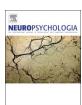


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Neural correlates of babyish adult face processing in men



Hirokazu Doi^a, Minoru Morikawa^b, Nobuyuki Inadomi^b, Katsuhiko Aikawa^b, Masataka Uetani^b, Kazuyuki Shinohara^a,*

- Graduate School of Biomedical Sciences, Nagasaki University, Nagasaki, Japan
- ^b Department of Radiology, Nagasaki University School of Medicine, Nagasaki, Japan

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ABSTRACT

The morphological characteristics of an infant's face are collectively referred to as baby schema or babyishness. It has been well established that infant traits are implicitly projected, or overgeneralized, to adults with babyish facial features. However, few studies to date have investigated the neural underpinnings of such overgeneralization. In the present study, we addressed this issue by comparing neural activations elicited by babyfaced and mature-faced adult faces in men using fMRI. We found increased activations in clusters surrounding the bilateral insula, bilateral anterior cingulate cortex, and right inferior frontal gyrus, which have been previously linked to the processing of facial attractiveness and infant-related information. We also discovered increased activation in the left medial prefrontal cortex, which might be related to emotional or empathic responses directed towards baby-faced adults. The activated region also included the left premotor cortex, which presumably reflects an embodied response or approach motivation directed toward infant-related information. Furthermore, the activation level of the left caudate correlated with the salivary concentration of oxytocin. Taken together, these findings indicate that passive viewing of babyish adult faces induces increased responses in neural regions linked to facial attractiveness and infant-related information processing, and that these responses are partially influenced by oxytocinergic factors.

1. Introduction

Mammalian infants universally share a set of morphological facial characteristics, such as large eyes, round contours, large foreheads, and small noses. According to the influential theory by Lorenz (1943), these facial features, collectively termed *Kindchenschema* (baby schema), evolved as a releaser for care-taking behavior in adults, consequently ensuring the survival of infants throughout the most vulnerable stage of their development. Baby-like visual features effectively capture visual attention in humans (Brosch et al., 2008, 2007) as well as in nonhuman primates (Sato et al., 2012). Additionally, the presentation of infant faces is known to induce enhanced sympathetic activity (Esposito et al., 2014) and positive implicit-association in adults (Senese et al., 2013).

It is widely recognized that the faces of some adults exhibit high levels of baby-like morphological characteristics, and that these morphological features are among the primary determinants of facial impression. This point was clearly illustrated in a series of insightful studies by Zebrowitz and her colleagues on the "overgeneralization effect" of baby faces (Zebrowitz et al., 1992, 1993, 1998; Sparko and Zebrowitz, 2011). According to their theory, baby-faced people are

more likely to be judged as warm, honest, and trustworthy, but also as vulnerable, incompetent, and less intelligent than their mature-faced counterparts, because infant characteristics are implicitly projected onto them. Consequently, baby-faced people are more likely to be exonerated from punishment (Zebrowitz et al., 1991) or to receive a greater degree of assistance from others (Keating et al., 2003; Livingston and Pearce, 2009; Lishner et al., 2008). At the same time, they are often thought to be less competent at handling situations compared with those who are mature-faced (Gorn et al., 2008). Taken together, these studies indicate that in addition to the often-studied dimensions of attractiveness and trustworthiness, baby-like facial features exert a strong influence on the facial impressions.

Despite a recent surge in interest regarding the neural bases of infant-related information processing and facial impression formation (Kranz and Ishai, 2006; O'Doherty et al., 2003; Bartels and Zeki, 2000; Glocker et al., 2009; Hahn and Perrett, 2014; Swain, 2011; Rilling, 2013), few studies have investigated the neural mechanisms underlying the perception of "babyish" adult faces. An exception (Zebrowitz et al., 2009) compared brain activity in females who viewed images of baby faces, mature-faced adults, and baby-faced adults. The results indicated that amygdala activation elicited by baby-faced men was comparable

E-mail address: kazuyuki@nagasaki-u.ac.jp (K. Shinohara).

^{*} Corresponding author.

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with that elicited by baby faces, thus highlighting the pivotal role of the connectivity between the amygdala and the fusiform face area in inducing the overgeneralization of babyish characteristics. However, the authors did not fully elucidate the neural responses to the images of baby-faced adults because they adapted a hypothesis-driven region-of-interest (ROI) approach.

In the present study, we sought to increase our understanding of how the brain processes facial images of baby-faced and mature-faced adults. To this end, we used functional magnetic resonance imaging (fMRI) to examine brain activity in childless men. We adopted a passive viewing paradigm with no overt responses, as we sought to investigate the neural activation induced automatically by face presentation with a minimal task requirement. We excluded female participants to avoid the influence of fluctuations in endocrinological functions during the menstrual cycle (Sprengelmeyer et al., 2009). Although several recent studies have investigated the ways in which brain function is altered by fatherhood (Mascaro et al., 2014; Kuo et al., 2012), little is known about how childless men process infant-related information, including babyish adult faces. From this perspective, the present study complements previous research in which only female participants were recruited (Glocker et al., 2009; Bos et al., 2010; Liang et al., 2010).

According to the over-generalization hypothesis (Zebrowitz et al., 1992, 1993, 1998; Sparko and Zebrowitz, 2011), stereotypical impressions attributed to babies, e.g. warmth, weakness, and incompetence, are implicitly projected onto adults with babyish facial morphology. Likewise, the baby schema is considered to release feelings and actions that are generally directed to co-specific infants (Lorenz, 1943). On the basis of these previous findings, we hypothesized that the presentation of baby-faced adult faces would enhance activation in neural regions that show increased activation in response to infant faces. We predicted the following neural regions to be candidates for increased activation in response to baby-faced compared to mature-faced adult faces. First, a number of studies have revealed that the reward system, which is composed mainly of the ventral tegmental area, nucleus accumbens (NAcc), basal ganglia, and the orbitofrontal cortex (Schultz, 2000; Sescousse et al., 2013), is recruited when processing images of infants (Bartels and Zeki, 2000; Glocker et al., 2009; see for a review, Hahn and Perrett, 2014; Swain, 2011; Rilling, 2013), which presumably explains why infant faces are considered to be a pleasant stimuli. Second, some types of infant stimuli that are closely linked to attachment behavior, such as the sound of crying, are known to induce increased activation in the inferior frontal gyrus (IFG), anterior insula and anterior cingulate cortex (ACC) (Riem et al., 2011; Voorthuis et al., 2014). Thus, we hypothesized that the images of baby-faced adults should increase activation in the dopamine-associated reward system, IFG, anterior insula and ACC compared with images of mature-faced adults.

People with babyish faces tend to be judged as more attractive (Cunningham, 1986; Kuraguchi et al., 2015; Little, 2012) and trustworthy (Pivonkova et al., 2011; Little, 2012; Zebrowitz et al., 1992, 1993, 1998). Thus, we also hypothesized that the presentation of babyfaced adult faces would increase activation in neural regions associated with facial impressions of attractiveness and trustworthiness. Neuroimaging and neuropsychological studies have revealed augmented activation of occipito-temporal regions (Chatterjee et al., 2009; Iaria et al., 2008; Vartanian et al., 2013) and the reward system (Chatterjee et al., 2009; Cloutier et al., 2008; Liang et al., 2010; Martín-Loeches et al., 2014; O'Doherty et al., 2003) in response to attractive faces. Additionally, judgment of faces as 'untrustworthy' has been associated with stronger activation in the amygdala (Mende-siedlecki et al., 2013; Baron et al., 2011). On the basis of these data, we hypothesized that viewing babyish adult faces increases activity in the reward system and occipito-temporal regions, while decreasing that in the amygdala.

Recent behavioral and neuroimaging studies have revealed that the endocrine system can modulate how infant-related stimuli are processed (Bos et al., 2010; Hahn et al., 2015; Sprengelmeyer et al., 2009). To further investigate this, we conducted a preliminary analysis of the endocrinological basis of individual differences in neural responses to images of baby-faced adults.

As a primary measure of endocrinological differences, we evaluated the concentration of testosterone and oxytocin in saliva. Studies of parenting have identified testosterone as a reliable predictor of parenting behavior, especially in men. For example, a pioneering study by Fleming et al. (2002) revealed that males with low testosterone levels show higher sympathy and more enhanced physiological responses to infants' crying compared with those with high testosterone levels. Additionally, a number of longitudinal studies have reported a negative association between the level of parental investment by fathers and their testosterone levels (Gettler et al., 2011; see Gray and Campbell, 2009, for a review). Likewise, an increasing number of studies have identified the neuropeptide oxytocin as a key modulator of human social relationships (Kosfeld et al., 2005; Domes et al., 2007; Scheele et al., 2012), especially those between infants and their parents (Feldman et al., 2012; Weisman et al., 2012). Of particular relevance to the present study, a recent study by Weisman et al. (2013) revealed that intranasal administration of oxytocin enhanced fathers' interactive behaviors toward their infants.

Interestingly, previous studies have shown that both testosterone and oxytocin exert modulatory influences on the activation of reward system that we hypothesized would exhibit increased activation in response to baby-faced compared to mature-faced adults. The reward system is rich with oxytocin receptors (Skuse and Gallager, 2009). Indeed, previous neuroimaging studies have shown a positive association between activation levels in reward-related regions, such as NAcc and the striatum, and oxytocin levels (Groppe et al., 2013, Scheele et al., 2013). Of particular relevance to the present study, Strathearn et al. (2009) have shown a positive correlation between the oxytocin response after interaction with own infant and ventral striatum activation elicited by videos of own infant faces.

Testosterone has long been associated with specific behavioral tendencies such as aggression (Dabbs and Hargrove, 1997), impulsivity (Booth et al., 1999) and competitiveness (Casto and Edwards, 2016). Moreover, influential animal studies have shown that administration of testosterone induces hedonic response (Arnedo et al., 2000; Alexander et al., 1994), which is considered to be mediated by NAcc (Frye et al., 2002). In addition to these, recent studies have indicated that there is a positive relationship between testosterone and sensitivity to rewarding stimuli, including infant faces (Hahn et al., 2015). Likewise, several studies show that the exogenous administration of testosterone increases activation in the ventral striatum (Hermans et al., 2010; Bos et al., 2010, 2013). Of particular relevance to the present study, Kuo et al. (2012) found a positive correlation between left caudate activation and salivary testosterone levels when fathers viewed the faces of their infants. On the basis of these findings, we predicted that oxytocin and testosterone would modulate activation in the reward-related regions, especially NAcc and the striatum, elicited by viewing babyfaced adult faces.

2. Method

2.1. Participants

Sixteen right-handed males (mean =21.2 years old; SD =3.6) with normal or corrected-to-normal visual acuity participated in the study. The experiment was conducted in the evenings from 6 pm to 8 pm. No participant had a history of psychiatric disorders or was currently taking any medication. Written informed consent was obtained from all participants before the experiment according to the requirements of the Ethics Committee of Nagasaki University.

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