 and 3.4 for description of these measures) further than 3 *SD* from the group mean in at least one condition (one 8-year-old, one 12-year-old). A statistically deviant σ or aftereffect was taken as an indication of inattentiveness or poor understanding of the task.

2.2. Stimuli

Stimuli were the same as in a previous study using a similar method (Wilson et al., 2011). Stimuli were synthetic faces constructed as in previous research (Wilson, Loffler, & Wilkinson, 2002; Wilson et al., 2011). These synthetic faces are based on the layout of real faces, so that it is possible to recognize an individual from the synthetic version of his/her face (Wilson, Loffler & Wilkinson, 2002). Importantly, these faces yield judgments of head orientation comparable to those made from photographs of live models (Wilson et al., 2000; Wilson et al., 2011). The face identity presented in the current study was the mean of 40 individual male faces. As in Wilson et al. (2011), all face images were bandpass filtered to 10 cycles/face width, a value within a range of low to mid spatial frequencies important for face identification in adults and children as young as age 5 (youngest tested) (Deruelle & Fagot, 2005; Gao & Maurer, 2011; Leonard, Karmiloff-Smith, & Johnson, 2010). Images of the face were rendered with the following orientations: 0° (frontal), and 2°, 4°, 6°, and 20° to the left and right (see Fig. 1). Face images were 3.22° wide and 4.56° high at the testing

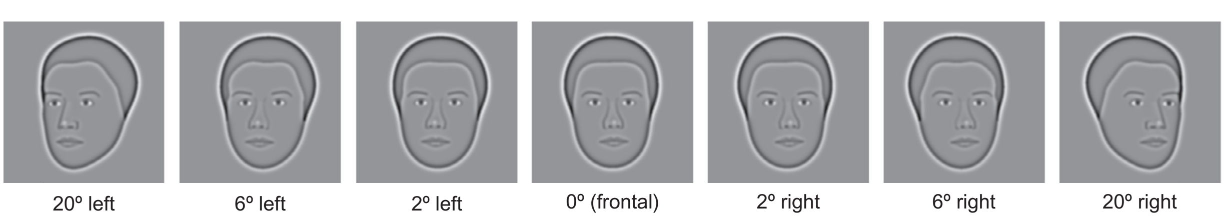

Fig. 1. Examples of stimuli presented in the current experiment.

distance of 131 cm. Stimuli were displayed on a Dell P1130 Trinitron 21 inch display set to a resolution of 1152 x 870 and a refresh rate of 75 Hz. The display had a mean luminance of 52.8 cd/m^2, as measured with a Minolta LS-200 photometer at a distance of 50 cm. The mean luminance of each face image and the background against which all stimuli were presented were set to the mean luminance of the display. The experiment was run in MATLAB R2008a (MathWorks, Natick, MA, USA) using the Psychophysics Toolbox extensions (Brainard, 1997) on an Apple computer.

2.3. Apparatus

Participants sat 131 cm from the center of the screen. They used a chin rest to maintain a constant head position. They entered responses by pressing designated keys on a keyboard placed on a table in front of them. The experimenter used a second keyboard to advance trials.

2.4. Design

Each participant completed a practice block, followed by three test blocks. In the practice block, participants viewed a frontally oriented adapting face, followed by a test face directed 6° to left (4 trials) or right (4 trials). At the beginning of each trial, a white fixation cross appeared at the center of the screen. When the participant appeared to fixate the cross, the experimenter pressed a key to display the adapting face. The adapting face appeared behind the cross, at a random position within 21 arcmin (0.35°) from the center of the screen. To disrupt low-level contour adaptation, the position of the adapting stimulus changed once per second, to a random position within 21 arcmin from the previous position. After 5 s, the adapting face disappeared and the screen returned to the mean luminance for 1 s. The test face was then flashed for 200 ms. A black question mark then appeared at the center of the screen. Participants pressed a key to indicate whether the test face was directed to the left or right. During practice trials, participants received feedback indicating whether their responses were correct or not (a cartoon image of a happy face with a 1000 Hz tone for correct responses and a cartoon image of a sad face with a 400 Hz tone for incorrect responses). Participants were allowed three attempts to reach a criterion of 75% accuracy. All participants met this criterion on the first attempt.

After completing the practice block, participants began the test blocks. The purpose of the test blocks was to measure the influence of adaptation on participants' sensitivity to head orientation (i.e., precision in discriminating differences in head orientation) and on perceived head orientation. The orientation of the adapting face was held constant within each test block. In the first block, the adapting face always had a frontal orientation. In the second and third blocks, the adapting face was oriented 20° to the left or right. Half of the participants received the left adapting orientation in the second block and the right adapting orientation in the third block, with the other half receiving the opposite order. In each block, participants received 8 trials with each of 7 test orientations (6° left to 6° right, in 2° steps), for a total of 56 trials per block. To assess attentiveness, we included three catch trials that appeared at random positions within each block, with the constraint that catch trials were never fewer than five trials apart. In each catch trial, a cartoon image of rocks appeared on the screen. Participants were instructed to press a button to sound an alarm when they saw this image. During the test blocks, participants received general encouragement but no trial-specific feedback.

2.5. Procedure

After the procedure was explained, written consent was obtained from adult participants, and from the parent of each child participant. Verbal assent was also obtained from each child participant. After positioning each participant appropriately in the apparatus, the experimenter displayed a cartoon image of the inside of a cave, and explained the task as follows:

My friend James is an explorer who loves to search for buried treasure. He has been out searching for treasure deep in this cave, and now he is lost! To find his way out of the cave, James has to face straight ahead. Sometimes James gets distracted and turns his head to this side [experimenter points to left of display] *or to this side* [points to right]. *Your job will be to help James stay on course by deciding which way his head is pointing. You're going to see a white cross in the middle of the screen, with a face behind it. When the cross is on the screen, stare directly at it. When the cross disappears and James' face flashes up on the screen, press one of these two buttons to show where his face was pointing* [points to response buttons]. *If the face is pointing this way* [points to left] *press this button* [points to left button]. *If the face is pointing this way* [points to right] *press this button* [points to right button].

The experimenter then initiated practice trials. Once the participant reached criterion, the experimenter displayed a photograph of rocks, and delivered the following instruction:

James is lost in a part of a cave that has lots of rocks. If you see rocks like these, you can sound an alarm to warn James so that he does not trip on the rocks. To sound the alarm, press this button [experimenter points to silver star button].

The experimenter then initiated the first test block. The experimenter carried out visual screening after the first test block, and offered a break after the second test block. Participants typically completed the entire procedure in 35–40 min.

3. Results

3.1. Accuracy on catch trials

Accuracy (expressed here as the proportion of correct responses) on catch trials was high in 8-year-olds (M = .93, SD = .09, range = .67–1.00), 10-year-olds (M = .96, SD = .07, range = .78–1.00), 12-year-olds (M = .96, SD = .11, range = .78–1.00), and adults (M = .98, SD = .05, range = .89–1.00). We carried out a mixed ANOVA with age and order (i.e., whether the participant received the right or left adaptation block first) as between-subject variables, adapting condition (frontal, left, right) as a within-subject variable, and accuracy as the dependent variable. There were no main effects or interactions, $ps > .65$. The high accuracy in each age group and the absent effect of age on accuracy suggest that participants in all age groups were attentive throughout the procedure.

3.2. Curve fitting

For each participant, adapting orientation, and test orientation, we calculated the proportion of rightward responses (see Fig. 2). For each adapting orientation, we fit each participant's data with a cumulative Gaussian function. All fits were carried out with the Palamedes Toolbox (Prins & Kingdom, 2009) extensions in MATLAB R2011b. For each fit, we assessed goodness of fit by calculating deviance, defined as:

$$D = 2[l(\theta_{max}; y) - l(\hat{\theta}; y)] \quad (1)$$

where $l(\theta_{max}; y)$ is the likelihood of a model that has a free parameter for each empirical data point, and therefore has no residual error (i.e., the "saturated" model), and $l(\hat{\theta}; y)$ is the likelihood of the

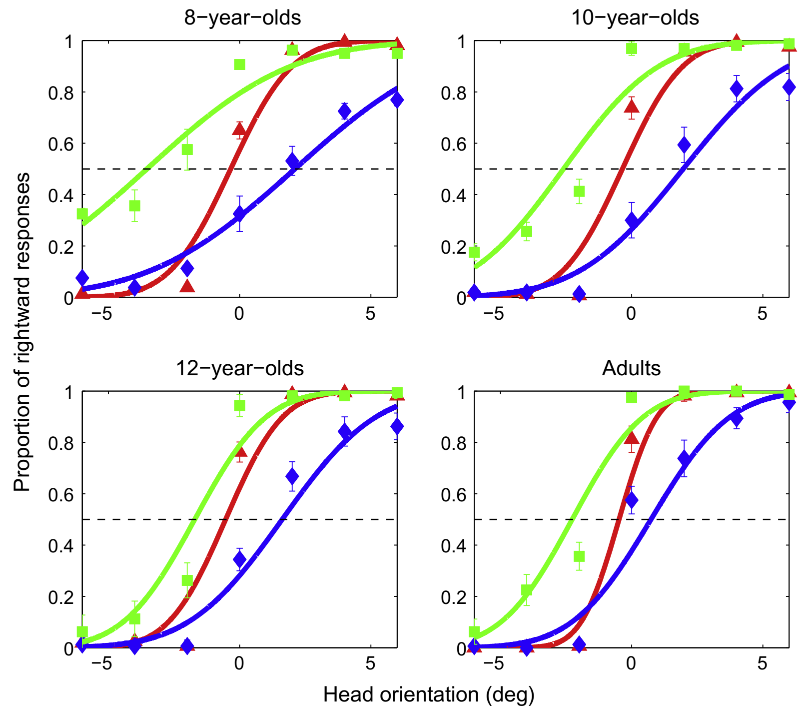

Fig. 2. Cumulative Gaussian functions fit to the mean proportion of rightward responses (±1 SE) as a function of head orientation (in degrees), adapting condition, and age group. In each plot, the green, red, and blue curves and data points represent the data for the 20° left, frontal and 20° right adaptation conditions, respectively. Negative values on the *x* axis refer to leftward orientations and positive values refer to rightward orientations. The dashed black horizontal line marks the 0.5 point on the *y* axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

best-fitting model (McCullagh & Nelder, 1989; Prins & Kingdom, 2009; Wichmann & Hill, 2001). A larger deviance value indicates greater discrepancy between the model and data. We compared the observed deviance value against a distribution of deviance values computed using a bootstrap method with 1000 iterations per fit (Prins & Kingdom, 2009). Deviance values below the 5th percentile in the deviance distribution are taken as evidence of a poor fit (Prins & Kingdom, 2009). All fits in the current experiment had deviance values above the 5th percentile.

From each fitted function, we extracted the parameter β, which controls the slope of the function. As in a previous study using a similar method (Wilson et al., 2011), we converted β to σ, the standard deviation of the Gaussian distribution, by taking the reciprocal of β (Prins & Kingdom, 2009). A smaller σ (steeper slope) reflects higher sensitivity to head orientation (i.e., the ability to detect smaller deviations from a frontal orientation). σ is linearly related to the 75% discrimination threshold (threshold = 0.68σ) reported in previous research (Chen et al., 2010; Wilson et al., 2000; Wilson et al., 2011), which provides an estimate of the smallest deviation from a frontal head orientation required for the participant to reach 75% accuracy in detecting the deviation. We also extracted the point of subjective equality (PSE), which is the head orientation at which the fitted function crossed the 0.5 point on the *y* axis (i.e., the head orientation corresponding to the transition between 'left' and 'right' responses). Values of the PSE were coded so that a positive value indicates a shift of perceived head orientation to the left of frontal, whereas a negative value reflects a rightward shift.

3.3. Adaptation to frontal face view

We did not expect frontal adaptation to produce large shifts in perceived head orientation. For this reason, we carried out separate analyses for the frontal and 20° side adaptation conditions, as in a previous study using a similar method (Wilson et al., 2011). For the frontal adaptation condition, we carried out a univariate ANOVA with age as the independent variable and PSE as the dependent variable (see Fig. 3A). There was no effect of age, $p > .75$. However, a single-sample t-test indicated that the PSE differed from 0 ($M = -.32°$, $SD = .45$), $t(79) = 6.40$, $p < .0001$, $d = .71$. This result indicates that across age groups, there was a small but significant bias to perceive the head as being oriented to the right. This bias seems likely to reflect a very minor asymmetry in the face used in the current study (see Fig. 1).

We also carried out a univariate ANOVA with age as the independent variable and σ as the dependent variable (see Fig. 3B). There was no effect of age, $p > .45$.

3.4. Adaptation to 20° side view

3.4.1. Preliminary analyses of order

Group differences in the extent to which participants' performance varied between the second and third blocks of the experiment (e.g., greater fatigue in young children) could lead to group differences in performance across these blocks. To evaluate this possibility, we carried out two mixed ANOVAs (one with aftereffect size [see Section 3.4.2 for description of this measure] as the dependent variable, one with σ as the dependent variable) with order (i.e., whether a participant completed the left or right adaptation block first), age, and direction of adaptation (left, right) as independent variables. In each ANOVA, there was no effect of order, and order did not interact with any other variable, *ps* > .6. This pattern suggests that in each age group, performance did not vary between the second and third blocks of the experiment. Hence, data were collapsed across orders for all further analyses.

3.4.2. Aftereffect size

We expected that as in previous research (Chen et al., 2010; Wilson et al., 2011), adaptation to a 20° side view would lead to repulsive aftereffects in which perceived head orientation is

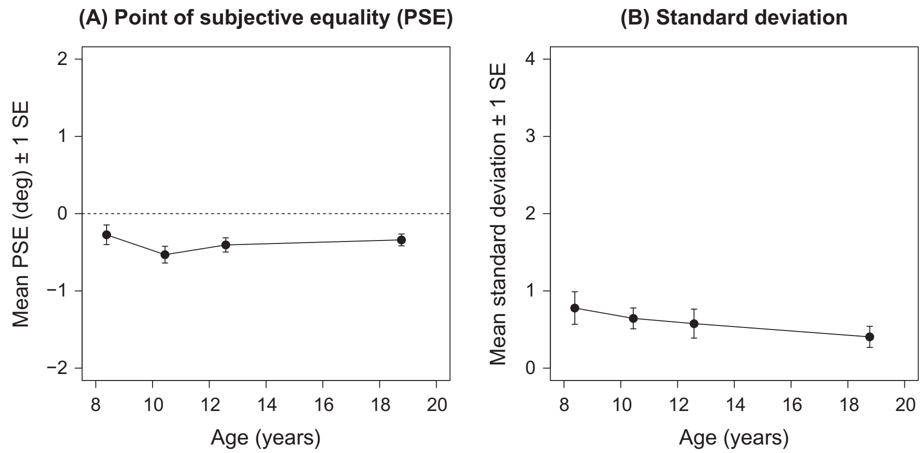

Fig. 3. Results for the frontal adaptation condition. (A) Mean point of subjective equality (PSE) (in degrees, ±1 *SE*) as a function of age. (B) Mean standard deviation (±1 *SE*) as a function of age.

shifted in a direction opposite to the orientation of the adapting stimulus. In the current paradigm, these aftereffects are indicated by a shift of the PSE toward the adapting orientation. For each participant and direction of adaptation (left, right), we calculated the size of the aftereffect from the difference in PSE between the frontal and 20° side adaptation conditions. Values of the difference were coded so that larger aftereffects in the expected direction lead to more positive values.

We carried out a mixed ANOVA with age and direction of adaptation (left, right) as independent variables and aftereffect size as the dependent variable (see Fig. 4A). There was a significant effect of age, $F(3, 76) = 4.09$, $p < .01$, $f^2 = .11$, with no effect of direction and no interaction, $ps > .064$. A Dunnett's post hoc following up the effect of age indicated that aftereffects were larger in 8-year-olds ($M = 2.96°$, $SD = 1.06$) than in adults ($M = 1.48°$, $SD = 1.17$), $p < .003$, and were larger in 10-year-olds ($M = 2.54°$, $SD = 1.55$) than in adults, $p < .03$, with no difference between 12-year-olds ($M = 2.03°$, $SD = 1.13$) and adults, $p > .2$.

The absent effect of adapting direction on aftereffect size, and the absent interaction between age and adapting direction indicate that the slight rightward bias observed in the frontal adaptation condition (see Section 3.3 for details) did not lead to a difference in aftereffect size between the 20° left and 20° right adapting directions, and that the influence of adapting direction did not differ between age groups. Hence, the bias observed in the frontal adaptation condition does not affect our interpretation of the results for the 20° side adaptation conditions.

3.4.3. Standard deviation (σ)

We carried out a mixed ANOVA with age and direction as independent variables and σ as the dependent variable (see Fig. 4B). There was an effect of age $F(3, 76) = 7.35$, $p < .0005$, $f^2 = .23$, but there was no effect of direction and no interaction, $ps > .07$. A Dunnett's post hoc following up the effect of age indicated that σ was larger in 8-year-olds ($M = 3.37$, $SD = 1.86$) than in adults ($M = 1.14$, $SD = 0.91$), $p < .001$, and was larger in 10-year-olds ($M = 2.22$, $SD = 1.63$) than in adults, $p < .05$, with no difference between 12-year-olds ($M = 1.67$, $SD = 1.74$) and adults, $p > .3$. Since there was no difference between the left and right adapting directions, we collapsed across directions for all further analyses of σ.

In light of previous research indicating that sensitivity to head orientation is greater when the adapting and test orientations are the same than when they differ by 15–60°, and our finding of a main effect of age following 20° side adaptation, but not following frontal adaptation, it was of interest whether sensitivity would differ between the frontal and 20° side adaptation conditions in each age group. To evaluate this possibility, we first carried out a mixed ANOVA with adapting direction (frontal, 20° side) and age as the independent variables and σ as the dependent variable. There was an effect of age, $F(3, 76) = 7.07$, $p < .001$, $f^2 = .22$, an effect of

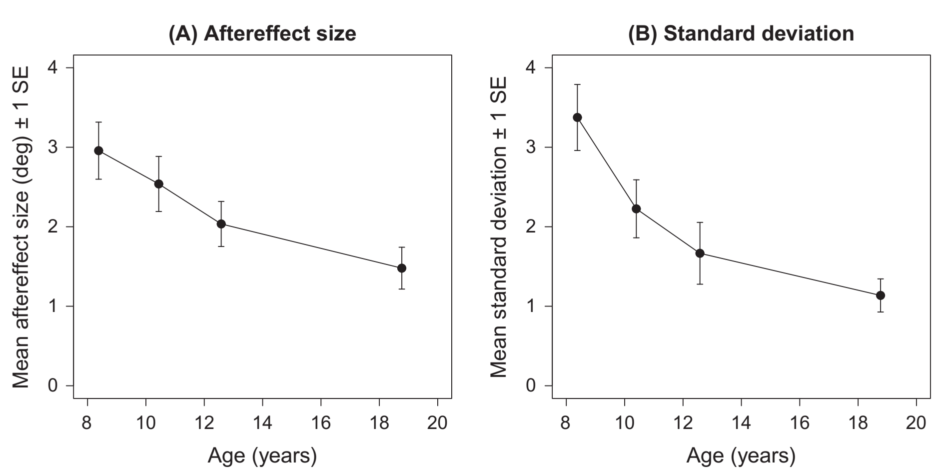

Fig. 4. Results for the 20° side adaptation conditions. (A) Mean aftereffect size (in degrees, ±1 *SE*) as a function of age. (B) Mean standard deviation (±1 *SE*) as a function of age.

adapting direction, $F(1, 76) = 69.21$, $p < .001$, $f^2 = .28$, and a significant interaction, $F(3, 76) = 4.94$, $p < .004$, $f^2 = .07$. We followed up the interaction with Holm–Bonferroni-corrected (Holm, 1979) paired-samples t-tests (one per age group) evaluating differences between adapting directions for each age group. σ was larger following adaptation to a 20° side view than for frontal adaptation (8-year-olds: $M = .78$, $SD = .94$, 10-year-olds: $M = .54$, $SD = .60$, 12-year-olds: $M = .58$, $SD = .84$, adults: $M = .40$, $SD = .61$) in 8-year-olds, $t(19) = 6.94$, $p < .0001$, $\alpha = .01$, $d = 1.76$, 10-year-olds, $t(19) = 3.88$, $p < .002$, $\alpha = .025$, $d = 1.37$, 12-year-olds, $t(19) = 2.75$, $p < .015$, $\alpha = .05$, $d = .80$, and adults, $t(19) = 3.18$, $p < .005$, $\alpha = .017$, $d = .94$. Inspection of the group means and effect sizes suggests that the interaction between age and adapting direction arose from a decrease in the difference in sensitivity between the 20° side and frontal adaptation conditions with increasing age.

3.5. Computational neural model

To interpret our results, we developed a model based on previous models of aftereffects for head orientation (Chen et al., 2010; Wilson et al., 2011) and grating orientation (Clifford et al., 2001). In view of evidence that expression of the inhibitory neurotransmitter GABA increases throughout childhood (Pinto et al., 2010), and that GABA inhibition is inversely related to tuning bandwidths and spontaneous activity in visual cortical neurons (Leventhal et al., 2003; Thiele et al., 2012; Wang et al., 2003), we first attempted to model the data for 8-year-olds and adults (the youngest and oldest groups in the current study, respectively) as a consequence of developmental changes in one or both of these characteristics. We also attempted to model the data as a consequence of developmental changes in inhibition.

As in previous models (Chen et al., 2010; Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001), we used a circular Gaussian (Von Mises) function to simulate the tuning function of neurons selective for head orientation, defined as:

$$R_w(\theta) = \exp\{\beta(\cos(\theta - \theta_0) - 1)\} \tag{2}$$

where β is inversely related to the bandwidth of the curve and θ_0 is the head orientation leading to the peak response (see Figs. 5 and 6A). We assume that the tuning curves are evenly distributed, with θ_0 ranging from −180° to 180° in 10° steps. The number of curves does not appear to be critical, as using half or double the number of curves had little effect on model results.

We simulated adaptation by reducing response magnitude by A_w, a factor proportional to the response to the adapting stimulus. The proportionality factor was set to 0.5, a value within the range used in previous models of head orientation aftereffects (Chen et al., 2010; Wilson et al., 2011), so that $A_w = 1 - 0.5 \cdot R_w(0)$.

We used vector population decoding to estimate predicted head orientation from the population of model neurons (see Clifford et al., 2001; Georgopolous, Kalaska, & Caminiti, 1982; Pouget et al., 2003). In this method, each model neuron contributes a vector in the direction of its preferred view direction, with a length proportional to its response to the stimulus. Predicted head orientation is calculated from the vector sum of the responses of all model neurons. Without adaptation, the perceived orientation predicted by the model matched the true orientation (see Figs. 5 and 6B). We calculated the size of the predicted aftereffect from the difference in predicted head orientation with and without adaptation (see Figs. 5c and 6C). We did not incorporate the slight rightward bias in perceived head orientation observed in the frontal adaptation condition (see Section 3.3 for details) into the model because the bias was quite small (0.32°), did not differ between age groups, did not lead to a significant difference in aftereffect size between the 20° left and 20° right adapting conditions, and seems likely to reflect a small asymmetry in the stimuli instead of a bias in neural mechanisms for decoding head orientation.

To model participants' sensitivity to head orientation, we first took into account the influence of adaptation on the slope of the function relating predicted head orientation to true head orientation (see Figs. 5B and 6B). Adaptation increases the steepness of the slope at and near the adapting orientation, and decreases the steepness away from the adapting orientation. The former may increase perceived differences in head orientation, leading to increased sensitivity, whereas the latter would have the opposite effect (Clifford et al., 2001). As in previous models (Chen et al., 2010; Clifford et al., 2001), we estimated the change in perceived differences (δ) from the slope of the function relating perceived head orientation to true head orientation following adaptation (see Fig. 5 and 6D).

We also took into account the influences of additive internal noise (Wilson et al., 2011) and the magnitude of the population neural response (Clifford et al., 2001) on sensitivity to head orientation. On each of 10,000 simulated trials, we added Gaussian noise ($M = 0$, SD varied to fit data) to the response of each model neuron, and estimated perceived head orientation as described above. A separate noise sample was generated for each trial and model neuron. The response of each model neuron was constrained so that noise could not lead to a negative response. We calculated the standard deviation of the estimates of perceived head orientation across all simulated trials (σ_{noise}) (see Figs. 5E and 6E). A larger σ_{noise} reflects lower sensitivity. Adaptation increases σ_{noise} at and around the adapting orientation (see Figs. 5 and 6E). This reduction in sensitivity reflects a decrease in signal to noise ratio caused by a decrease in the magnitude of the population response at and around the adapting orientation (see Figs. 5 and 6A).

We then calculated $\sigma_{predicted}$, an estimate of standard deviation combining information from σ_{noise} and δ:

$$\sigma_{predicted}(\theta) = \sigma_{noise}(\theta) \cdot \left(\frac{1}{\delta(\theta)^{\lambda}}\right) \tag{3}$$

where λ controls the extent to which δ influences σ. λ was set to 5.75 for all fits (see Figs. 5 and 6F). Hence, the model yields estimates of sensitivity ($\sigma_{predicted}$) in the same units (σ) as our measures of human sensitivity.

To fit the aftereffect and sensitivity data for 8-year-olds and adults, it was necessary to vary bandwidth (β) and the standard deviation of additive internal noise. To fit adults' data, we set β to 32.5. This value of β corresponds to a full width at half height (FWHH) of 23°, a value similar to that used for young adults (27°) in a previous study using a similar method (Wilson et al., 2011). We set the standard deviation of additive internal noise to .01. These parameter values yielded simulated aftereffect (see Fig. 5C) and $\sigma_{predicted}$ (see Fig. 5F) values similar to the aftereffect (see Fig. 4A) and σ (see Figs. 3 and 4B) values observed in adults. Increasing bandwidths and internal noise by setting β to 14.5 (FWHH = 34°) and setting the noise parameter to .05 yielded simulated aftereffect (see Fig. 8C) and $\sigma_{predicted}$ (see Fig. 6F) values similar to the aftereffect (see Fig. 4A) and σ (see Figs. 3 and 4B) values observed in 8-year-olds.

The model captures our finding of no significant age difference in sensitivity to head orientation following frontal adaptation, with much lower sensitivity in 8-year-olds than adults following 20° side adaptation. Following frontal adaptation, the higher internal noise (σ_{noise}) in 8-year-olds (see Fig. 6E) is offset by large perceived differences (δ, see Fig. 6D), a pattern leading to only slightly lower predicted sensitivity in 8-year-olds than adults (see Fig. 5F and Fig. 6F). Following 20° side adaptation, the higher σ_{noise} in 8-year-olds (see Fig. 6E) is no longer offset by large δ (see Fig. 6D), a pattern leading to much lower predicted sensitivity in

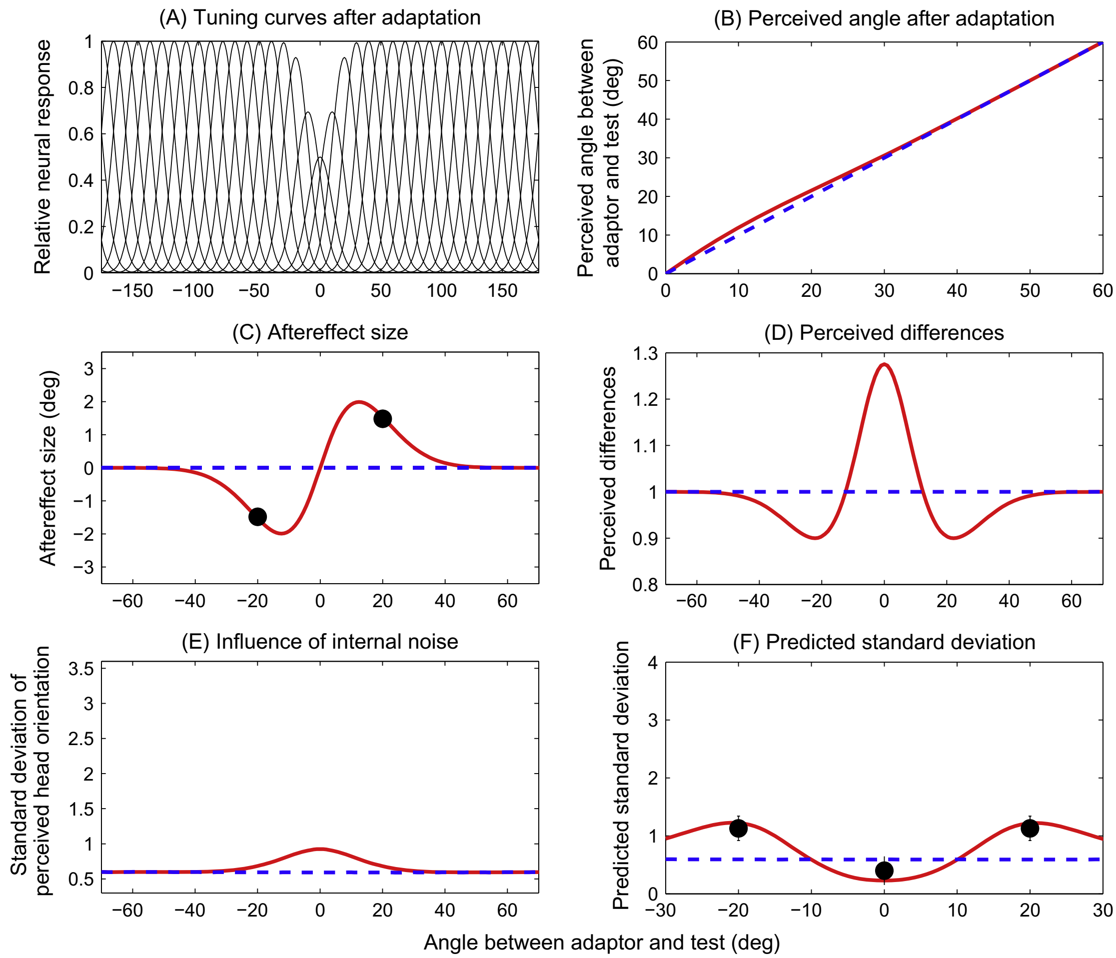

Fig. 5. Computational model fit to adults' data. For each plot, the red line shows the model prediction following adaptation, and the dotted blue line shows the model prediction without adaptation. For each plot, the *x* axis shows the difference between the adapting orientation and the test orientation (in degrees), with positive values referring to adapting orientations to the right of the test orientation, and negative values referring to adapting orientations to the left. (A) Relative response of each model neuron following adaptation. (B) Predicted perceived angle (in degrees) between the adaptor and test. (C) Predicted aftereffect size (in degrees). The black data points show the mean aftereffect (±1 *SE*) observed in adults. (D) Predicted perceived differences (δ). (E) Standard deviation (σ_{noise}) of perceived head orientation over 10,000 simulated trials. (F) Predicted sensitivity ($\sigma_{predicted}$), an estimate of sensitivity to head orientation taking into account information from δ (panel D) and σ_{noise} (panel E). The black data points show the mean standard deviation σ (±1 *SE*) observed in adults. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

8-year-olds than in adults (see Fig. 5F and Fig. 6F). The model also captures our finding of larger aftereffects following 20° side adaptation in 8-year-olds than in adults. The wider bandwidths in 8-year-olds (see Fig. 6A) cause adaptation to spread over a wider range of orientations than in adults (see Fig. 5A), a pattern leading to larger predicted aftereffects in 8-year-olds (see Figs. 5 and 6C). Hence, our model indicates that developmental changes in judgments of head orientation after age 8 can be modeled as a consequence of decreasing additive internal noise and decreasing bandwidths.

We also investigated whether the developmental changes observed during childhood could be modeled as a consequence of increasing inhibition after age 8. To test this possibility, we incorporated lateral inhibition to control the tuning bandwidths of the simulated neurons, so that increasing inhibition decreased the tuning bandwidths. The tuning functions were replaced by:

$$R_w(\theta) = \left[A_w \cdot \exp\{\beta(\cos(\theta-\theta_0)-1)\} - G \cdot \sum_{\alpha=\pm1} \exp\{\beta(\cos(\theta-\theta_0)-1)\}\right]_+ + \eta \tag{4}$$

where G is the gain of lateral inhibition, and $\alpha = \pm 1$ represents summation over adjacent tuning curves. The subscripted bracket $[X]_+$ is a threshold function indicating that any negative values of X are set to zero, so that lateral inhibition cannot generate negative responses. The noise term η was set to $-0.24G + .14$. Hence, noise decreased with increasing inhibition, as is reported physiologically (Leventhal, Wang, Pu, Zhou, & Ma, 2003). We used a spacing of 2.5° between adjacent tuning curves instead of the 10° spacing used in the previous version of the model, because the smaller spacing allowed a slightly smoother δ curve. However, the spacing does not appear to be critical, as we were able to fit the data equally well with the 10° spacing. We used a bandwidth parameter of 14 (FWHH = 36°) for both 8-year-olds and adults, so that only G was varied to fit the data as a function of age. All other details were the same as in the previous version of the model. To fit the data for young adults, we set G to 0.49, a value similar to that used for young adults (0.50) in a previous study using a similar method (Wilson et al., 2011). To fit the data for 8-year-olds, we set G to 0.15. These parameter values yielded simulated aftereffect (see Fig. 7C and Fig. 8C) and $\sigma_{predicted}$ (see Fig. 7F and Fig. 8F) values similar to those observed in 8-year-olds and adults. Hence, our refined model indicates that developmental changes in judgments of head

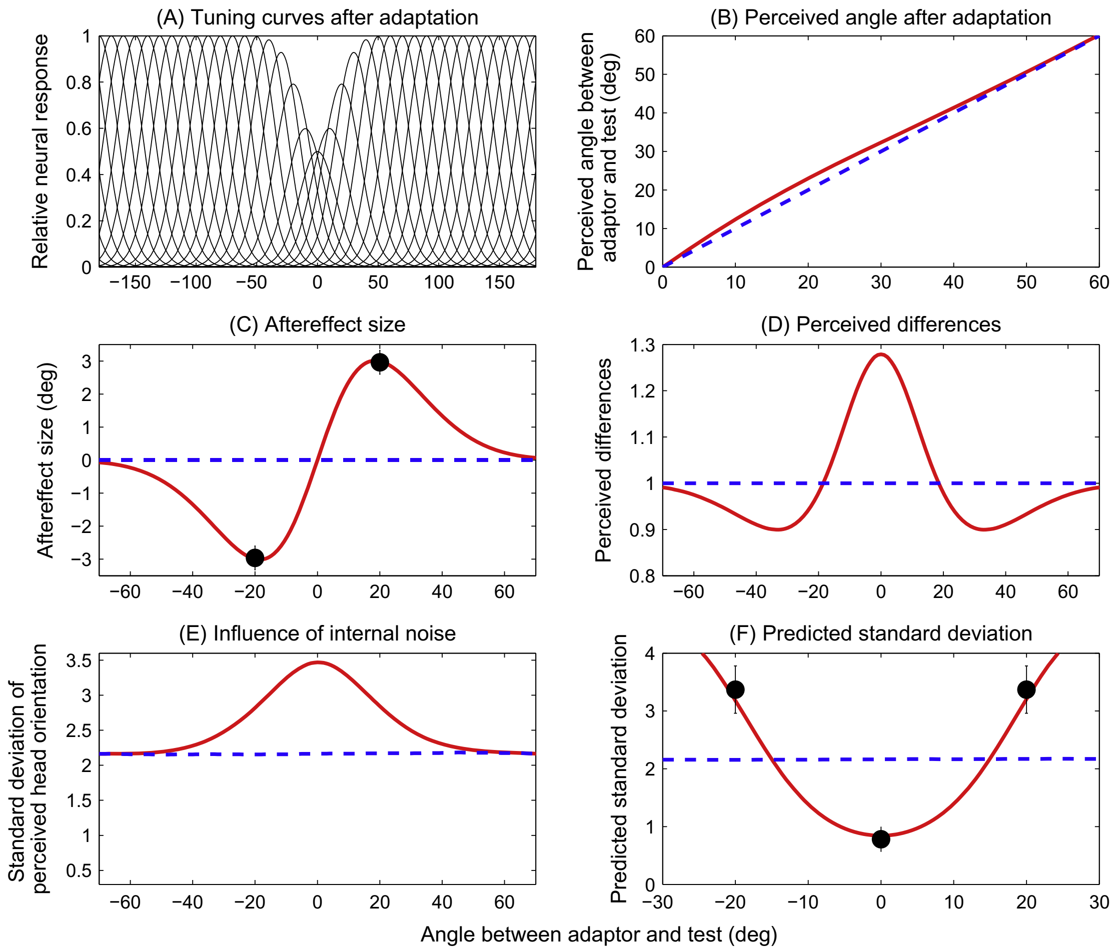

Fig. 6. Computational model fit to 8-year-olds' data. All other details as in Fig. 5.

orientation can be modeled as a consequence of increasing inhibition after age 8.

4. Discussion

The current study provides the first information on the development of fine-grained sensitivity to head orientation and aftereffects for head orientation during childhood. We found no differences between children and adults in judgments of head orientation following adaptation to a frontally oriented head. However, following adaptation to a 20° side view, aftereffects were larger in 8- and 10-year-olds than in adults, by factors of 2.0 and 1.7, respectively. In addition, sensitivity was lower in 8- and 10-year-olds than in adults, by factors of 3.0 and 2.0, respectively. There were no differences between 12-year-olds and adults. Our computational model indicates that the data for 8-year-olds and adults can be modeled as a consequence of decreasing additive internal noise and decreasing tuning bandwidths after age 8, by factors of 5.0 and 2.2, respectively. A revised version of the model indicates there may also be an influence of increased inhibition after age 8 (by a factor of 3.3); such inhibition is inversely related to internal noise and tuning bandwidths in visual cortical neurons (Leventhal et al., 2003; Thiele et al., 2012; Wang, Fujita, Tamura, & Murayama, 2003) and hence the two models overlap. Together, the results suggest that although young children can make adult-like judgments of head orientation under some conditions, neural mechanisms underlying sensitivity to head orientation undergo considerable refinement after age 8.

The lower sensitivity observed in 8- and 10-year-olds following adaptation to a 20° side view could reflect poorer attentiveness, motivation, and/or understanding of the task in younger children. However, at least three findings in the current study provide evidence against these hypotheses. First, there were no age differences in performance on catch trials included to assess attentiveness, and performance on catch trials did not vary across blocks. In addition, children's sensitivity was adult-like following frontal adaptation. Finally, sensitivity and aftereffect size did not vary between the second and third blocks of the experiment in any age group, a pattern suggesting that children did not become more fatigued than adults toward the end of the experiment. Hence, it seems unlikely that age differences in attentiveness, motivation, and/or understanding of the task can account for the lower sensitivity observed in younger children after 20° side adaptation.

The lower sensitivity to head orientation observed in 8- and 10-year-olds following 20° side adaptation could also reflect differences in sensitivity to low-level visual information. However, contrast sensitivity and letter acuity are adult-like at age 7 (Ellemberg et al., 1999). Also, adults and children as young as age 5 (youngest tested) (Deruelle and Fagot, 2005; Gao and Maurer, 2011; Leonard, Karmiloff-Smith, & Johnson, 2010) rely on the same range of low to mid spatial frequencies to discriminate facial identity. Hence, it seems unlikely that the age differences observed in the current study reflect differences in sensitivity to low-level visual information.

The developmental changes observed in the current study are similar to those reported in a previous study of healthy aging using the same stimuli and a similar method (Wilson et al., 2011). In that

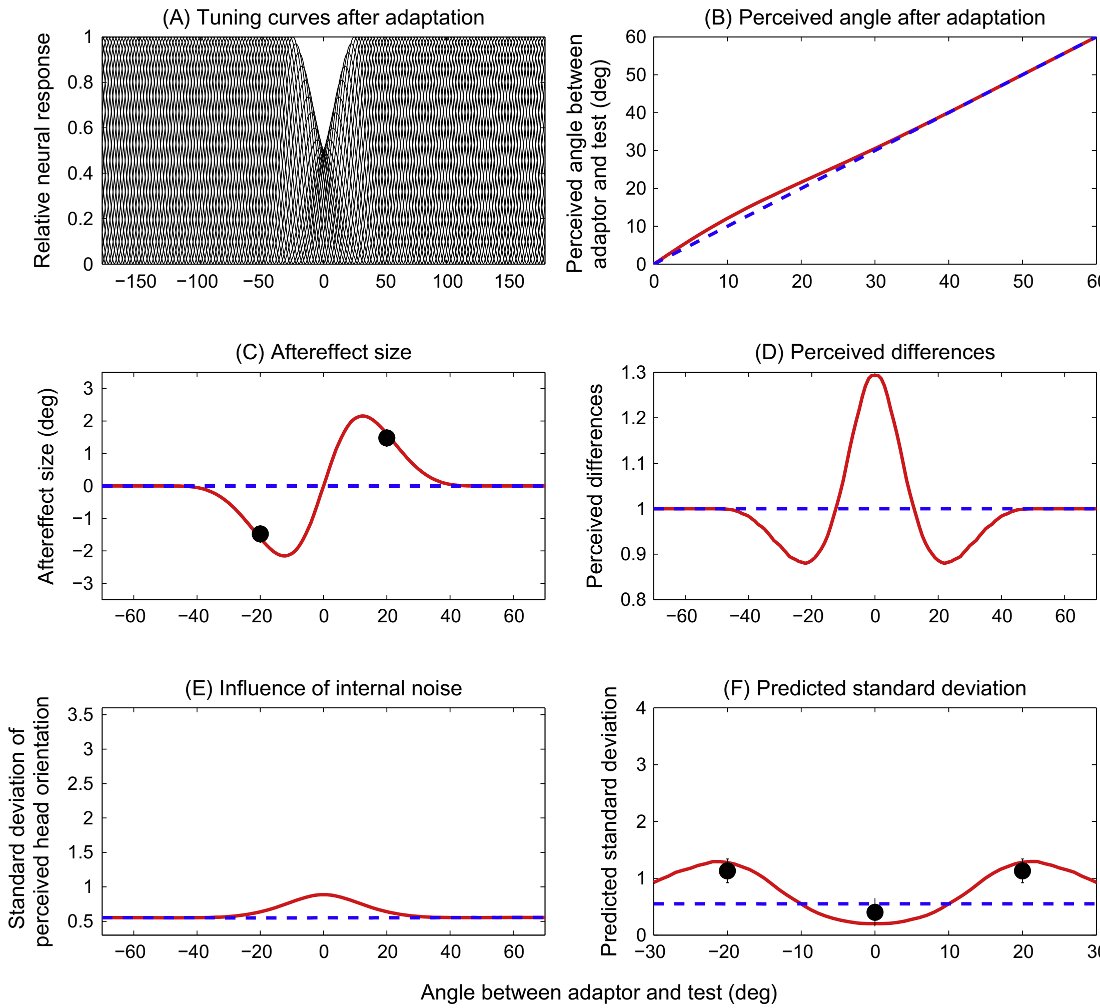

Fig. 7. Computational model with lateral inhibition fit to adults' data. All other details as in Fig. 5.

study, there were no age differences following frontal adaptation. However, after adaptation to a 20° side view, sensitivity was 2.0 times lower and aftereffects were 2.4 times larger in older adults. A computational model indicated that the changes observed in aging could be modeled as a consequence of increasing additive internal noise by a factor of 1.7, and increasing bandwidths by a factor of 2.5. The effect of aging could also be modeled as a consequence of a decrease in inhibition, by a factor of 2.5 (Wilson et al., 2011). Developmental changes in expression of the inhibitory neurotransmitter GABA provide a plausible explanation for our results and those of Wilson et al. (2011). The amount of available GABA is inversely related to tuning bandwidths and spontaneous activity in visual cortical neurons (Leventhal et al., 2003; Thiele et al., 2012; Wang et al., 2003). GABA expression increases during childhood (Pinto, Hornby, Jones, & Murphy, 2010), and decreases in healthy aging (Leventhal et al., 2003; Pinto et al., 2010). Hence, the former may allow more adult-like processing of head orientation, whereas the latter may degrade processing of head orientation, leading to behavioral performance similar to that of young children in the current study.

The current results may have implications for understanding developmental changes in humans' ability to recognize faces across changes in head orientation (e.g., learning a facial identity with one head orientation, then later recognizing the identity despite a change in head orientation). Judgments of head orientation were not fully adult-like until after age 10, an age at which children make more errors than adults in recognizing faces across changes in head orientation, but not across changes in eye gaze or facial expression (Mondloch, Geldart, Maurer, & Le Grand, 2003, but also see Jeffery, Rathbone, Read, & Rhodes, 2013). Similarly, the effect of aging on judgments of head orientation (Wilson et al., 2011) is accompanied by a decline in the ability to match faces across changes in head orientation, with no corresponding decline in the ability to match faces within the same head orientation (Habak, Wilkinson & Wilson, 2008). In hierarchical neural models of object recognition, higher visual cortical areas compute a viewpoint-invariant neural representation of object identity from viewpoint-selective responses in lower visual areas (see Axelrod & Yovel, 2012; DiCarlo, Zoccolan, & Rust, 2012). From this perspective, it seems possible that immature or degraded processing of head orientation could lead to lower accuracy in recognizing faces across changes in head orientation. Future studies could investigate this possibility by using adaptation to manipulate participants' sensitivity to head orientation (e.g., adapting to a 20° side view will decrease sensitivity to deviations from frontal, whereas frontal adaptation will increase sensitivity (Chen et al., 2010)), and measuring the effect of this manipulation on accuracy in recognizing faces across changes in head orientation.

One remaining question is whether the developmental changes observed in the current study are specific to judgments of head orientation, or whether the results could reflect changes in more general mechanisms of object processing. Evidence for neural mechanisms specialized for coding head orientation comes from findings that a subset of neurons in macaque superior temporal

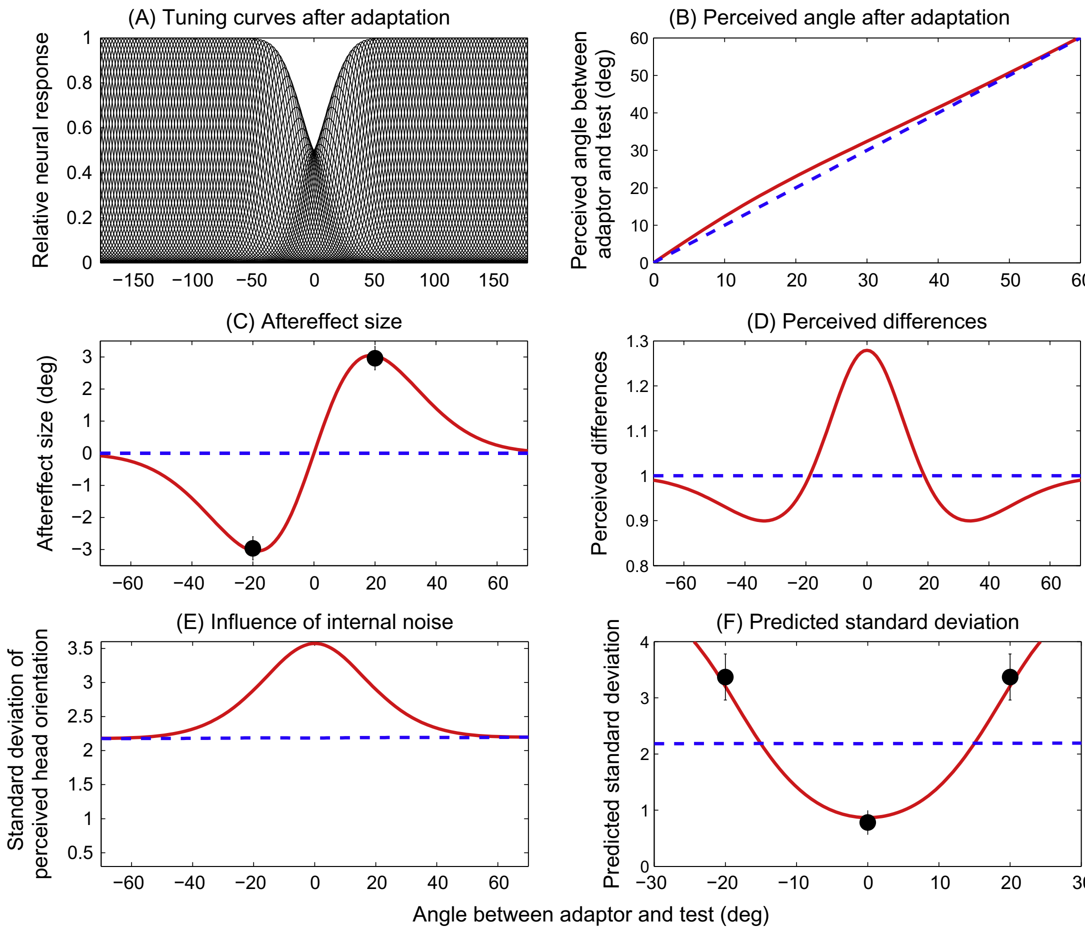

Fig. 8. Computational model with lateral inhibition fit to 8-year-olds' data. All other details as in Fig. 5.

sulcus respond selectively to images of heads over other body parts (e.g., hands, hair). The majority of these cells respond selectively to a particular head orientation, with the preferred orientation varying between cells (Perrett et al., 1991; Perrett et al., 1992). The current results could reflect changes in this neural population. However, our results could also reflect changes in more general mechanisms of object processing. For example, cells in macaque inferior temporal cortex are tuned to a wide variety of complex shapes, and vary widely in selectivity for viewing angle (see DiCarlo, Zoccolan & Rust, 2012, for review). Future studies could evaluate the specificity of the developmental changes observed in the current study by repeating the current study with complex objects other than heads (e.g., bodies, cars, houses).

Another remaining question is whether the current results are limited to the perception of head orientation for orientations at or near frontal. It is possible that neural mechanisms underlying the perception of head orientation are specialized for orientations at or near frontal, perhaps because humans receive more experience with this range of orientations than with orientations far from frontal. Evidence consistent with this hypothesis comes from the finding that adults are able to detect smaller differences in head orientation between sequentially presented faces when these faces are oriented around frontal or 15° to the side than when they are oriented around 30° to the side (Wilson et al., 2000). Future studies could investigate whether neural mechanisms underlying the perception of head orientation are specialized for orientations at or near frontal by repeating the current study with test faces oriented far from frontal.

5. Conclusions

We examined developmental changes in sensitivity to head orientation and head orientation aftereffects during childhood. We found no age differences in judgments of head orientation following adaptation to a frontally oriented head. However, after adaptation to a 20° left or right side view, aftereffects were larger and sensitivity was lower in 8- and 10-year-olds than in adults, with no differences between 12-year-olds and adults. We modeled the data for 8-year-olds and adults as a consequence of decreases in additive internal noise and neural bandwidths after age 8, and/or as a consequence of increases in inhibition after age 8. Together, these results provide the first evidence that neural mechanisms underlying the perception of head orientation are refined during mid to late childhood. These results also provide the first evidence of parallels between childhood and healthy aging (Wilson et al., 2011) in the development of mechanisms underlying the perception of head orientation, a pattern that could reflect changes throughout the lifespan in expression of the neurotransmitter GABA (Pinto et al., 2010).

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References

Axelrod, V., & Yovel, G. (2012). Hierarchical processing of face viewpoint in human visual cortex. *Journal of Neuroscience, 32*, 2442–2452.

Bi, T., Su, J., Chen, J., & Fang, F. (2009). The role of gaze direction in face viewpoint aftereffect. *Vision Research, 49*, 2322–2327.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–439.

Chen, J., Yang, H., Wang, A., & Fang, F. (2010). Perceptual consequences of face viewpoint adaptation: Face viewpoint aftereffect, changes of differential sensitivity to face view, and their relationship. *Journal of Vision, 10*, 1–11.

Clifford, C. W. G., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Research, 41*, 151–159.

D'Entremont, B., Hains, S. M. J., & Muir, D. W. (1997). A demonstration of gaze following in 3- to 6-month-olds. *Infant Behavior and Development, 20*, 569–572.

Deruelle, C., & Fagot, J. (2005). Categorizing facial identities, emotions, and genders: Attention to high- and low-spatial frequencies by children and adults. *Journal of Experimental Child Psychology, 90*, 172–184.

DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object ecognition? *Neuron, 73*, 415–434.

Doherty, M. J., & Anderson, J. R. (1999). A new look at gaze: preschool children's understanding of eye direction. *Cognitive Development, 14*, 549–571.

Ellemberg, D., Lewis, T. L., Maurer, D., Liu, C., & Brent, H. P. (1999). Spatial and temporal vision in patients treated for bilateral congenital cataracts. *Vision Research, 39*, 3480–3489.

Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron, 45*, 793–800.

Fang, F., Ijichi, K., & He, S. (2007). Transfer of the face viewpoint aftereffect from adaptation to different and inverted faces. *Journal of Vision, 7*, 1–9.

Gao, X., & Maurer, D. (2011). A comparison of spatial frequency tuning for the recognition of facial identity and facial expressions in children and adults. *Vision Research, 51*, 508–519.

Georgopolous, A., Kalaska, J., & Caminiti, R. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience, 2*, 527–1537.

Habak, C., Wilkinson, F., & Wilson, H. R. (2008). Aging disrupts the neural transformations that link facial identity across views. *Vision Research, 48*, 9–15.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6*, 65–70.

Jeffery, L., Rathbone, C., Read, A., & Rhodes, G. (2013). Children's face identity representations are no more view specific than those of adults. *Journal of Experimental Psychology: Human Perception and Performance, 39*, 450–463.

Leonard, H. C., Karmiloff-Smith, A., & Johnson, M. H. (2010). The development of spatial frequency biases in face recognition. *Journal of Experimental Child Psychology, 106*, 193–207.

Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., & Ma, Y. Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science, 300*, 812–815.

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models*. London: Chapman and Hall.

Mondloch, C. J., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology, 86*, 67–84.

Perrett, D. I., Hietanen, J. K., Oram, M. W., Benson, E. T., Rolls, P. J., et al. (1992). Organization and functions of cells responsive to faces in the temporal corte. *Philosophical Transactions: Biological Sciences, 335*, 23–30.

Perrett, D. I., Oram, M. W., Harries, M. H., Bevan, R., Hietanen, J. K., Benson, P. J., et al. (1991). Viewed-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research, 86*, 159–173.

Pinto, J. G., Hornby, K. R., Jones, D. G., & Murphy, K. M. (2010). Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. *Frontiers in Cellular Neuroscience, 4*.

Pouget, A., Dayan, P., & Zemel, R. S. (2003). Inference and computation with population codes. *Annual Review of Neuroscience, 26*, 381–410.

Prins, N., & Kingdom, F. A. A. (2009). *Psychophysics: A practical introduction*. Academic Press.

Ryu, J., & Chaudhuri, A. (2006). Representations of familiar and unfamiliar faces as revealed by viewpoint aftereffects. *Vision Research, 46*, 4059–4063.

Scaife, M., & Bruner, J. S. (1975). The capacity for joint visual attention in the infant. *Nature, 253*, 265–266.

Thiele, A., Herrero, J. L., Distler, C., & Hoffmann, K. (2012). Contribution of cholinergic and GABAergic mechanisms to direction tuning, discriminability, response reliability, and neuronal rate correlations in macaque middle temporal area. *The Journal of Neuroscience, 32*, 16602–16615.

Turati, C., Bulf, H., & Simion, F. (2008). Newborns' face recognition over changes in viewpoint. *Cognition, 106*, 1300–1321.

Wang, Y., Fujita, I., Tamura, H., & Murayama, Y. (2003). Contribution of GABAergic inhibition to receptive field structures of monkey inferior temporal neurons. *Cerebral Cortex, 12*, 62–74.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*, 1293–1313.

Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research, 42*, 2909–2923.

Wilson, H. R., Mei, M., Habak, C., & Wilkinson, F. (2011). Visual bandwidths for face orientation increase during healthy aging. *Vision Research, 51*, 160–164.

Wilson, H. R., Wilkinson, F., Lin, L. M., & Castillo, M. (2000). Perception of head orientation. *Vision Research, 40*, 459–472.