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From Caregivers to Peers: Puberty Shapes Human Face Perception

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Abstract

Puberty prepares mammals to sexually reproduce during adolescence. It is also hypothesized to invoke a social metamorphosis that prepares adolescents to take on adult social roles. We provide the first evidence to support this hypothesis in humans and show that pubertal development retunes the face-processing system from a caregiver bias to a peer bias. Prior to puberty, children exhibit enhanced recognition for adult female faces. With puberty, superior recognition emerges for peer faces that match one's pubertal status. As puberty progresses, so does the peer recognition bias. Adolescents become better at recognizing faces with a pubertal status similar to their own. These findings reconceptualize the adolescent "dip" in face recognition by showing that it is a recalibration of the face-processing system away from caregivers toward peers. Thus, in addition to preparing the physical body for sexual reproduction, puberty shapes the perceptual system for processing the social world in new ways.

Keywords

puberty, adolescence, face recognition, peers

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Pubertal development transforms sweet-smelling, cuddly children into tall, stinky, hairy, self-conscious, moody teenagers. What is much less obvious is whether and how puberty prepares adolescents to take on the adult social roles that mark the end of adolescence (Dahl, 2004). Some of the essential ways adolescents must prepare for adulthood include gaining increasing autonomy from parents while developing more confiding relationships and exploring romantic partnerships with peers (Havighurst, 1972). While some of these behaviors may not be directly related to sexual reproduction, they are equally, if not more, important for successful adaptation to adulthood (Roisman, Masten, Coatsworth, & Tellegen, 2004). Researchers are now theorizing about how pubertal development might support this social metamorphosis in humans (e.g., Scherf, Behrmann, & Dahl, 2012).

We have hypothesized that puberty instigates and causally influences changes in face processing in adolescence (Scherf et al., 2012; Scherf & Scott, 2012). Successful navigation through the social world critically depends on how people perceive others' faces. Faces are the preeminent social signal from which people extract information related to the identity, age, sex, attractiveness, and intentions of others—characteristics that are relevant to the complex social relationships that characterize adulthood, which individuals begin to learn to navigate in adolescence. We have argued that social developmental tasks (salient tasks that are specific to a developmental period; Havighurst, 1972) fundamentally shape the "computational goals" of the perceptual system (Marr, 1982), which are ultimately reflected in face-processing biases (i.e., superior recognition for some kinds of faces over others). In other words, developmental tasks are derived from the social, emotional, and contextual milieu of an individual's environment, and the computational goals of the perceptual system are instantiations of the solutions to these tasks. The social developmental tasks of childhood, adolescence, and young adulthood are distinct. Children are focused on learning self-mastery while still depending on primary caregivers. Adolescents are developing increasing autonomy from caregivers as they engage in confiding friendships and explore romantic partnerships with peers. Young adults are immersed in romantic and sexual

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relationships with peers, whom they are evaluating for long-term partnerships and coparenting relationships. We expect that these differential tasks shape face-processing biases in functionally distinct ways.

Formation of attachment relationships with caregivers in infancy and childhood likely shapes the computational goals of the visuoperceptual system by tuning face-processing behavior toward caregivers (Scherf & Scott, 2012). In support of this hypothesis, infants and young children are better at recognizing adult faces than infant faces, and this is particularly true of adult female faces compared with adult male faces (Macchi Cassia, Bulf, Quadrelli, & Proietti, 2014; Quinn et al., 2010), unless the primary caregiver is male (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). In adolescence, social developmental tasks change, and the influx of gonadal hormones during puberty likely influences motivation to accomplish these tasks. Therefore, we predicted that the computational goals of the visuoperceptual system change to retune face-processing behavior away from caregivers and toward peers, who are the primary focus of the newly emerging relationships in adolescence. This visuoperceptual retuning toward peers likely increases into young adulthood as social developmental tasks continue to be focused on peers until parenthood. Note that this set of predictions suggests that the face-processing behavior of both children and young adults, but not adolescents, will be tuned to adult faces, but for different reasons.

We are not the first to hypothesize about adolescent-specific changes in face-processing behavior and their relation to puberty. Diamond, Carey, and Back (1983) reported that girls in the midst of pubertal change make more errors in face recognition than do pre- or postpubescent girls. Since this early study, several other researchers reported an age-related dip in face-recognition behavior between 12 and 13 years (Lawrence, Campbell, & Skuse, 2015; McGivern, Andersen, Byrd, Mutter, & Reilly, 2002; Vetter, Leipold, Kliegel, Phillips, & Altgassen, 2013). Importantly, these studies used adult face stimuli and were not specifically designed to evaluate the influence of puberty irrespective of age. An alternative, untested interpretation of the adolescent dip in performance is that children and adults have face-processing biases toward adult faces, whereas adolescents' biases are retuned toward peer faces instead of adult faces.

In the existing literature, face-processing biases toward same-age individuals reflect an *own-age effect* (for a review, see Scherf & Scott, 2012). For example, adults tend to be more accurate at recognizing other adult faces of a similar age as their own, compared with faces from other age groups, including child faces (Harrison & Hole, 2009). Although previous work has evaluated the own-age effect in children and adolescents, the findings are inconsistent (see Scherf & Scott, 2012). There are no studies tracking the developmental progression of the own-age effect with age-matched faces from early childhood through adolescence and into adulthood. The existing data are consistent with the interpretation that an own-age effect in preadolescent children is much less robust than in adults.

Here, we conducted the first empirical test of the social-metamorphosis hypothesis that puberty evokes a transition from a *caregiver bias* to a *peer bias* in face processing. We define peers not by age alone, but also by pubertal status, given our hypotheses about how social developmental tasks of childhood and adolescence shape face-processing biases. We hypothesized that prepubescent children's face-recognition behavior would be characterized by a caregiver bias evident in superior recognition of adult faces, particularly adult female faces. Importantly, we predicted that there would be a qualitative transition from this caregiver bias to a peer bias in adolescence, in which peer faces become the primary category of faces to which the visual system is tuned. Furthermore, we predicted that puberty continually shapes this process; as adolescents progress through puberty, their face-recognition bias also shifts to peers of similar pubertal status. Finally, we expected the peer bias to be largest in young adults given their strong social focus on peers.

Method

To test these hypotheses, we employed a novel experimental paradigm in which the facial stimuli mirrored the participant groups in age and pubertal status. We tested individuals across the full range of pubertal status: prepubescent children, age-matched adolescents in early and later stages of pubertal development, and adults. This design enabled us to evaluate changes in face recognition related to the transition from late childhood into adolescence, as well as the transition from early to later pubertal development during adolescence, while controlling for age.

Participants

The final sample contained 116 participants. The demographic characteristics of the four pubertal groups (i.e., prepubescent children, early-puberty adolescents, late-puberty adolescents, and sexually mature adults) are given in Table 1. The ethnic distribution of the participants reflected the ethnic distribution of the town from which we recruited them. A sample size of 28 individuals for each pubertal group was determined a priori to give us 80% power to detect a moderately sized Group × Condition interaction effect (η^2) at a significance level of .05. We ended data collection for all four groups when we

Table 1. Demographic Characteristics of the Four Pubertal Groups

Group	Males (*N*)	Females (*N*)	Age (years)		
			M	*SD*	Range
Prepubescent children	15	15	7.33	0.61	6–8
Early-puberty adolescents	14	14	11.50	0.63	11–14
Late-puberty adolescents	14	14	11.85	0.97	11–14
Sexually mature adults	15	15	19.97	2.40	18–24

reached the minimum sample size for the two adolescent groups. The two groups of adolescents were matched on age (M = 12 years), $t(54) = 1.63$, $p = .110$ (see Fig. 1a), but differed in pubertal status, $t(54) = 12.13$, $p < .001$ (see Fig. 1b). The mean pubertal stage of all four groups was significantly different. An additional 6 children, 6 adolescents, and 5 adults were excluded from the analyses because their average total performance was below chance. One additional adolescent participant did not complete the testing session.

Participants were medically healthy and did not regularly use medication; further, neither they nor their first-degree relatives had a history of autism, neurological or psychiatric illness, acquired brain injury, learning disabilities, developmental disabilities, school problems, or substance abuse. Child and adolescent participants were recruited through the Families Interested in Research Studies database at Pennsylvania State University and through several outreach initiatives with the Discovery Space museum of Central Pennsylvania. Adult participants were recruited via print advertisements and from the Pennsylvania State University Department of Psychology undergraduate subject pool. All participants were paid $10 for their participation in the study, with the exception of the subject-pool participants, who received 1 credit hour. Prior to testing, written informed consent was obtained from the adult participants and parents of the children and adolescents, along with written assent from the children and adolescents, using procedures approved by the Pennsylvania State University Institutional Review Boards. Parents were given the option of completing the experiment-relevant paperwork in the same room with children and adolescents while they executed the computer tasks. Those who did were given explicit instructions not to interact with their child during testing. Children and adolescents whose parents were in the room wore headphones during the experiment.

Pubertal assessments

Pubertal development of both children and adolescents was assessed. Parents provided assessments of children and adolescents, and adolescents also completed self-assessments. In this way, we acquired multirater and multimeasure assessments of pubertal development in the adolescents.

The pubertal-development measures assessed developing secondary sex characteristics. They included the self- and parent-report versions of the Sexual Maturation Scale (SMS; Morris & Udry, 1980), which consist of line drawings of five progressive stages of pubertal development that range from Stage 1 (prepubescent) to Stage 5 (sexual maturity). For males, the drawings combine pubic hair and genital development. For females, the drawings combine pubic hair and breast development. Adolescent participants and their parents separately examined the line drawings and indicated which image they or their child most closely resembled. The other pubertal-development measure, the Pubertal Development Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988), is a written questionnaire that assesses multiple aspects of pubertal development, including the occurrence of a growth spurt, growth of body hair, skin changes, breast development and menstruation for girls, and voice changes and facial hair for boys. The PDS was developed as an alternative to physician rating measures and has been shown to have adequate reliability and validity (Petersen et al., 1988) and to be predictive of free testosterone in adolescent males (Hibberd, Hackney, Lane, & Myers, 2015). Both of these measures have been used to assess pubertal status in recent developmental studies (e.g., Shirtcliff, Dahl, & Pollak, 2009) and are reported to be in moderate to excellent agreement with physical exams (see Herting, Gautam, Spielberg, Dahl, & Sowell, 2015).

Only children who were identified as being in Tanner Stage 1 by parents were included in the prepubescent group. To take advantage of the multirater and multimeasure approach to assessing pubertal status, we created a composite score for assigning adolescents to the early- and late-pubertal groups. We recoded both sets (parent, adolescent self-report) of PDS responses to parallel the SMS scoring (Shirtcliff et al., 2009), which resulted in four measures of pubertal development on a 5-point scale (1 = prepubescent, 5 = adult sexual maturity). As in previous work (Herting et al., 2015), we defined early pubertal development for the adolescents as Tanner Stages 1 and 2

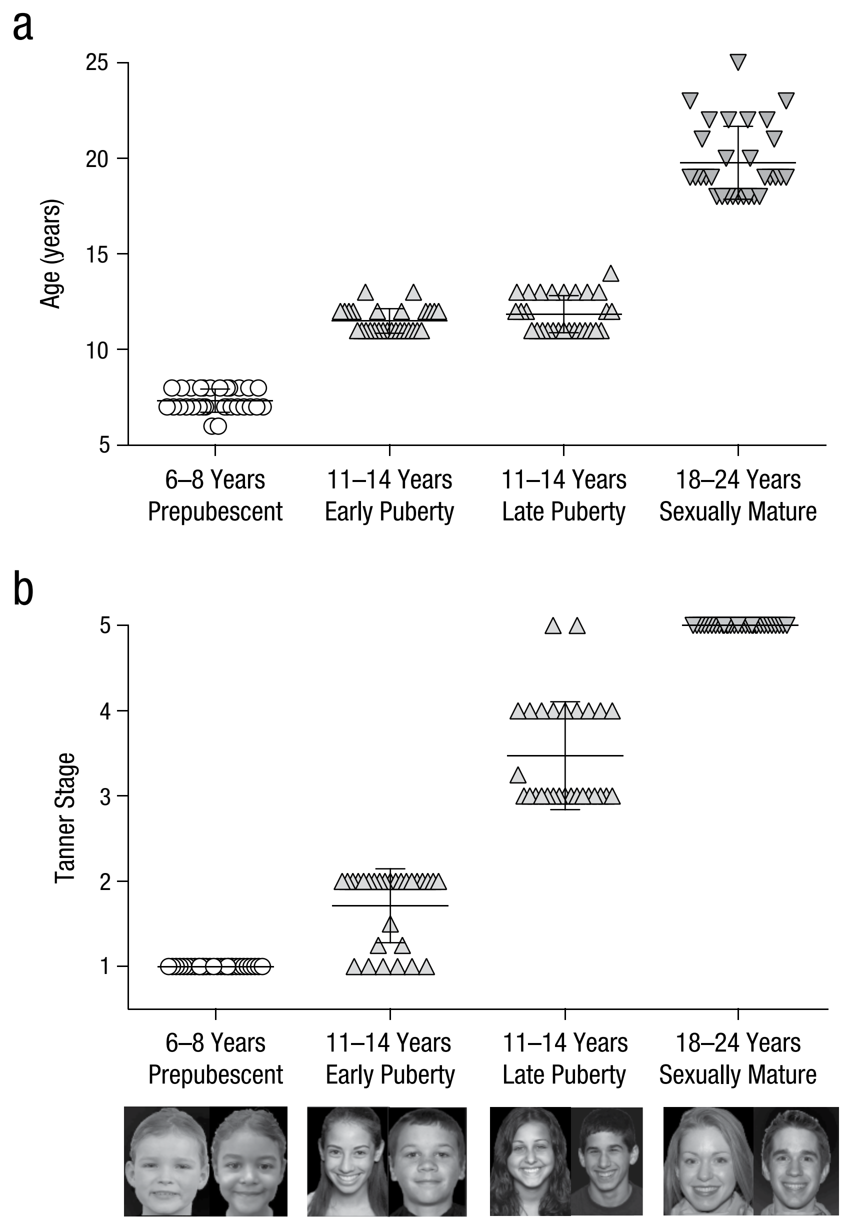

Fig. 1. Age (a) and Tanner stage (b) of each of the four pubertal groups. For each group in each graph, the mean (horizontal bar) is given, along with data points for individual participants. Error bars represent ±1 *SE*. Tanner stage was assessed using self- and parent reports from the Sexual Maturation Scale (Morris & Udry, 1980) and Pubertal Development Scale (Petersen, Crockett, Richards, & Boxer, 1988). The example stimuli shown here for each face category were taken from the Radboud Faces Database (Langner et al., 2010), the National Institute of Mental Health Child Emotional Faces Picture Set (Egger et al., 2011), and the NimStim database (Tottenham et al., 2009).

and late pubertal development for adolescents as Tanner Stages 3 through 5. Unlike in previous studies, we required all four scores and to be consistent when categorizing adolescents into these groups. For example, an adolescent in the late-puberty group could have the following scores across the four measures—self PDS: 5, self SMS: 4, parent PDS: 3, parent SMS: 3. Since all four scores fall in the late category (3–5), this adolescent would be classified as a late-puberty adolescent. If, however, the adolescent and the parent reports differed across category (e.g., parent report: 2 and self-report: 4), the adolescent would not have been included in the final data set. Using these criteria, four adolescents were excluded because of a lack of reporter agreement about pubertal status.

Stimuli

The stimuli consisted of 120 gray-scale photographs of faces with neutral and happy expressions (see Fig. 1 for examples). There were 30 images from each of the four face categories (which corresponded to the pubertal groups): 6- to 8-year-old children, 11- to 14-year-old early-puberty adolescents, 11- to 14-year-old late-puberty adolescents, and sexually mature young adult faces. The individuals represented in the early- and late-adolescent face stimuli did not differ significantly in age, $t(38) = 1.58$, $p = .12$. The ethnic distribution of the stimuli reflected the ethnic distribution of the town from which we recruited participants. For each face category, there were five male and five female target identities, and five male and five female distractor identities. There were two images of each target identity, one presented at encoding and the other presented at test.

Photographs were acquired from five face databases: NimStim (Tottenham et al., 2009), Karolinska (Lundqvist, Flykt, & Öhman, 1998), the National Institute of Mental Health Child Emotional Faces Picture Set (NIMH-ChEFS; Egger et al., 2011), JimStim (Tanaka, Campbell, Hagen, & Xu, 2016), and the Radboud Faces Database (RaFD; Langner et al., 2010). In addition, approximately half of the images of late-puberty adolescents were taken at the Pennsylvania State University campus. Luminance and image size were standardized across images. Any extreme blemishes or scars were masked to eliminate any potential cues to recognition other than facial features. Hair and clothing were not cropped out of the images, which is consistent with procedures in previous face-perception research involving children (Saxton et al., 2010). All images were presented on a black background.

Although the age of the adolescents and children in the face stimuli was known, the pubertal status was not. Faces undergo dramatic biological changes with puberty; they become sexually dimorphic (Farkas, 1988; Silveira, Fishman, Subtelny, & Kassebaum, 1992). Males develop more prominent mandibles, brow ridges, and facial hair. Females develop more prominent cheekbones and lips. These changes are linked with the timing and tempo of pubertal maturation (Silveira et al., 1992). To determine an approximate pubertal status for the adolescent faces, we asked an additional independent set of 25 sexually mature adults to rate the images for pubertal status and sexual maturity. Ratings were made using a scale from 1 to 5 that mirrored the Tanner stages on the SMS. Adults were given an example of a prepubescent 6-year-old "baby" face for the lowest ranking (1) and a sexually mature "grown-up" face for the highest ranking (5). These faces were not included in the stimulus set. The examples were present on the screen while participants judged each face to anchor the extreme ends of the rating scale. The stimuli that were selected to be used in the study as early-puberty adolescents were ranked closer to baby faces ($M = 2.32$, $SD = 0.45$), whereas the stimuli that were selected to be used in the study as late-puberty adolescents were ranked closer to grown-up faces ($M = 3.57$, $SD = 0.47$). The set of early-puberty and late-puberty faces used in the experiment were ranked as being significantly different from each other in sexual maturity, $t(18) = 6.09$, $p < .001$. Thus, just as the adolescent participants were matched for age and varied on pubertal status, so did the stimuli.

Face-memory task

Participants from each of the four pubertal groups were asked to recognize face stimuli from all four face categories (i.e., prepubertal child faces, early-pubertal 11- to 14-year-old adolescent faces, late-pubertal 11- to 14-year-old adolescent faces, and sexually mature adult faces). Face-recognition abilities were measured in a developmentally sensitive old/new recognition paradigm using a computerized game adapted from a recent study (Ewing, Pellicano, & Rhodes, 2013). After studying 10 target faces, participants identified whether each face in a set of 20 faces (10 targets, 10 distractors) had been in the study group ("old") or had not been seen before ("new"). The task was presented in a counterbalanced blocked design with each block containing face stimuli from one of the four categories. Participants first completed a practice session, which consisted of an abbreviated version of each phase of the task. During practice, the experimenter sat with the participant in a quiet room and guided him or her through each portion of the task (i.e., encoding, delay, recognition). At the end of practice, participants were instructed to "try to remember the person and not the picture" to encourage them to create an invariant representation of the face identity. In addition, participants were instructed to complete the task as quickly and as accurately as possible.

Each task block was divided into three sections, encoding, delay, and recognition, in the context of a movie-theater scenario. During the encoding phase, participants were presented with 10 target faces and were told that these were faces of people who were going to a movie; each face had a neutral expression. Adults and adolescents had 2,000 ms to encode each face, whereas the children had 3,000 ms. In the delay period, all participants watched a trailer for a movie (~1.5 min). During the test phase, participants were presented with the 10 target faces, except that now the individuals in the photographs were smiling. These target faces were shown with 10 distractor faces, which were also smiling. By presenting perceptually transformed images of the target faces (i.e., different affect) during the test phase, we were able to assess participants' invariant representation of face identity (not image-specific memory). The faces were each presented for 3,000 ms for adults and adolescents and 5,000 ms for children. Participants responded "yes" ("I recognize this face") or "no" ("I do not recognize this face") by pressing a key.

General analysis strategy

We computed sensitivity (*A*) rather than accuracy because it accounts for response biases in signal and noise distributions that are nonparametric (Zhang & Mueller, 2005). Sensitivity (*A*) is based on the hit rate (*H*) and false alarm rate (*F*) and is calculated as follows:

$$A = \begin{cases} \frac{3}{4} + \frac{H-F}{4} - F(1-H) & \text{if } F \le .5 \le H; \\ \frac{3}{4} + \frac{H-F}{4} - \frac{F}{4H} & \text{if } F \le H \le .5; \\ \frac{3}{4} + \frac{H-F}{4} - \frac{1-H}{4(1-F)} & \text{if } .5 < F \le H. \end{cases}$$

Sensitivity ranges from 0 to 1, with higher scores reflecting better performance. Prior to analyses, the data were evaluated for violations of normality and outliers, separately for each pubertal group's responses to each face category. For each group, values were Winsorized at 2 standard deviations above or below the mean, as appropriate (Dixon & Tukey, 1968).

First, to evaluate whether we replicated the adolescent dip in face-recognition behavior, we computed a one-way analysis of variance (ANOVA) on sensitivity for the adult face category using the between-subjects factor of pubertal group. We also conducted a planned contrast to test whether prepubertal children and adults would perform better than both groups of adolescents (e.g., Diamond et al., 1983; Lawrence et al., 2015; McGivern et al., 2002; Vetter et al., 2013). Following this analysis, we tested our prediction that each group would exhibit a different pattern of recognition bias by evaluating the significance of an omnibus Face Category (prepubertal, early puberty, late puberty, sexually mature) × Pubertal Group (prepubertal, early puberty, late puberty, sexually mature) interaction in a repeated measures analysis of covariance (ANCOVA) with age as a covariate. The presence of the omnibus interaction would indicate that one or more groups had a robust pattern of recognition bias. To determine whether the patterns of bias were consistent with our predictions, we decomposed the interaction by evaluating simple main effects of condition within each group.

Identifying biases within groups. For groups with a main effect of category, face-recognition biases were operationalized by comparing responses to the primary category of interest (caregiver, peer) with the average of all other face categories using paired-samples *t* tests. The rationale for this approach is that if the visual system is tuned to recognize faces from a particular category, then recognition for faces from that category should be relatively better than for faces from all other categories. This approach of using a composite score to represent "other" faces directly reflects the nature of the hypothesis and leverages the power and repeated measures design of the study without requiring the use of multiple post hoc comparisons (6 per group = 24), which were unnecessary to address the central questions of the study.

For the child and adolescent groups, the caregiver bias was defined as sensitivity to adult faces compared with average sensitivity for all other faces (prepubescent child, late-puberty adolescent, and early-puberty adolescent). The peer bias was determined separately for each group. For example, a peer-bias score for an adolescent participant in the early-puberty group was computed by comparing sensitivity to early-puberty adolescent faces with average sensitivity for all other faces (prepubescent child, late-puberty adolescent, sexually mature adult). We bootstrapped significant *t* tests with 1,000 iterations to determine the 95% confidence intervals (CIs) around the responses to compare the robustness of effects.

Comparing biases across groups. To test our hypotheses about differences in the presence and magnitude of the caregiver and peer bias across groups, we computed difference scores reflecting these operational definitions and submitted them to one-way ANOVAs using planned contrasts that reflected our a priori hypotheses. For example, to examine the caregiver bias, we computed a difference score between the sensitivity to adult faces and the average sensitivity to faces in the three other face categories. We did not include the adults in the analysis of the caregiver bias because this is the equivalent of a peer bias in the adults. Only prepubescent children were expected to exhibit a caregiver bias. Given the existing evidence of a female-caregiver bias in infants and young children, we also hypothesized that prepubescent children, but not adolescents, might also have a female-caregiver bias. We tested this hypothesis using a repeated measures ANOVA with pubertal group (prepubertal children, early puberty adolescents, late puberty adolescents) and stimulus sex (male, female) on sensitivity to recognize adult faces.

All groups except the prepubescent children were expected to exhibit a peer bias. We explored this in two planned contrasts. The first tested whether the magnitude of the peer bias was not present in the children but was present in all other groups. The second tested whether the magnitude of the peer bias increased linearly across the full sample. Finally, to address whether the peer bias

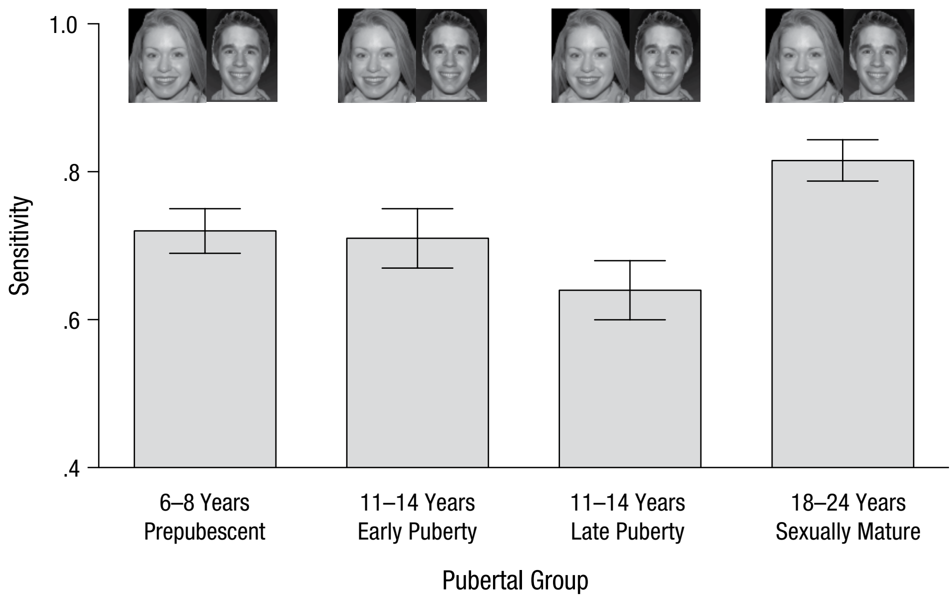

Fig. 2. Mean sensitivity for recognition of adult faces, separately for each of the four pubertal groups. Error bars indicate 95% confidence intervals. The example face stimuli shown here were taken from the NimStim database (Tottenham et al., 2009).

specifically changed as a function of pubertal development during adolescence, we compared the recognition abilities for the two adolescent groups in a 2 (pubertal group) × 2 (face category) repeated measures ANOVA to assess their performance on early- and late-pubertal adolescent faces.

Results

To evaluate whether we could replicate the adolescent dip in face recognition, we analyzed group differences in sensitivity for recognizing adult faces. The main effect of pubertal group in the one-way ANOVA was significant, $F(3, 112) = 4.55$, $p = .005$, as was the planned contrast testing whether prepubertal children and adults performed better than both groups of adolescents, $t(98) = 2.66$, $p = .01$. These findings indicate that there was a dip in sensitivity among both groups of adolescents compared with the prepubertal children and adults (see Fig. 2). Levene's test indicated unequal variances across the groups, $F = 2.78$, $p = .04$, so we report the planned contrast with corrected degrees of freedom. These results replicated the reported adolescent dip in face recognition that is observed when testing recognition of adult faces.

Next, we tested for the larger 4 (face category) × 4 (pubertal group) interaction, controlling for age, in the repeated measures ANCOVA, which revealed a significant interaction, $F(9, 333) = 3.70$, $p < .001$, $\eta^2 = .09$. Critically, there were no main effects of face category, $F(3, 333) = 0.42$, $p = .74$; age, $F(1, 111) = 0.00$, $p = 1.0$; or pubertal group, $F(3, 111) = 0.47$, $p = .71$, and no interaction between age and face category, $F(3, 333) = 0.43$, $p = .73$. The lack of a main effect of pubertal group and age reveals that the paradigm was developmentally sensitive for all participants and that there was no consistent difference across the groups on the basis of age or pubertal status in memory performance. To decompose the interaction, we investigated the simple effects of condition within each group.

Identifying biases within groups

Among the prepubertal children, there was a main effect of face category overall, $F(1, 29) = 4.24$, $p = .049$ (see Fig. 3a). To determine whether the children had a caregiver bias, we compared their recognition of adult faces with their average recognition of faces in the three other categories. An independent-samples, two-tailed *t* test was significant, $t(29) = 2.25$, $p = .032$, as was the 95% CI for the mean difference between the two conditions ([.01, .14]), which did not include 0 ($p < .05$). We evaluated whether this effect existed when defined as better recognition for adult faces than for peer faces (i.e., children's faces), $t(29) = 1.97$, $p = .058$, and it remained nearly significant at the two-tailed level; the 95% CI for the mean difference between the two conditions ([.002, .150]) was significant ($p < .05$). In other words, prepubescent children were significantly better at recognizing adult faces than child faces. Children do not have a peer bias; they have a caregiver bias. This was confirmed by the comparison of peer faces to the average of faces from the other three categories, which was nonsignificant, $t(29) = 0.77$, $p = .45$.

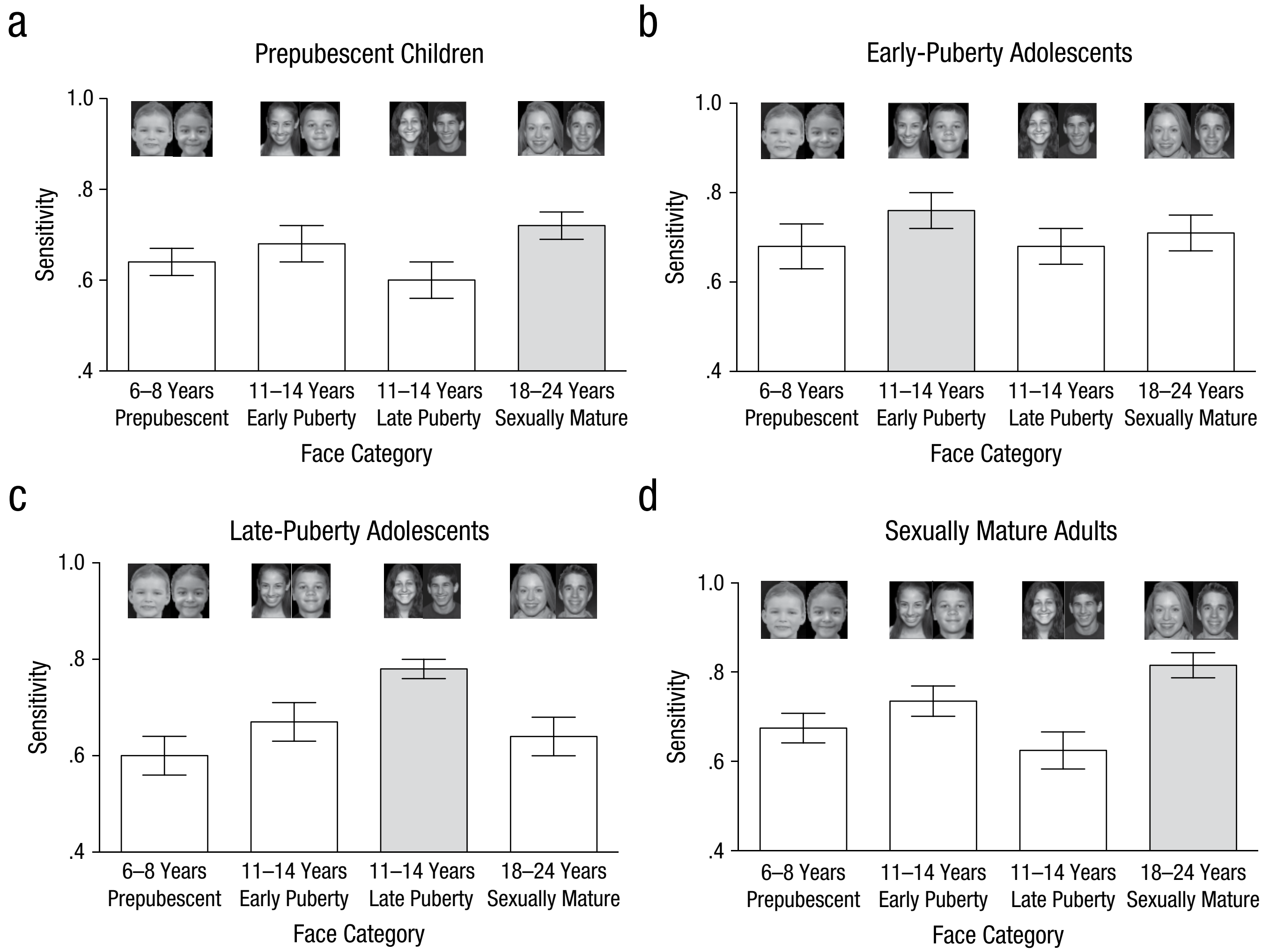

Fig. 3. Mean sensitivity for recognition of each face category, separately for (a) prepubertal children, (b) early-puberty adolescents, (c) late-puberty adolescents, and (d) sexually mature adults. The dark bar in each graph indicates the face category in which that pubertal group exhibited superior performance compared with the average of the three other face categories. Error bars indicate 95% confidence intervals. The example stimuli shown here for each face category were taken from the Radboud Faces Database (Langner et al., 2010), the National Institute of Mental Health Child Emotional Faces Picture Set (Egger et al., 2011), and the NimStim database (Tottenham et al., 2009).

Among early-puberty adolescents, there was also a main effect of face category overall, $F(1, 27) = 5.97$, $p = .021$ (see Fig. 3b). In contrast to the prepubescent children, the early-puberty adolescents did not exhibit a caregiver bias, $t(27) = 0.10$, $p = .46$. Instead, they evinced a peer bias, which was evident in their superior recognition for other early-puberty adolescent faces compared with their recognition for the other three face categories combined, $t(27) = 2.80$, $p = .001$ (see Fig. 4a), and in the 95% CI for the mean difference between the two conditions ([.02, .13]), which was also significant ($p < .01$). This superior recognition was nearly significant when we contrasted recognition performance for other early-puberty adolescent faces and for adult faces, $t(27) = 1.38$, $p = .09$, which suggests that these early adolescents are transitioning from a caregiver to a peer bias.

The late-puberty adolescents also exhibited a main effect of face category in their recognition behavior, $F(1, 27) = 8.98$, $p = .006$ (see Fig. 3c). Like the early-puberty adolescents, the late-puberty adolescents did not evince a caregiver bias, $t(27) = 0.12$, $p = .45$. However, like the early-puberty adolescents, they also demonstrated a strong peer bias, $t(27) = 4.40$, $p = .001$ (see Fig. 4a), and the 95% CI for the mean difference between conditions ([.08, .20]) was also significant ($p < .001$). Unlike in the early-puberty adolescents, this bias for late-puberty adolescent faces remained significant when contrasted with performance for recognizing adult faces, $t(27) = 2.88$, $p = .004$, which indicates that they were no longer transitioning from a caregiver bias but that they were strongly rooted in a peer bias.

Finally, among the adults, there was a strong main effect of face category in face-recognition behavior, $F(1, 29) = 16.13$, $p = .001$ (see Fig. 3d). We could evaluate the

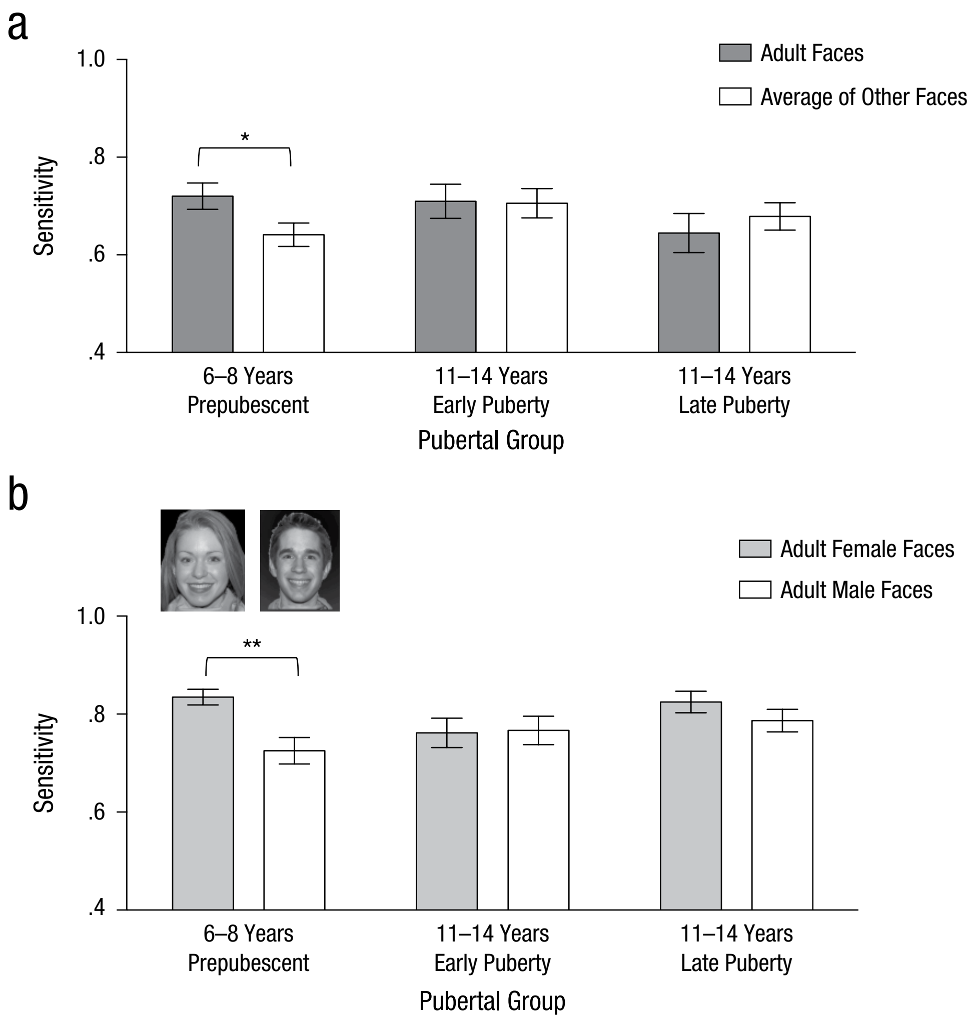

Fig. 4. Mean sensitivity of each of the three youngest pubertal groups as a function of face category. Sensitivity is shown separately for (a) adult faces and the average of the other three face categories and (b) adult female and adult male faces. Asterisks indicate significant differences in sensitivity between face categories (*$p < .05$, **$p < .01$). Error bars indicate 95% confidence intervals. The example face stimuli shown here were taken from the NimStim database (Tottenham et al., 2009).

adults only for a peer bias, which was significant, $t(29)$ = 3.14, p = .000, as was the 95% CI for the mean difference between conditions ([.05, .23], p = .005; see Fig. 4a).

Comparing biases across groups

The caregiver bias dominates childhood face recognition and disappears in adolescence. To evaluate group differences in the magnitude of the caregiver bias, we compared sensitivity to adult faces with sensitivity to faces in the three other categories (i.e., difference scores) across the three pubertal groups (excluding the adults). The one-way ANOVA revealed a main effect of group, $F(1, 83)$ = 4.52, p = .036. The planned contrast revealed that the prepubescent children indeed had a higher caregiver bias than did both groups of adolescents, two-tailed $t(83)$ = 1.99, p = .05 (see Fig. 4a).

Further, we evaluated whether participants had an adult-female-caregiver bias, given the previous evidence in infants and young children of a female-caregiver bias (Macchi Cassia et al., 2014; Quinn et al., 2010). We tested this for each pubertal group by comparing sensitivity for recognizing adult female faces with sensitivity for recognizing adult male faces using a repeated measures 3 (pubertal group) × 2 (stimulus sex) ANOVA. This analysis uncovered a Pubertal Group × Stimulus Sex interaction, $F(2, 83)$ = 3.35, p = .040. To decompose this interaction, we computed difference scores that represented the female bias (female recognition – male recognition) for each participant. Given our predictions about prepubescent children having the largest female-caregiver bias, we tested this hypothesis using a planned contrast on the difference scores. The prepubescent children had a higher female-caregiver bias than did both groups of adolescents, two-tailed $t(83) = 2.41$, $p = .018$ (see Fig. 4b). Only prepubertal children exhibited superior recognition for adult female compared with adult male faces, $t(29) = 3.50$, $p = .002$, 95% CI = [.05, .17]. Early-puberty adolescents, $t(27) = 0.14$, $p = .89$, and late-puberty adolescents, $t(27) = 1.31$, $p = .20$, did not evince a female-caregiver bias. Consistent with our predictions, these findings indicate that the caregiver bias dominates prepubertal children's, but not adolescents', face-recognition behavior despite the vast experience that children have with peer faces in school.

Emergence and fine-tuning of the peer bias for face recognition during puberty. To evaluate the second part of our hypothesis that the peer bias emerges with pubertal development, we compared sensitivity to faces from one's own pubertal group with sensitivity to faces from each of the other three pubertal groups (see Fig. 5a). First, we investigated the emerging sensitivity to the peer bias across the full spectrum of pubertal development by computing group-appropriate peer-bias difference scores (i.e., own-group faces – average of faces from the three other groups). The one-way ANOVA evaluating differences in the magnitude of the peer-bias scores across groups revealed a main effect of group, $F(3, 112) = 3.77$, $p = .013$. Levene's test indicated unequal variances ($F = 3.73$, $p = .01$), so degrees of freedom were adjusted appropriately. The planned contrast confirmed that prepubescent children were the only group who did not exhibit the peer bias, two-tailed $t(55.5) = 3.31$, $p = .002$. An exploratory planned contrast also revealed a systematic linear increase in the magnitude of the peer bias from childhood through early and late adolescence to sexually mature emerging adulthood, two-tailed $t(73) = 2.94$, $p = .004$ (see Fig. 5a).

Finally, to investigate whether the peer bias changes as a function of pubertal development, we compared the two adolescent groups' recognition abilities in a 2 × 2 repeated measures ANOVA that assessed their performance on early- and late-pubertal faces. We uncovered a Pubertal Group × Stimulus Status interaction, $F(1, 54) = 15.67$, $p < .001$, $\eta^2 = .23$ (Fig. 5b). That is, adolescents in early puberty had a peer bias for recognizing other early-puberty adolescents, $t(27) = 2.26$, $p = .032$, 95% CI for the mean difference = [.01, .15], and late-puberty adolescents had a peer bias for recognizing other late-puberty adolescents, $t(27) = 3.41$, $p = .002$, 95% CI for the mean difference = [.06, .18]. In other words, with the onset of pubertal development, superior recognition emerges for peer faces that match one's pubertal status. As pubertal development progresses, so does the recognition bias; individuals with more advanced pubertal development become better at recognizing faces of other individuals with similarly advanced pubertal development.

Discussion

We investigated whether, in face-recognition behavior, prepubertal children have a caregiver bias and whether puberty influences the emergence and developmental course of a peer bias. As predicted, prepubertal children's face-recognition behavior is superior for adult faces compared with child and adolescent faces. With the emergence of puberty, this bias shifts so that superior recognition for peer faces (compared with adult and child faces) emerges. Furthermore, this peer bias is shaped by pubertal status such that early-puberty adolescents are better at recognizing other early-puberty adolescents, and late-puberty adolescents are better at recognizing other late-puberty adolescents. This is not a function of age, given that age was matched across the two adolescent groups and face stimuli, and was controlled for in our analyses. Adults also have a peer bias for other adult faces. These results indicate that puberty plays a critical role in the adolescent-specific shift that occurs in the prioritization of information that is extracted from faces.

Our finding that the caregiver bias dominates children's face-recognition behavior expands on a literature reporting the same bias in infants' and toddlers' behavior (Macchi Cassia, 2011; Quinn et al., 2010). Our findings reveal that this caregiver bias, particularly for adult female faces, exists long after children become immersed in their age-matched peer group at school. We suggest that this extended caregiver bias reflects the instantiation of a computational goal within the visuoperceptual system that addresses the social developmental tasks of childhood. It makes identification of adult faces a priority for young children who are still largely dependent on their caregivers.

We also discovered that the caregiver bias systematically decreases with the onset of adolescence. This finding allows us to recast the prior findings on the adolescent dip in face-recognition abilities (e.g., Diamond et al., 1983). Recall that all previous work investigated adolescent recognition abilities for adult faces. We replicated this dip and also showed that it is concurrent with the emergence of the peer bias.

This is the first study to show that the peer bias in face recognition emerges in early adolescence as a function of pubertal development. Previous studies have all considered a peer bias with respect to the age of the stimulus face and observer. Work investigating an own-age effect in children's face-recognition behavior has been sparse and largely inconsistent, and it has not systematically measured the effect in adolescents. One group reported an own-age effect in 8-year-olds' recognition of other 8-year-olds' faces (Hills & Lewis, 2011) that disappeared when participants became 9 years old (Hills, 2012). However, the remaining

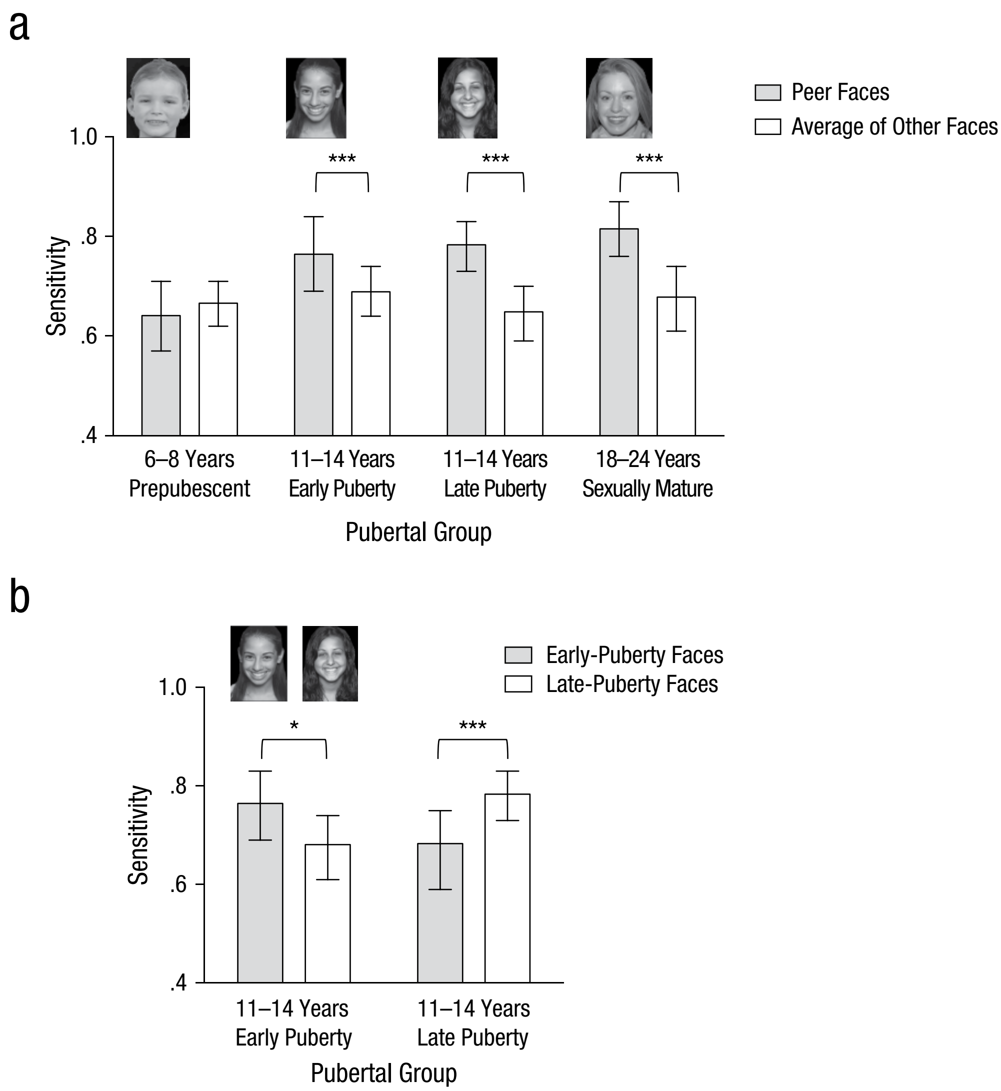

Fig. 5. Mean sensitivity for (a) each of the four pubertal groups and (b) the two pubertal adolescent subgroups. In (a), sensitivity is shown for peer faces and for the average of the three other face categories. In (b), sensitivity is shown for early- and late-puberty faces. Asterisks indicate significant differences in sensitivity between face categories (* $p < .05$, *** $p < .001$). Error bars indicate 95% confidence intervals. The example stimuli shown here for each face category were taken from the Radboud Faces Database (Langner et al., 2010), the National Institute of Mental Health Child Emotional Faces Picture Set (Egger et al., 2011), and the NimStim database (Tottenham et al., 2009).

face-recognition studies in children have all failed to find an own-age effect (Chung, 1997; Goldstein & Chance, 1964; Rehnman & Herlitz, 2006), and in fact, some report evidence of a caregiver bias (Gilchrist & McKone, 2003). The inconsistencies in this work may be due in large part to the fact that researchers defined peer biases in terms of age, which is often broadly defined. Furthermore, age alone is not necessarily a relevant measure of peerhood (i.e., the organizational characteristics of peer groups), particularly in adolescence, when the timing and tempo of puberty differ greatly between individuals (Marceau, Ram, Houts, Grimm, & Susman, 2011), which contributes to adolescent-peer-group structure (Crockett & Petersen, 1987). This is why we suggest that pubertal maturation, together with age, may be more indicative of peerhood.

We suggest that the emergence of a superior ability to recognize peer faces from one's own pubertal group reflects our thinking that adolescents' perceptual systems are becoming organized to subserve the social developmental tasks of adolescence (Scherf & Scott, 2012). Specifically, the diminished caregiver bias reveals an emerging autonomy from parents, the beginning peer bias in early puberty signifies the orienting toward peers as they begin to seek out loyal confiding friendships, and the fine-tuning of the peer bias in late puberty reflects how they are beginning to think of peers as potential romantic and sexual partners. Therefore, these biases are likely manifestations of transitional computational goals within the perceptual system, which facilitate the accomplishment of developmental tasks in specific developmental periods. Future work linking the magnitude of the biases with progress toward each of these developmental tasks will help evaluate this interpretation of these findings.

But how could pubertal development shape the brain and behavior to influence the way the visuoperceptual system recognizes faces and processes social information more generally? Regions within the neural circuitry supporting face recognition, including the occipital and temporal cortices and the amygdala, are rich with sex-hormone receptors (Perlman, Webster, Kleinman, & Weickert, 2004; Sarrieau et al., 1990), and naturally occurring fluctuations in both women's and men's intrinsic gonadal hormones are related to alterations in their perceptions of faces (Little, Jones, Burt, & Perrett, 2007). These findings lead us to suggest that the influx of sex hormones during adolescence likely mediates the emergence of the peer bias via their influence on the neural architecture of the face-processing system (Scherf et al., 2012; Scherf, Smith, & Delgado, 2013). For example, the peer bias in face recognition may result from a shift in the attribution of relevance of peer faces that is mediated by the amygdala, which is extensively connected with cortical and subcortical regions. Pubertal hormones likely influence the initiation of the motivation to reevaluate these stimuli, given the presence of sex-hormone receptors in the amygdala. Changes in amygdala inputs to the rest of the face-processing network could then induce extensive functional reorganization within this network, enabling it to retune toward peers (Scherf et al., 2013). Future developmental neuroimaging work will need to assess this mechanistic hypothesis of our behavioral findings.

We provide evidence for the role of pubertal development in shaping face-processing behaviors that likely support the navigation of peer-oriented relationships in adolescence and ultimately facilitate the adolescent transition into adult social roles. We reconceptualized the adolescent dip by showing that it is explained as a recalibration of the face-processing system away from caregivers and toward peers. In so doing, we uncovered the emergence of the peer bias during adolescence and showed how it is related to the onset and development of puberty. We have provided the first evidence that puberty shapes social human behaviors that are not directly sexual.

Action Editor

Jamin Halberstadt served as action editor for this article.

Author Contributions

G. Picci and K. S. Scherf contributed equally to designing the study. G. Picci collected the data. G. Picci and K. S. Scherf contributed equally to the analysis of the data and the writing of the manuscript.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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