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Original Research Article

Fluctuating Asymmetry Predicts Human Reactive Aggression

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ABSTRACT Fluctuating asymmetry (FA) represents non-directional deviations from perfect symmetry in morphological characters. Prenatal stressors contribute to the imprecise expression of symmetrical phenotypes and display of agonistic behavior in children and adults. Because prenatal stress affects neurological function and overt behavior, and FA is often used as a marker for prenatal stress, we hypothesized that high FA would be associated with elevated levels of human reactive aggression. Data were collected from 100 males and females (average age = 20.1) on FA of 11 bilateral traits (second, third, fourth, and fifth digit length, palm height, wrist diameter, elbow width, ear height, ear width, foot breadth, and ankle circumference). Additional relationships were also investigated among FA, testosterone (T), and type of provocation to test a comprehensive aggression model. Experimental participants solicited donations for a fictitious charity organization via telephone and selected follow-up letters after the calls. High FA and T values were independently associated with elevated reactive aggression (force of terminating the call) under low provocation in males, and under high provocation in females. In the absence of phenotypical markers, i.e., FA and T, sex differences in response to provocation disappeared and a "passive-aggressive" response emerged. Both males and females selected hostile follow-up letters, but showed low reactive aggression when terminating the call under high provocation. This pattern was reversed under low provocation. Taken together, these data suggest that individuals' phenotype and intensity of provocation are important determinants of individual and sex differences in aggression. Am. J. Hum. Biol. 16:458–469, 2004. © 2004 Wiley-Liss, Inc.

Fluctuating asymmetry (FA) refers to random, minor deviations from perfect symmetry in paired traits, such as hand width and ear height. Because the development of the left and right sides of a paired trait is presumably controlled by an identical set of genetic instructions, these small imperfections in symmetry are considered to reflect genetic and environmental perturbations experienced during ontogeny. Individuals are presumably buffered against such developmental insults by employing homeostatic mechanisms to produce the ideal phenotype (Clarke and McKenzie, 1992). Thus, FA may be used to quantify developmental stressors and decreased buffering capacity against environmental and genetic perturbations (van Valen, 1962; Adams and Niswander, 1967; Livshits et al., 1988; Leung and Forbes, 1996; Vollestad et al., 1999; Klingenberg, 2001). Indeed, FA increases with prenatal stress under controlled laboratory conditions in nonhuman animals (Mooney et al., 1982; Siegel et al., 1977; Siegel and Smookler, 1973). In humans, stressors such as inbreeding (Markow and Martin, 1993) and poor maternal health during pregnancy (Kieser et al., 1997; Kieser, 1992; Wilber et al., 1993) are associated with increased FA in the offspring.

Taken together, these data suggest that perturbations experienced during ontogeny leave enduring signs in the adult body marked by high FA. Genetic and environmental stress during development may also adversely affect executive function and overt behavior. The development of the central nervous system (CNS) is concurrent with the development of traits that show minor deviations from the symmetrical phenotype. Thus, high FA should be associated with various neurological disorders. Indeed, schizophrenia

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(Reilly et al., 2001; Yeo et al., 1999; Green et al., 1994; Mellor, 1992; Markow and Wandler, 1986), attention deficit and hyperactivity disorder (AD/HD) (Burton et al., 2002, 2003), developmental delays in childhood (Naugler and Ludman, 1996), and Down syndrome (Barden, 1980) are positively correlated with FA. Because disruptions in developmental homeostasis, marked by increased FA, are suggestive of impaired CNS function, as shown by the relationship between FA and neurological disorders, we hypothesized that human reactive aggression would be elevated in individuals with high FA. Supporting evidence indicates a significant positive association between FA and poor impulse control in normal populations (Shackelford and Larsen, 1997). Poor impulse control is in turn implicated in CNS dysfunction (Oades, 1998) and aggression (Serocyznski et al., 1999). Therefore, a significant correlation between high FA and aggressive reaction to provocation may be observed because of poor impulse control, possibly reflecting exposure to developmental stressors. The joint contribution of prenatal stressors, such as maternal tobacco and alcohol consumption, to the imprecise expression of symmetrical phenotypes (Keiser, 1992; Kaiser et al, 1997; Wilbur et al., 1983) and agonistic behaviors (reviewed in Raine, 2002a,b) supports this hypothesis.

The relationship between aggression and FA remains unspecified in humans. Symmetrical adult and adolescent human males are more aggressive on self-reported measures (Furlow et al., 1998; Manning and Wood, 1997). In contrast to these self-report data, psychopathic and nonpsychopathic violent offenders charged with homicide, sexual assault, and armed robbery are more asymmetrical than nonoffenders (Lalumiere et al., 2001). In an attempt to better examine the association between FA and agonistic behaviors, we conducted our experiments in a realistic setting during a staged aggressive interaction. Our experiment differed from other studies that used either self-reported questionnaires in survey or clinical experiments, or examined aggressive people (e.g., violent offenders) at some point temporally distant from the aggressive behavior. The current study investigated the association between FA and human reactive aggression. Reactive aggression was operationally defined as an angry-like response to frustration goal blocking, provocation, or threat (Berkowitz, 1989). Additional relationships regarding the sex steroid hormone, testosterone (T) in response to provocation were also investigated.

Aggressive behavior in humans and nonhuman animals shows a sexually dimorphic pattern, with males generally more overtly aggressive than females. T is implicated in this sexual dimorphism. Specifically, T exerts its influence on agonistic behavior through its organizational effects on neural tissue during ontogeny and its activational effects on androgen receptors, generally after puberty and in adulthood (Nosenko and Reznikov, 2001; Rubinov and Schmidt, 1996). Although the organizational and activational role of T on aggression is fairly well established in several species, such as mice and rats (Book et al., 2001; Nosenko and Reznikov, 2001), the evidence is not compelling in other species, including humans (reviewed in Albers et al., 2002; Harris, 1999). For example, meta-analyses indicate a positive, weak correlation between T and aggression in humans (Archer, 1991; Book et al., 2001). Self-reported measures of aggression in criminal and normal populations, however, do not consistently correlate with T concentrations (reviewed in Harris, 1999). Indeed, one study reported a negative correlation between aggressive behavior and T in women (Gladue, 1991). Clinical, randomized, placebo-controlled studies also yielded mixed results. In some studies, androgen administration in supra-physiological amounts to eugonadal men did not result in anger and aggression (O'Connor et al., 2002; Anderson, et al., 1992; Tricker et al., 1996). In other studies, a positive association between androgen administration and aggressive behavior was observed (Kouri et al., 1995; Pope et al., 2000; Su et al., 1993). We hypothesized that if sufficient anger arousal is induced by provocation, then T may regulate the expression of aggression. Previously reported positive relationships between T and anger (Persky et al., 1971; van Honk et al., 1999), tension, threat, and selective attention to angry faces (van Honk et al., 1999) and words (Benderlioglu and Nelson, unpubl. data) suggest that proclivity for anger may be associated with high T. Consequently, we predicted that aggressive reaction to provocation would generally increase as a function of FA and T for both sexes. We hypothesized that this response would be moderated by the type of provocation, because unprovoked males are generally more aggressive than females (Bettencourt and Miller, 1996). By testing a comprehensive model of aggression that included several phenotypical characteristics of individuals, such as FA and T values, and the nature of provocation, we aimed to control for factors that may independently contribute to aggressive behavior in general and sex differences in particular.

SUBJECTS AND METHODS

One hundred (51 male, 49 female, mean age = 20.1, SD = 1.4) college students participated in our experiment for course credit. In Phase I of the experiments, the participants were told they were part of a study that investigated the effects of circulating hormones on soft and hard tissue components in the body and on behavior. In this phase, participants first completed a questionnaire that asked several demographic variables, such as age, sex, and ethnicity. Only participants who were born and raised in the US were solicited to take part in the study to control generally for the environmental factors involved in physical growth and development.

FA measurements

Participants were initially measured with a digital caliper to the nearest 0.01 mm on 11 bilateral traits: 1) second, 2) third, 3) fourth, and 4) fifth digit length, 5) palm height, 6) ear height, 7) ear width, 8) wrist diameter, 9) elbow width, 10) foot breadth, and 11) ankle circumference. Injuries were noted and traits with broken bones or sustained injuries were eliminated. Each subject was measured twice by the same investigator. The digits on the right side of the body, right hand, wrist, elbow, ear, ankle, and foot were measured first in this exact order. The data on the left side of these traits were then collected. This procedure was repeated for the second measurements without reference to the prior data. There was about a 20-minute lag between the two measurements.

Preparing the FA indices

Because the size difference between two sides of a single trait is rather small and can be partially attributed to measurement error, we employed three separate methods to assess and control for this error. First, two methods aimed to eliminate traits that showed a clear indication of measurement error. A one-way repeated measures ANOVA with measurement as the repeated factor and R-L of each trait as the dependent variable revealed ear width differed between the two measurements ($F_{[1,95]} = 11.43$, $P = 0.0010$). Therefore, this trait was eliminated from further analysis. Following a mixed model two-way ANOVA (side × subject) with repeated measurements on each side (Palmer, 1994), we further tested whether the between-side variance is significantly greater than the error in measurement for the remaining traits. The presence of a significant interaction effect (i.e., side × subject) for each trait would support our previous conclusion that the traits were correctly measured with negligible measurement error. This was indeed the case. The interaction effects were significant for the remaining traits (2nd digit: $F_{[1,99]} = 5.51$, $P < 0.0001$; 3rd digit: $F_{[1,99]} = 3.78$, $P < 0.0001$; 4th digit: $F_{[1,99]} = 9.48$, $P < 0.0001$; 5th digit: $F_{[1,99]} = 3.55$, $P < 0.0001$; hand: $F_{[1,99]} = 1.54$, $P = 0.0052$; wrist: $F_{[1,99]} = 4.89$, $P < 0.0001$; elbow: $F_{[1,99]} = 5.07$, $P < 0.0001$; ear height: $F_{[1,99]} = 7.27$, $P < 0.0001$; ankle: $F_{[1,99]} = 10.13$, $P < 0.0001$; foot: $F_{[1,99]} = 31.78$, $P < 0.0001$). The third method further reduced the measurement error by averaging the two replicates (Graham et al., 2003).

We then performed student's t-test and normality tests on the signed FAs (R-L) for each trait. The effects of early stressors on perfect symmetry are assumed random, independent, and cumulative (Palmer, 1994; Palmer and Strobeck, 1986). Hence, the frequency distribution of the difference between the right and left (R-L) measurements of a particular trait approximates a normal distribution at the population level, with a mean around zero (Palmer, 1994; Palmer and Strobeck, 1986; van Valen, 1962). Ankles and wrists showed directional asymmetry; that is, the corresponding sample mean of the signed R-L was significantly different from zero ($t_{wrist} = -4.46$, $P < 0.0001$; $t_{ankle} = -8.58$, $P < 0.0001$). These were also excluded from the analyses.

There is evidence that digit lengths (Manning et al., 1998; Brown et al., 2002), dermatoglyphic asymmetry (Jamison et al., 1993) and patterns (Jamison et al., 1994) are influenced by circulating androgens. Soft tissue components of the traits may also be responsive to circulating hormones (Manning et al., 2002), rendering overall trait FAs unreliable indicators of developmental stress. Accordingly, among the traits that showed ideal FA, we also tested whether FA of these traits varied as a function of sex steroid hormone, T. Average FA of the digits increased with T in males (*beta* = 0.23, $P = 0.0182$; age, weight, height, and handedness controlled). Thus, deviations from ideal FA could not be considered random and independent. We therefore excluded digits from the calculations of average FA. No significant relationships were observed for other individual trait FAs and composite FA excluding the digits ($P > 0.05$).

The remaining ideal FAs were then corrected for trait size, i.e., $|R\text{-}L|/0.5(R+L)$ (Palmer, 1994). A composite asymmetry score was calculated by summing and averaging size corrected, unsigned ideal FAs, namely, palm height, elbow width, ear height, and foot breadth, following the methods described in similar FA studies with humans (e.g., Thornhill and Gangestad, 1986; Furlow et al., 1998; Trivers et al., 1999; Lalumiere et al., 1999, 2001). Size-scaling, however, may confound the individual differences in FA measures when FAs do not actually vary as a function of size. To avoid this confounding factor, we conducted analyses on size dependence by regressing absolute asymmetry ($|R\text{-}L|$) of each trait on the average size of that particular trait [$(R+L)/2$] (Palmer and Strobeck, 1986) controlling for sex. We found no indication of size dependency for any of these traits (all $P > 0.05$). We thus converted R-L values for each trait to standard normal deviates and summed these standard deviates to construct a composite measure of individual FA. We conducted all of our analyses on this new composite score. We also performed our analyses on a different FA index that summed and averaged absolute R-L values for each individual without standardization and size correction (i.e., no significant size effect on any of the trait FAs was found). Analyses conducted with these three different FA indices yielded identical results. Therefore, we present our results on the size-corrected first composite measure (i.e., $|R\text{-}L|/0.5(R+L)$ to establish direct comparison with previously published studies on human violence and FA (i.e., Furlow et al., 1998; Lalumiere et al., 2001).

Handedness

Participants completed a slightly revised version of the "Waterloo Handedness Questionnaire-Revised" (WHQ-R) (Elias et al., 1998). Questions on hand preference consisted of 38 scaled items to assess self-reported hand preference and performance. Responses of a) left always, b) left usually, c) equal, d) right usually, e) right always were scored from –2 to 2 with equal being scored as zero.

Testosterone (T)

Upon completion of the questionnaires and FA measurements, saliva samples were collected from consenting participants. Salivary measurements offer advantages for behavioral research because they are noninvasive. Salivary testosterone represents a biologically active fraction (free) of testosterone. Participants were instructed to rinse their mouths with water 15–20 minutes prior to collection. We collected 5–7 ml saliva in a polyethylene tube from participants chewing sugar-free bubblegum, which has been shown to have no cross-reactivity with free T radioimmunoassay (RIA) (Dabbs, 1991). Samples were frozen at –80°C until assayed. All samples were analyzed in a single RIA using a Coat-A-Count kit for Total Testosterone (Diagnostics Products, Los Angeles, CA).

Aggression measures

In the second phase, participants were invited to join a study that purported to measure persuasive ability. In this phase, they were asked to raise money for a fictitious charity organization. The participants were informed that there is a relationship between the pitch of the voice and persuasive ability. They were led to believe that they scored high in T, which lowers the pitch of the voice, hence they should be able to convey messages more assertively. Also, they were promised two free tickets to a local movie theater if they were able to obtain any donations. In order to increase the credibility of our experimental manipulation, we prepared a telephone directory with fictitious names and phone numbers, except those of our two confederates. The entries showed "yes" and "no" and corresponding dollar values for donations. The last entry before the participants' call list began was listed as $20. We believed that the high expectations to succeed (i.e., false high T scores), incentives, and success of previous callers would increase the level of frustration and anger arousal when rejected.

Participants called two male confederates who both refused to donate.

Conversations between the participants and confederates were tape-recorded. The confederates were uninformed about the conditions of the experiment. The first calls were always placed under low provocation. The confederate in the low provocation condition appeared to be amenable to charity donations. He did not challenge the caller and declared persuaded by the worthiness of the donation. However, he cited lack of money as a reason not to contribute. The second calls were always made under high provocation. The confederate in this condition was confrontational. He directly challenged the caller and worthiness of the donation. The force applied when hanging up the telephone was an indicator of reactive aggression. Force was measured by a balance plate (Bertec, Columbus, OH) built into the desk where the participants made the calls. Participants were alone when they placed and terminated the calls. Therefore, the force measured served as a reliable indicator of emotional arousal because of "minimal sanctions against slamming it" (Kulik and Brown, 1979).

After these two unsuccessful calls the participants were asked to send prepared follow-up letters to be attached to programs and brochures of the fictitious charity organization. They were told that no identification, such as name and signature, should be included. They made the choice of cover letters in a discreet manner. The tone of the letters carried three main themes. The first had a self-effacing tone; e.g. apologizing for "the imposition on your time." The second was assertive, but neither self-effacing nor outwardly aggressive "...at a time when assistance is critical, rejection is often received." The third was outwardly aggressive "you are performing a disservice to the community" (Kulik and Brown, 1979). The letters were coded as 0, 1, and 2 to reflect aggression scores. Previous analyses indicated that letters significantly differed in their tones and were found "self-effacing," "moderate," and "aggressive" by an independent panel of judges (Kulik and Brown, 1979).

The experimental conditions involving the charity organization, follow-up letters, and balance plate were adapted from a previous study (Kulik and Brown, 1979). After choosing the letters, a second saliva sample was collected from the participants. Following saliva collection, participants were debriefed and told the real purpose of the study. Debriefings indicated that none of the subjects was aware of the real conditions of the study and none had suspected the authenticity of the charity organization. An independent judge, who was uninformed about the experimental conditions, evaluated taped conversations between the participants and confederates. In her evaluation, 51% of the participants appeared "neutral," 47% "frustrated/upset" during solicitation (2% "undecided"). Most participants were rated as "frustrated/upset" or "angry" after the calls in an overall assessment. This assessment was based on such cues as "slamming down the phone," use of profanity, and other emotionally charged words and sentences.

Preliminary analyses

The first set of analyses sought to determine whether T concentrations changed because of frustration. A one-way repeated measures ANOVA with phase of the experiment (Phase I vs. Phase II) as the single factor showed a nonsignificant decrease in T after frustration both for males and females ($P > 0.05$). We therefore performed our analyses on T samples obtained in the neutral condition (i.e., Phase I).

The second set of analyses sought to establish relationships between FA and aggression, as well as T and aggression based on the nature of provocation for each sex. This second set of analyses involved testing a generalized linear model with *type* of provocation (low vs. high) within subject factor and FA, T, age, weight, and handedness as covariates for each sex. Results indicate that FA and aggression relationship was moderated by the nature of provocation. That is, the effect of $type \times FA$ on reactive aggression as measured by force in kg was significant both for males ($F_{[1,47]} = 7.27$, $P = 0.0097$) and females ($F_{[1,32]} = 4.73$, $P = 0.0370$), whereas the main effect of FA on force was not significant for either of the sexes ($P > 0.05$).

The model also tested the same moderated effect between T and aggression with *type* within subject factor and weight, age, handedness as covariates. The results were in congruity with those pertaining to the FA analyses. T and aggression relationship was moderated by the type of provocation for each sex. The interaction effect, $type \times T$, on reactive aggression as measured by force when terminating the call was significant for both sexes (Males: $F_{[1,46]} = 4.71$, $P = 0.0352$; Females: $F_{[1,32]} = 5.68$, $P = 0.0243$). No significant relationship was observed for the main effect of T on force for neither males nor females ($P > 0.05$). Written aggression scores were not correlated in any of these measures. We then performed regression analyses to investigate further the nature of the relationships between FA and aggression, as well as T and aggression under low and high provocation.

RESULTS

Regression analyses indicate that composite FA was positively associated with reactive aggression (force in kg) under low provocation in males (*beta* = 0.37, $P = 0.0151$, T, weight, age, handedness controlled) (Fig. 1). In females, composite FA was positively associated with reactive aggression under high provocation (*beta* = 0.41, $P = 0.0135$; T, age, weight, and handedness controlled) (Fig. 2). The overall aggression model was significant both for males ($R^2 = 0.30$, $P = 0.01$, low provocation condition) and females ($R^2 = 0.40$, $P = 0.01$, high provocation condition). The same nature of the relationship was observed for T and aggression. That is, there was a positive relationship between T concentrations and aggression in males under low provocation (*beta* = 0.44, $P = 0.0059$; age, weight, handedness controlled) (Fig. 3). In females, there was a positive association between T concentrations and aggression only under high provocation (*beta* = 0.37, $P = 0.0131$; weight, age, handedness controlled) (Fig. 4). No significant associations were found between FA and aggression (*beta* = –0.11, $P = 0.5880$), as well as T and aggression (*beta* = 0.10, $P = 0.5754$) in females under low provocation. The relationship between FA, as well as T and reactive aggression, were not significant in the high provocation condition for males (*beta* = 0.03, $P = 0.8430$ for FA; T, weight, age, handedness controlled; *beta* = –0.07, $P = 0.6899$ for T; weight, age, handedness controlled).

A closer investigation of the relationships among FA, T, and aggression presented in Figures 1–4 indicates potential single influential cases, especially for T and aggression in

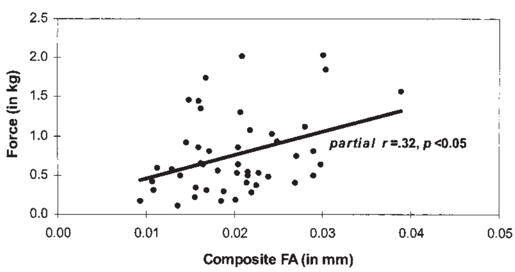

Fig. 1. FA and male reactive aggression in the low provocation condition.

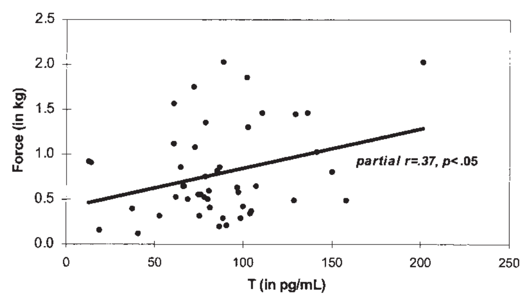

Fig. 3. T and male reactive aggression in the low provocation condition.

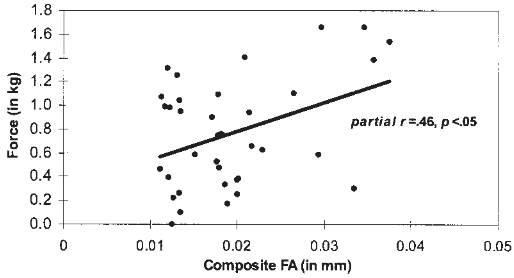

Fig. 2. FA and female reactive aggression in the high provocation condition.

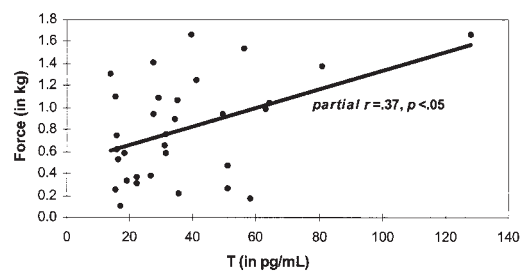

Fig. 4. T and female reactive aggression in the high provocation condition.

the male and female samples. We therefore performed Grubbs' test (1969) on outliers and attempted to confirm the test results by running the analyses without the outliers. We then applied corrective measures (i.e., winsorization) to reduce the effects of such influential cases.

The Grubb's test yielded two outliers for T concentrations in each sample (T = 201.42 pg/mL; $z = 3.19$ for males and T = 127.99 pg/mL; $z = 2.94$ for females, both significant at $alpha = 0.05$). No significant outliers were detected for FA values ($P > 0.05$), although in males an FA value of 0.038 mm appeared to be high. We therefore excluded all these cases from our total sample and reran the regression analyses. Regression results pertaining to T and aggression confirmed that the two previously identified outliers by the Grubb's test were indeed influential. The significant effect of T disappeared in the male sample with the removal of the outlier ($beta = 0.22$, $P = 0.1466$), whereas the FA and aggression relationship remained significant ($beta = 0.31$, $P = 0.0432$). Likewise, when the outlier in the female sample was removed there was no significant effect of T on aggression ($beta = 0.30$, $P = 0.1160$), although FA still had a significant influence on aggression ($beta = 0.42$, $P = 0.0244$). The removal of a potential influential case in the male sample pertaining to the FA values still yielded significant relationship between FA and aggression ($beta = 0.33$, $P = 0.0373$; T, weight, age, handedness controlled).

There is considerable intraindividual and interindividual variability in circulating T (Vermeulen and Kaufman, 1997). The mean T concentrations ($M_{males} = 85.63$ pg/mL; $M_{\mathrm{females}} = 38.10$ pg/mL), standard deviations ($Std_{males} = 37.11$; $Std_{\mathrm{females}} = 22.94$) and ranges ($Range_{males} = 114.19$; $Range_{\mathrm{females}} = 188.62$) in our sample are within normal limits for males and females reported elsewhere (Dabbs, 1990; Dabbs and Mallinger, 1999; Vittek et al., 1985). Because of significant individual variability in T, concurrence with normal limits, and our small sample size, the removal of outliers is not recommended unless warranted by error in data entry and experimental design (see Weinberg and Goldberg, 1990; Sokal and Rohlf, 1995; Bollen, 1989, for a detailed discussion). We therefore winsorized the data as recommended in biometrical (Sokal and Rohlf, 1995) and other statistical applications (Armstrong, 2000; Armstrong and Collopy, 1992). In this procedure, data including the outliers (i.e., T concentrations) were ordered in an array and the influential cases were replaced by the next highest adjacent value (Sokal and Rohlf, 1995). The procedure was conducted separately for males and females. The analyses were then rerun with the winsorized data. Winsorization has been shown to be efficient to reduce the impact of the outliers without biasing the pertinent statistical analyses (Armstrong, 2000; Armstrong and Collopy, 1992; Sokal and Rohlf, 1995).

Regression analyses with winsorized data yielded significant relationships between T and aggression for males under low provocation ($beta = 0.37$, $P = 0.0179$; weight, age, handedness controlled) and for females under high provocation ($beta = 0.41$, $P = 0.0309$ for females; weight, age, handedness controlled), concurrent with the original results. Likewise, new analyses with winsorized data indicated a significant positive correlation between FA and aggression in the low provocation condition for males ($beta = 0.31$, $P = 0.0406$; T, weight, age, handedness controlled) and in the high provocation condition for females ($beta = 0.45$, $P = 0.0109$; T, weight, age, handedness controlled). The overall aggression model also remained significant after winsorizing data ($R^2 = 0.20$, $P = 0.04$ for males, $R^2 = 0.28$, $P = 0.04$ for females). As in previous analyses, no significant correlations were observed between FA and aggression, as well as T and aggression under high provocation in males ($P > 0.05$) and under low provocation in females ($P > 0.05$).

A three-way ANOVA with sex between subjects and type of aggression (letters vs. force) and condition of provocation (low vs. high) within subject factors was performed to test the differences in aggression scores in the absence of phenotypical characteristics, i.e., FA levels and T concentrations. Aggression scores for the letters and force were z-scored for comparison. The interaction effect of the type of aggression and condition of provocation was significant ($F[1,90] = 51.97$, $P < 0.0001$). No sex differences were found ($P > 0.05$). Written (i.e., letter) aggression scores towards the actor in the high provocation condition were significantly higher than those towards the actor in the low provocation condition (least square means comparison at $P < 0.05$ with Tukey-Kramer adjustment). No significant mean differences in force scores were observed regarding the provocation condition ($P > 0.05$). The reactive aggression scores mea-

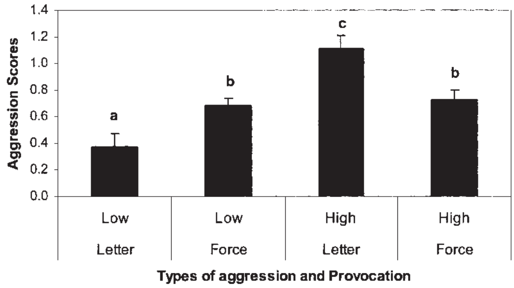

Fig. 5. Mean aggression scores across type of aggression (letters vs. force) and provocation (low vs. high). Mean scores carrying the same letter are not significantly different from each other. No sex differences were observed ($P > 0.05$).

sured by force were significantly higher than those measured by letters for the actor under low provocation ($P < 0.05$, Tukey-Kramer). In contrast, the reactive aggression scores measured by letters were significantly higher than those measured by force under high provocation ($P < 0.05$, Tukey-Kramer) (Fig. 5). Although it is unlikely that anyone would donate any money in response to a letter describing the recipient as a "disservice to community," 33% of the respondents chose such letters.

DISCUSSION

The present study explored the effects of developmental perturbations indicated by nondirectional deviations from perfect bilateral symmetry, FA, and adult free T concentrations on aggression in a realistic experimental setting. In doing so, it also tested whether the nature of provocation moderated the relationships among FA, T, and aggression. In our experiment, the participants attempted to persuade two confederates to contribute via telephone to a fictitious charity organization under low and high provocation conditions. Males with high FA scores displayed high aggression towards the confederate only under low provocation when terminating the phone call. In contrast, high FA scores among females were associated with high aggression towards the actor only under high provocation. Consistent with the FA findings, high T concentrations in males were associated with high force towards the confederate only in the low provocation condition, whereas high T concentrations in females were associated with high force only when the type of provocation was high. It should be noted that the correlations pertaining to T and aggression both for males and females were of low magnitude and our small sample size, as well as the presence of influential cases, imposed limitations on our study. After corrective measures were applied to the influential cases, the results on sex differences in general and the association between T and aggression in particular remained statistically significant. The observed sex differences regarding provocation condition and the subsequent aggressive response warrant further attention. Sexual dimorphism in response to provocation in general, and behavioral and physiological responses to conflict and threatening situations in specific, may help explain these relationships.

Men and women have different reactions to heightened arousal during conflict (Levenson and Gottman, 1985). Although women score higher on general arousability and trait anxiety measures (Saliba et al., 1998), they can generally better tolerate high levels of physiological arousal during conflict compared to men (Levenson and Gottman, 1985; Buysse et al., 2000). In contrast, men consider this level of arousal as aversive (Levenson and Gottman, 1985). Indeed, physiological reactions to anger and fear, as measured by skin conductance rate, is greater for men than women (Kring and Gordon, 1998). There is also evidence that men are more attentive than women to changes in their bodily states, such as heartbeat and respiratory resistance (Harver et al., 1993). It follows that men may be more motivated than women to quickly withdraw from conflict situations, because they are more readily aware of the physiological changes induced by the interaction and find such experiences more aversive compared to women (Levenson and Gottman, 1985; Buysse et al., 2000). In addition, both anecdotal and empirical evidence indicate that men tend to conceal their emotions (see Kring and Gordon, 1998, for a review). Suppression of emotions in turn reduces expressive behavior and somatic activity in laboratory experiments (Gross and Levenson, 1993). It is possible that males in our study found the high provocation condition more aversive, and thus were more motivated than females to quickly withdraw from the agonistic encounter, resulting in null effects of FA and T on aggression. Also, because males were sufficiently aroused by the previous frustrating conversation (i.e., significant main effects under low provocation), they might have used this aversive experience to guide their behavior in the second encounter and suppress their anger accordingly, resulting in low behavioral expression as measured by force exerted when hanging up the phone.

The observed sex differences in expression of aggression can also be partially attributed to sexual dimorphism in response to provocation. Although unprovoked men are generally more aggressive than women, under provocation the gender differences either greatly diminish (Bettencourt and Miller, 1996), or show a female bias (Anderson, 1993; Frodi et al., 1977; Hoaken and Pihl, 2000; Schuck et al., 1971; Taylor and Epstein, 1967). The enhanced reaction to provocation in females (Anderson, 1993; Frodi et al., 1977; Hoaken and Pihl, 2000; Schuck et al., 1971; Taylor and Epstein, 1967) may explain why female aggression was manifested in the high provocation condition, but muted when the target of aggression was less provocative. Taken together, FA and T partially contribute to reactive aggression in both males and females, but the magnitude of provocation and differential responses to heightened arousal appear to determine how this aggressive response is manifested in each sex.

The mechanisms in which reactive aggression is expressed appear to be different for FA and T. Genetic and environmental perturbations during ontogeny have adverse consequences for the developing individual and leave enduring signs in the adult body, marked by high FA. Apart from these visible signs, there is strong evidence that prenatal insults adversely affect executive function and overt behavior (reviewed in Raine, 2002b). Specifically, exposure to maternal tobacco use (Day et al., 2000; Brennan et al., 1999; Rasanen et al., 1999), alcohol consumption (Raine, 2002a,b; Fast et al., 1999; Streissguth et al., 1999; Olson et al., 1997), and wartime famine (Neugebauer et al., 1999) are positively associated with indicators of aggressive behavior. Many of these prenatal insults, such as maternal tobacco and alcohol consumption, jointly contribute to the imprecise expression of symmetrical phenotypes (Keiser, 1992; Kaiser et al, 1997) and conduct disorders (reviewed in Raine, 2002a,b). Moreover, poor impulse control, implicated in CNS dysfunction (Oades, 1998) and aggression (Serocyznski et al., 1999) is positively correlated with FA in normal populations (Shackelford and Larsen, 1997). Therefore, our results pertaining to the FA and aggression relationship may underline poor impulse control under provocation. In contrast, the influence of T on reactive aggression may indicate a proclivity for anger. Previously reported positive associations between T and anger, tension (Persky et al., 1971; von Honk et al., 1999), and selective attention to threat (von Honk et al., 1999) support this proposition. The presence of two complementary mechanisms in expression of aggression has important implications for individuals with elevated T and FA. Specifically, aggressive reactions under provocation may be exacerbated in such individuals by combined effects of heightened anger arousal because of elevated T, and poor impulse control as a result of high FA.

In the absence of phenotypical characteristics measured by FA levels and adult free T concentrations, our overall results showed that both men and women restrained their aggression when choosing letters towards the first confederate in the low provocation condition. In contrast, participants selected harsher letters, including such sentences as "your attitude is a disservice to the community" for the second confederate in the high provocation condition. However, the participants' use of force when terminating the calls was similar for both actors. Curiously, the reactive aggression scores measured by force were significantly higher than those measured by letters under low provocation. In contrast, the reactive aggression scores measured by letters were significantly higher than those measured by force under high provocation. There were no sex differences in this passive-aggressive behavior. Taken together, these data suggest that individual and sex differences in agonistic behavior can best be explained by phenotypical characteristics and the nature of provocation. In the absence of such variables, the observed relationships may not fully reflect the actual sex differences.

In summary, disruptions in development appear to adversely affect neurological functioning. It has been previously shown that such prenatal insults as prenatal nicotine exposure compromise the development of the noradrenergic neurotransmitter system (Levin et al., 1996) and disrupts neural development in the cerebellum, which is implicated in executive function (Raine, 2002b). Our study design and obvious ethical considerations involving human subjects do not permit us to determine the exact timing and type of the developmental insult. Nor can we conclusively establish that the observed positive relationship between FA and aggression is due to the impaired CNS functioning. However, previous research on the deleterious effects of common prenatal insults, such as maternal alcohol and tobacco use, on agonistic behavior (reviewed in Raine, 2002a,b) and the deleterious effect of nicotine on neurological functioning (Levin et al., 1996) may provide further insight in understanding the observed relationship between FA and human reactive aggression.

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