Implicit motives show sex-dimorphic associations with digit ratio

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Author note

OCS and AGR designed the studies; MF coordinated and supervised all data collection and initial data processing; SL and LM conducted most digit length measurements; DÖ, AO, and MS coded most PSE stories; OCS processed and integrated all data files and ran all statistical analyses; and OCS wrote the manuscript, with contributions by all co-authors during editing and revision phases. Partial results from study 2 were presented at the 47th annual conference of the International Society of Psychoneuroendocrinology, Zurich, September 7-9 2017. This research was supported by Deutsche Forschungsgemeinschaft grant SCHU 1210/3-1. We thank Alexander Weller for coding PSE stories in study 1 and Niklas Kinder and Lorena Els for their help measuring digit lengths in studies 1 and 2. Please send correspondence regarding this manuscript to oliver.schultheiss@fau.de or to Oliver C. Schultheiss, Department of Psychology, Nägelsbachstrasse 49b, 91052 Erlangen, Germany.

Abstract

Digit ratio represents a marker of prenatal steroid hormone effects on the developing brain. In a data set compiled from four studies (total $N = 618$), we examined relationships between 2nd and 4th digit lengths as assessed from participants' hands, implicit needs (*n*) for power, achievement, and affiliation, and activity inhibition (AI) as assessed from picture stories, and participant sex. We obtained robustly significant sex-dimorphic effects of nPower and AI on between-hand digit ratio differences and suggestive effects of nAchievement on average digit ratio. Women high in both nPower and AI had a male-typical negative digit ratio difference, whereas those high only in nPower had a particularly female-typical positive digit ratio difference. In women, nAchievement was positively associated with digit ratio; in men, it was negatively related. No effects emerged for nAffiliation. Thus, dispositional needs for power and achievement in adulthood appear to be shaped in part by the organizational effects of prenatal steroid exposure on brain development.

Keywords: implicit motives; activity inhibition; digit ratio; organizational hormone effects; sex differences

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Growing evidence suggests that motivation in adulthood is partly rooted in the organizing effects of hormones on central nervous system development (Beltz, Blakemore, & Berenbaum, 2013; Schulz & Sisk, 2016). In the present research we explored whether variations in implicit motivational needs for power, achievement, or affiliation in adults can be linked to the ratio of the second to the fourth digit (2D:4D), a marker of prenatal exposure to the sex steroids testosterone and estradiol (Manning, 2002).

Digit ratio as a marker of prenatal sex steroid exposure

Digit ratio has been identified as a sex-dimorphic morphological trait (Phelps, 1952), with men typically showing lower 2D:4D scores than women, due to the relatively longer ring finger (4D) in the former compared to the latter (the index finger, 2D, serves as a control for variations in overall size). Digit ratio has been studied intensively in recent years (for reviews, see Breedlove, 2010; Manning, 2002; Manning, Kilduff, Cook, Crewther, & Fink, 2014), because several lines of evidence, reviewed below, suggest that exposure to testosterone and estradiol during early prenatal development is one important source of digit ratio variations. Digit ratio thereby provides an estimate of the developing brain’s exposure to these hormones. From the seventh week post-conception onward, that is, during a time when the central nervous system still undergoes fundamental stages of differentiation, genetically male and female embryos are exposed to markedly different hormonal milieus (Becker et al., 2005). Males’ gonads start producing testosterone, which in turn organizes the development of a male phenotype. In female embryos, this testosterone surge is lacking, and development proceeds towards a female phenotype. Consistent with this early hormonal differentiation, the sex difference in 2D:4D is present after the first trimester of pregnancy and does not change subsequently (Malas, Dogan, Evcil, & Desdicioglu, 2006). After birth, the gender difference in 2D:4D persists and digit ratio measurements show considerable stability throughout postnatal development (Knickmeyer, Woolson, Hamer, Konnecker, & Gilmore, 2011; Trivers, Manning, & Jacobson, 2006).

Multiple lines of research point to an influence of prenatal steroids on digit ratio in humans (Brown, Hines, Fane, & Breedlove, 2002; Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004; van Hemmen, Cohen-Kettenis, Steensma, Veltman, & Bakker, 2017; Ventura, Gomes, Pita, Neto, Taylor, 2013; Warrington et al., 2018) and other species (Saino, Rubolini, Romano, & Boncoraglio, 2007; Talarovicova, Krskova, & Blazekova, 2009). However, the by far strongest evidence for a causal effect of prenatal hormones on digit ratio comes from Zheng and Cohn's (2011) comprehensive series of experimental studies on mice. These authors could show that in males and females, (a) testosterone treatment resulted in a more male-like, and estradiol treatment in a more female-like digit ratio, (b) that this effect depended on androgen and estrogen receptors, respectively, (c) that it affected primarily the fourth, but not the second digit or other digits, (d) that it was limited to the early phase of gestation, and (e) that it was asymmetric, with stronger effects for the right paw than the left.

The last finding matches meta-analytic findings in humans showing that sex differences in digit ratio are more pronounced for the right hand than the left, leading to the conclusion that right-hand 2D:4D may be a better indicator of prenatal steroid exposure than left-hand 2D:4D (Hönekopp & Watson, 2010). Some research therefore uses the difference between right-hand and left-hand 2D:4D – D_{R-L} – as an additional marker of prenatal steroid effects, with lower (more negative) scores on this measure reflecting greater exposure to testosterone and/or less exposure to estradiol prenatally (Manning et al., 2014). A large-scale study has found D_{R-L} to be associated with handedness, with those using the right hand for writing exhibiting higher D_{R-L} scores than those using the left hand (Manning & Peters, 2009). Because handedness emerges as a stable trait early in life (e.g., Hepper, Wells, & Lynch, 2005), this observation suggests that D_{R-L} is a marker of fundamental variations in lateralized brain function. Consistent with this, Kalmady et al (2013) found in a brain-imaging study that lower (i.e., more negative) D_{R-L} was associated with more right-hemispheric activation. These observations are also generally consistent with findings documenting that high testosterone prenatally is associated with asymmetric brain development in favor of the right hemisphere (Geschwind & Galaburda, 1987).

Robust associations between digit ratio and behavioral outcomes have been reported for sexual preferences (Grimbos, Dawood, Burriss, Zucker, & Puts, 2010), reproductive success (Manning et al., 2000; Manning & Fink, 2008), and athletic prowess (Hönekopp & Schuster, 2010). In contrast, self-report measures of personality show either very small or no consistent associations at all with digit ratio (Hönekopp & Watson, 2011; Manning & Fink, 2008; Voracek, Pietschnig, Nader, & Stieger, 2011; Voracek, Tran, & Dressler, 2010).

Implicit motives and steroid hormones

Implicit motives represent capacities for enjoying certain types of incentives, which in turn makes individuals more likely to crave these incentives and act upon incentive-predicting cues (Schultheiss & Köllner, in press). So far, research has focused particularly on the needs (n) for power, defined as a capacity for deriving pleasure from having impact on others (Winter, 1973), achievement, defined as a capacity for getting a kick out of mastering challenging tasks (McClelland, Atkinson, Lowell, & Clark, 1953), and affiliation, defined as a capacity to enjoy establishing, maintaining, or restoring friendly, harmonious relationships (Atkinson, Heyns, & Veroff, 1958). These motives are implicit in the sense that meta-analytically, their measures have no significant overlap with self-ascribed motivational needs and goals in the same content domain (Köllner & Schultheiss, 2014). But they robustly predict behavioral outcomes, such as sociosexuality and reproductive success in the case of nPower (Hofer, Busch, Bond, Campos, Li, & Law, 2010; Peterson & Stewart, 1993), business success in the case of nAchievement (Collins, Hanges, & Locke, 2004), or nonverbal responses to social stimuli in the case of nAffiliation (e.g., Dufner, Arslan, Hagemeyer, Schönbrodt, & Denissen, 2015). Longitudinal research shows that variations in adult motive levels can be traced back to individual differences present even before age 5 (McClelland & Pilon, 1983), suggesting that motive dispositions have some roots in early development.

More relevant for the present research, implicit motives are associated with hormones (Schultheiss, 2013; Stanton & Schultheiss, 2009). For instance, nPower predicts testosterone responses in men, and estradiol responses in women, to winning or losing dominance contests (e.g., Schultheiss, et al 2005; Oxford, Tiedtke, Ossmann, Özbe, & Schultheiss, 2017; Stanton & Schultheiss, 2007) and is associated with basal salivary estradiol in women (Stanton & Schultheiss, 2007; Stanton & Edelstein, 2009). nAchievement predicts attenuated cortisol release in response to stressful challenges (Schultheiss, Wiemers, & Wolf, 2014). For affiliative needs, studies suggest a link with progesterone (e.g., Oxford et al., 2017; Schultheiss, Dargel, & Rohde, 2003) and estradiol (Edelstein, Stanton, Henderson, & Sanders, 2010). Thus, in adulthood implicit motives are linked to concurrent endocrine levels and level changes.

Researchers have started to explore whether implicit motives are also associated with organizational hormone effects. Schultheiss and Zimni (2015; *N* = 50) examined associations between digit ratio, averaged across both hands, and nPower, nAffiliation, and activity inhibition (AI). AI is a marker of functional hemispheric asymmetry, as suggested by the observation that high AI is associated with right-hemisphere functions such as heightened sensitivity to stimuli presented in the left visual field, negative affectivity, nonverbal expressiveness, physiological stress responses, cardiovascular activation, and low immunocompetence (Schultheiss, Riebel, & Jones, 2009). It frequently moderates motive-behavior relationships (Langens, 2010; Schultheiss et al., 2009). Schultheiss and Zimni (2015) found a positive, but non-significant association between nAffiliation and digit ratio and a significant nPower x AI effect, which was due to nPower being non-significantly associated with more male-like digit ratios in high-AI individuals and with more female-like digit ratios in low-AI individuals. Janson, Bleck, Fenkl, Riegl, Jägel, and Köllner (2018, *N* = 213; see also Köllner, Janson & Bleck, in press) extended research on associations between nPower and organizing effects of steroid hormones by looking at facial width-to-height ratio (FWHR), a sex-dimorphic marker of pubertal hormone levels (Geniole, Denson, Dixson, Carre, & McCormick, 2015). They report a significant nPower x AI effect, with a positive association between nPower and more male-typical FWHR scores in high-AI, but not low-AI individuals. However, this effect was significant in women only.

Taken together, these findings suggest (a) that nPower is associated with morphological markers of organizational hormone effects, (b) that AI may be one important moderator of this association such that individuals high in both nPower and AI appear to have been exposed to high levels of androgens and/or low levels of estrogens during critical developmental periods, and (c) that this effect may emerge as sex-dimorphic once sufficiently large samples are tested. The last effect would be consistent with observed gender differences in 2D:4D and FWHR and with the frequently observed sex-dimorphic associations between digit ratio and behavior (e.g., Grimbos et al., 2010; Manning et al., 2000).

However, it is unclear whether the the nPower x AI interaction on digit ratio effect observed by Schultheiss and Zimni (2015) can be replicated and whether it is moderated by participants' biological sex once larger samples are tested. Moreover, because prenatal hormones appear to influence not only 2D:4D, but also the left-right asymmetry of this effect, which may be associated with brain lateralization, digit ratio should be modeled with a separate score for each hand. Finally, in light of the reported associations between nAchievement and nAffiliation and hormones, possible associations between these motives with 2D:4D should also be explored.

The present study

To address these issues, we compiled data from 618 individuals tested in four similar studies in which motive measures and hand scans had been collected as part of a research project focusing on another topic (motives and emotional expression). Motives were assessed with a standard picture-story exercise (PSE; Schultheiss & Pang, 2007), followed by coding for nPower, nAchievement, and nAffiliation (Winter, 1991). AI was assessed by determining the frequency of the negation "not" in PSE protocols (Schultheiss et al., 2009). Lengths of the second and fourth digits were measured from hand scans, a frequently used, reliable, and valid method for assessing digit ratio (e.g., Kemper & Schwerdtfeger, 2009).

We tested associations between motives and digit lengths using generalized linear models (GLM) that treated finger and hand as separate within-subjects factors and motives as between-subjects factors. We focused on effects involving the factor Finger, implicating a 2D:4D effect, and effects involving a Finger x Hand interaction, reflecting D_{R-L}. With regard to the power motive, we hypothesized, based on the studies by Schultheiss and Zimni (2015) and Janson et al (2018), the emergence of an nPower x AI effect, with nPower being associated with a more male-typical digit ratio in high-AI individuals and a more female-typical digit ratio in low-AI individuals. We also explored whether the nPower x AI effect would be moderated by participants’ sex. With regard to nAffiliation and nAchievement, we examined both direct effects as well as possible interactions with participant sex and AI.

Method

Participants and procedure

Our sample was drawn from four studies conducted at Friedrich-Alexander University, Erlangen, Germany, from fall 2010 to summer 2012. Each study aimed at recruiting 80 women and 80 men (mostly university students) as part of an a-priori sampling plan specified in a grant proposal. In all four studies, participants' implicit motives and AI were assessed with a PSE administered at the beginning of testing sessions and digit ratio was assessed from hand scans obtained at the end. All participants provided written informed consent prior to study commencement, were fully debriefed after completing each study, and treated in accordance with the American Psychological Association's Ethics Code.

Table 1 provides an overview of initial sample sizes, reasons for missing data, final sample size, gender composition, and age for the four individual studies. For the full data set, initial sample size was 648, with missing data leading to the loss of a total of 30 participants and thus to a final data set of 618 participants, aged 22.08 years (*SD* = 2.78), and comprised of 312 women and 306 men. Data sets in SPSS and SYTAT formats, a SYSTAT processing and analysis script, and an output file are available from https://osf.io/xp96e/.

Motivational measures

To assess participants' motives and AI, we administered to all participants a computer-based version of the 6-picture PSE described by Pang and Schultheiss (2005; online materials: https://osf.io/6kfhz/) using standard instructions (see Schultheiss and Pang, 2007). For each study, stories were later coded for motivational imagery by two trained coders following Winter's (1994) manual. Coders A and B coded stories for Study 1, coders A and C for Study 2, coders C and D for Study 3, and coders A and D for Study 4. According to the manual, power imagery is scored when someone shows a concern for having impact on others through (1) strong, forceful actions, (2) controlling or manipulating others, (3) influencing, arguing with, or persuading others, (4) providing unsolicited help or advice to others, (5) impressing others or showing a concern with fame or prestige, or (6) eliciting strong emotions in others. Achievement imagery is scored for (1) adjectives suggesting good performance, (2) goals or performances that are portrayed in a positive way, (3) competing with someone or winning a competition, (4) failure leading to negative affect, and (5) unique accomplishments. Affiliation imagery is scored for (1) positive affect expressed in the context of a relationship between people, (2) sadness about relationship disruption or loss, (3) companionate activities, and (4) nurturant help and assistance. Scorers had previously exceeded 85% inter-scorer agreement on calibration materials contained in the manual. Table 1 lists, separately for each study, interrater reliability estimates for total motive scores, summed across all 6 pictures.

For Studies 1 and 2, AI frequency and story word counts were determined, and motive imagery coding was aided, by a MatLab script. For Studies 3 and 4, we used PSECoder (Frisch & Schultheiss, 2012; http://www.psych2.phil.uni-erlangen.de/%7Eoschult/humanlab/resources/resources_PSECoder.htm) for these purposes.

Within all four studies, motive and AI raw scores were not normally distributed according to the Shapiro-Wilk test, *ps* < .0033. Moreover, while PSE protocol length and nAchievement scores did not differ across studies, nPower, nAffiliation, and AI scores did (see Table 1), probably due to sample differences, differential coder bias (in the case of motive scores), or both. To correct for skew, we subjected motive and AI scores to a square-root transformation after adding a constant of 1. We then converted motive and AI scores to z scores within studies after regressing total word count from motive and AI scores within each study to remove not only the shared variance with narrative fluency (*r*s with transformed motive and AI scores > .325, *p*s < .001), but also between-study mean-level differences. The motive and AI scores resulting from these procedures were independent of PSE protocol length, had a mean of 0 and an SD of 1 within each study, and were used in all further analyses. nPower, nAchievement, and AI scores did not significantly differ from a normal distribution, Shapiro Wilk *p*s > .121. nAffiliation were no longer skewed, but somewhat leptokurtic, Shapiro Wilk *p* = .0053.

Digit length

Participants placed their hands on the platen of a Hewlett-Packard Scanjet G3010 scanner so that both hands and their creases were visible in detail. Scans had a 1699 x 2340 pixels format and a 200 dpi horizontal and vertical resolution. 2D and 4D lengths were measured from the tip of the finger to the midpoint of the bottom crease, using Image J (http://imagej.nih.gov/ij/). This has been shown to be a reliable method for determining digit length (Kemper & Schwerdtfeger, 2009). For the present research, second coders provided duplicate measurements for digit lengths from randomly selected participants for Study 1 (n = 16), Study 2 (n = 16), Study 3 (n = 32), and Study 4 (n = 30). Within each study and for each finger, intercoder reliability was excellent (see Table 1). 4D length, but not 2D length, showed some significant variability for both hands across studies, which also influenced digit ratio measures (see Table 1). Digit ratio was calculated separately for each hand by dividing 2D length by 4D length. A $D_{R\text{-}L}$ score was calculated by subtracting left- from right-hand digit ratio. Neither individual digit lengths nor any of the ratios derived from them differed significantly from a normal distribution, Shapiro-Wilk *p*s > .076. However, the D_{R-L} ratio difference had a positive skew, Shapiro-Wilk $p < .001$.

Results

Table 2 provides an overview of all relevant variables. Motive and AI scores showed typical patterns of low correlational overlap and gender differences (Drescher & Schultheiss, 2016; Schultheiss & Brunstein, 2001). None of the motive measures or AI showed any significant zero-order correlations with digit length measures. 2D and 4D lengths were comparable to those reported in earlier research (Peters, Mackenzie, & Bryden, 2002) and showed a strong gender difference reflecting the overall body height difference between women (M = 168.29 cm, SD = 6.16 cm) and men (M = 181.31 cm, SD = 6.63 cm), $t(616) = -25.29$, $d = -2.03$, $p < .001$. However, even after controlling for gender, height remained a significant predictor of finger length measures, $F(1, 615) = 362.95$, $\eta^2 = .3711$, $p < .001$, which is why we ascertained that all effects reported below remained robust when we controlled for this variable. Replicating earlier observations (Hönekopp & Watson, 2010), 2D:4D also reflected a moderate-sized gender difference, with women having relatively shorter 4D than men, and with the effect being stronger for the right hand than for the left. For digit ratio scores of both hands, correlation coefficients indicated that 4D length was the main determining factor. Finally, the difference between the right and the left hands' ratio scores was positive for women and negative for men, suggesting that in men, compared to women, the right-hand digit ratio tended to be more male-typical than the left-hand digit ratio. The effect was significant, but of small size. The ratio difference score showed the strongest overlap with right-hand 4D: the longer the right ring finger, the lower D_{R-L}.

To test our main hypotheses, we ran a GLM with digit length as dependent variable, hand and finger as within-subjects factors, and sex, nPower, nAchievement, nAffiliation, and AI as between-subjects factors, with the latter factors tested simultaneously up to the Sex x Motive x AI interaction for each motivational domain[1, 2]. This yielded the following results: First, we obtained a significant Sex x nPower x AI x Hand x Finger effect, $F(1, 602) = 10.12$, $\eta^2 = .0165$, $p = .0015$. This effect also prevailed when we reran the GLM including only the between-subjects factors sex, nPower, and AI constituting this effect, $F(1, 610) = 9.99$, $\eta^2 = .0161$, $p = .0017$, and then controlled for body height, $F(1, 609) = 9.83$, $\eta^2 = .0159$, $p = .0018$. As shown in Table 3, the overall effect was robustly significant even when we systematically removed individual study datasets, although (with the exception of Study 3) each study's dataset was too underpowered to reliably detect the effect on its own. Consistent with this observation, the factor Study did not moderate the Sex x nPower x AI x Hand x Finger interaction, $F(3, 586) < 1$, $p = .65$. When we probed the effect with digit ratio scores instead of individual finger length effects as our dependent measure, we found the Sex x nPower x AI x Hand interaction to be fully preserved, $F(1, 610) = 10.66$, $\eta^2 = .0172$, $p = .0012$, which suggests that 2D:4D scores capture and simplify effects that emerge for individual finger lengths rather well. Follow-up analyses revealed that the *difference* between digit ratio scores (D_{R-L}) best captured the between-subjects factors' three-way interaction in an ordinary least-squares regression, $B = -.00695$, $SE = .00213$, $\Delta R^2 = .0169$, $t(610) = -3.26$, $p = .0012$ (total $R^2 = .0314$)[3]. To illustrate the effect, we plotted predicted D_{R-L} group means for men and women 1 SD above (high) or below (low) nPower and AI means. As Figure 1 shows, the three-way interaction was mainly based on a nPower x AI interaction in women, $B = -.00532$, $SE = .00161$, $\Delta R^2 = .0340$, $t(308) = -3.30$, $p = .0011$ (total $R^2 = .0368$). Women high or low in both nPower and AI featured a male-typical, negative D_{R-L} score (cf. Table 1) that was highly similar to the D_{R-L} scores of men high or low in both variables. Women high only in either nPower or AI featured a particularly female-typical, positive D_{R-L} score. Men showed a reversed, non-significant pattern of relationships between nPower, AI, and digit ratio difference scores, within a more restricted and male-typical range, $B = .00164$, $SE = .00139$, $\Delta R^2 = .00459$, $t(302) = 1.18$, $p = .24$ (total $R^2 = .00465$).

Second, the overall GLM also suggested a Sex x nAchievement x Finger effect, $F(1, 602) = 7.39$, $\eta^2 = .0121$, $p = .0067$, that remained significant when we reran the GLM and only included the between-subjects factors sex and nAchievement constituting this effect, $F(1, 613) = 6.77$, $\eta^2 = .0109$, $p = .0095$, and then additionally controlled for body height, $F(1, 612) = 7.12$, $\eta^2 = .0115$, $p = .0078$. As shown in Table 4, the overall effect remained largely significant even when we systematically removed individual study datasets. Again, each study's dataset was too small to reliably detect the effect on its own. The factor Study did not moderate the Sex x nAchievement x Finger interaction, $F(3, 602) < 1$, $p = .89$. When we probed the effect with a digit ratio score averaged across both hands instead of individual finger length effects as our dependent measure, we found the Sex x nAchievement interaction to be preserved in an ordinary least-squares regression analysis, $B = .00594$, $SE = .00233$, $\Delta R^2 = .00994$, $t(614) = 2.55$, $p = .011$. Follow-up analyses revealed that the effect was due to a significant positive correlation between averaged 2D:4D scores and nAchievement in women, $B = .00358$, $SE = .00161$, $r = .125$, $t(310) = 2.22$, $p = .027$, and a non-significant negative correlation between these variables in men, $B = -0.00236$, $SE = 0.00166$, $r = -.0811$, $t(304) = -1.42$, $p = .16$. Figure 2, which was plotted for predicted group means for men and women 1 SD above (high) or below (low) nAchievement, shows that in comparison to individuals low in nAchievement, women high in nAchievement had a more female-typical digit ratio, whereas men high in nAchievement tended to have a more male-typical digit ratio.

Third, we also obtained significant Sex x nAchievement x Hand x Finger, $F(1, 613) = 3.99$, $\eta^2 = .0065$, $p = .043$, and nAchievement x AI x Hand x Finger (controlling for sex) effects, $F(1, 612) = 6.98$, $\eta^2 = .0113$, $p = .0085$. However, because these effects were not robust for the removal of individual datasets from the overall sample, we deemed them too unreliable to merit further reporting and discussion.

Fourth, analyses involving nAffiliation failed to reveal significant associations between this variable and 2D:4D, either in the overall GLM or in individual analyses focusing on main and interaction effects involving nAffiliation and AI only, ps > .05. We also explored possible interactions of nAffiliation and sex with nPower or nAchievement, but without obtaining significant effects, ps > .05.

In the Supplement we report findings from a second set of analyses using an alternative correction for word count (images per 1,000 words) and no further transformations for skew. These analyses yield essentially the same findings as the ones described above.

Discussion

The present research provides evidence that points to a role of prenatal hormones for implicit motives in adulthood. Women high in both nPower *and* AI, as well as those low in both variables, showed an asymmetry of 2D:4D suggestive of exposure to high prenatal testosterone and/or low estradiol, as indicated by a longer 4D on the right hand than the left. Conversely, women high in either nPower *or* AI showed the opposite asymmetry, with a relatively shorter 4D on the right hand than the left, suggestive of low prenatal testosterone and/or high estradiol levels. Men showed the mirror image of this pattern, but the association between 2D:4D differences and nPower and AI failed to become significant. The overall interaction effect representing this pattern of findings was highly robust for (a) controlling for body height, which had a unique effect on finger length after controlling for sex, (b) removal of individual study datasets from the overall sample or a testing for a moderator effect of study, and (c) using non-optimal corrections of nPower and AI scores for PSE protocol length (see Supplement). Although the overall effect is of a small size, its significance level was well below .005 and thus sufficient to satisfy even stringent criteria for statistical thresholding (Johnson, 2013). The effect broadly replicates the nPower x AI interaction for 2D:4D originally observed by Schultheiss and Zimni (2015), although it is more intricate, depending both on biological sex and the specific hand. Given the small sample size of the Schultheiss and Zimni (2015) study, these finer points were unlikely to be detected in that study. Our present findings are consistent with the study by Janson et al (2018) for a pubertal-hormone marker by showing that associations between nPower and AI with markers of a hormonal effect emerge more strongly and differently for women than for men.

We also observed an interaction effect between participants' sex and nAchievement on average digit ratio, based on a positive association between nAchievement and 2D:4D in women and a negative association in men. This finding suggests that high nAchievement in adulthood may be the result of low testosterone and/or high estradiol levels prenatally in women and high testosterone and/or low estradiol levels in men. The interaction was robust (a) for controlling for body height, (b) for removing individual datasets (although one dataset removal pushed the *p* level slightly above the .05 threshold), and (c) for using non-optimal procedures to correct for protocol length, although the effect then only emerged as a trend (see Supplement). In light of these results and also of a statistical threshold close to .01 in the primary analyses, we view this finding as suggestive, but not yet conclusive (see Johnson, 2013).

We failed to observe any association patterns between nAffiliation and digit ratio. This could suggest that sex steroid variations in the first trimester of pregnancy do not play a significant role in determining adult levels of this motive. However, we would not yet rule out an organizational effect of other hormones (e.g., progesterone) on nAffiliation. Another possible reason for this null finding may be the specific coding system we used (Winter, 1994), which is less detailed than other measures of nAffiliation (Atkinson et al., 1958; McAdams, 1980; McKay, 1991). Future studies examining the possibility of prenatal hormone effects on affiliative motives should therefore focus on other potential endocrine factors and employ other content-coding measures.

Emerging questions

If sex steroid levels during the first trimester of pregnancy influence nPower and nAchievement in adulthood, as our results suggest, then it will be important to identify brain areas that transmit the organizational effect of hormones to adult motivational preferences. Areas critically involved in motivational processes – including implicit motives (see Hall, Stanton, & Schultheiss, 2010; Schultheiss & Schiepe-Tiska, 2013) – are the hypothalamus, the striatum, the amygdala, and the orbitofrontal cortex (Schultheiss & Wirth, 2018). The structural development of these areas is influenced by prenatal sex steroids, and they remain functionally sensitive to sex steroids in adulthood (e.g., Baum, 2002; Gore, Martien, Gagnidze, & Pfaff, 2014; Heany, van Honk, Stein, & Brooks, 2016; Nelson, 2011; Tobiansky, Wallin-Miller, Floresco, Wood, & Soma, 2018). However, except for a few, small-sample studies looking at associations between digit ratio and structural and functional variations in motivational-brain areas (Darnai et al., 2016; Kalmady et al., 2014; Müller et al., 2018), systematic research on brain correlates of digit ratio is missing so far. Because our interest is not in finger length per se, but in the prenatal hormonal milieu it reflects and particularly the effect that this milieu has on the developing brain with its motivational proclivities in postnatal life, this is an important area for future research.

Our findings also raise the question of whether brain areas shaped by early sex steroid exposure and linked to motives in adulthood are as sex-dimorphic as the peripheral digit-ratio marker pointing to them (e.g., with women's nAchievement being associated with different brain areas than men's nAchievement) or whether they are the same (i.e., both sexes' nAchievement being associated with the same brain areas). In humans testosterone seems to exert its effects on the brain through an androgenic pathway that is separate from the effects of estrogen (Motta-Mena & Puts, 2017). Future research needs to determine whether testosterone in men and estradiol in women can have functionally equivalent prenatal effects on the development of brain areas involved in a given motive, despite causing differences in other parts of the body such as the fingers (see McCarthy & Konkle, 2005).

Our observation of an involvement of AI and D_{R-L} in the findings for nPower adds a further twist to the inferences we can draw about prenatal brain organization supporting adult nPower. Although both measures index aspects of brain lateralization, the correlations reported in Table 2 also show that these aspects are statistically independent. Consistent with this independence, the three-way interaction between sex, nPower, and AI on D_{R-L} indicates that both measures show congruent lateralization only for some combinations of nPower and sex, but not others. For instance, in high-nPower women higher AI was associated with lower $D_{R-L,}$ with both reflecting a congruent rightward lateralization that seems to be consistent with a general effect of increasing testosterone on hemispheric development (see Geschwind & Galaburda, 1987). In contrast, in low-nPower women higher AI was associated with higher D_{R-L}, reflecting incongruent lateralization. Perhaps this effect was due to a prenatal hormonal milieu characterized by high estradiol in combination with low testosterone. The interpretation of our results is complicated by the fact that little is known about the developmental factors that influence AI levels. Clearly, the Sex x nPower x AI effect on D_{R-L} we observed represents a riddle that needs to be solved in future studies. We anticipate that structural brain imaging or sophisticated neuropsychological methods are needed to pinpoint which structures and functions are lateralized in which manner in women and men with various combinations of nPower and AI.

Finally, in men we found only slight (nAchievement) or no direct associations (nPower x AI) of motives with 2D:4D. In this regard, our results resemble those of Janson et al (2018), who also obtained clear-cut results for associations between nPower and AI with a putative body marker of sex steroid exposure for women, but not for men, in a German sample. Perhaps the weak findings for men are specific to German samples -- past research has similarly failed to obtain digit ratio associations with behavioral outcomes, such as reproductive success, for German men that were found for German women or men with other ethnic backgrounds (Manning et al., 2000).

A difference in timing of sex steroid effects on finger development and the development of specific brain areas supporting motivation in women and men may be another explanation for our findings. According to this account, the hormonal fluctuations that affect specific brain substrates of implicit motives coincide closely with the development of digit length in women, but not in men. In this case, the digit ratio measures may better reflect variations in the neuronal correlates of implicit motives in women than in men.

A third explanation is based on the observation that testosterone's effect on cognition follows a curvilinear relationship, with testosterone in the low, female range showing a linear positive effect, but testosterone in the high, male range showing no further increases or even negative effects (e.g., Grimshaw, Sitarenios, & Finegan, 1995; Moffat & Hampson, 1996). If such effects also extend to the development of brain areas supporting power motivation in humans, then female digit length patterns would be more likely to reflect the linear positive effect of variations in the lower testosterone range, whereas male digit lengths would indicate the result of the nonlinear effect of variations in the higher testosterone range (in addition to the effect of estradiol). This explanation would also be broadly consistent with Geschwind and Galaburda's (1987) theory, according to which testosterone inhibits neuronal development in a dose- and laterality-dependent manner, with low to medium levels (i.e., female range and low male range) increasingly inhibiting left-hemispheric development while sparing right-hemisphere development, but very high levels (i.e., high male range) eventually also inhibiting development in the right hemisphere. Ultimately, the question whether nPower is influenced by prenatal sex steroids in men (and women) can best be answered through longitudinal studies that directly assess the endocrine milieu during early gestation.

Strengths and limitations

Strengths of our present research include a large sample, generalizability of the reported results across subsets of data, double coding of all motive imagery with satisfactory to good intercoder reliability, and exact measurement of fingers from scans, as reflected in excellent intercoder reliability for digit lengths and the equally excellent reliability for digit ratio scores derived from these measures. The only exception from the latter was the merely satisfactory reliability of the D_{R-L} scores, which reflects the reduced reliability of the subtractive difference of two imperfectly reliable scores more generally (see Cohen & Cohen, 1983).

One limitation of our research is the significant fluctuation of mean nAffiliation and nPower scores across studies. This may reflect specific coder biases of the different pairs of coders across studies. Or it may reflect sample or seasonal differences, because AI scores, which were determined by a word count software, also varied across studies, while nAchievement scores did not vary, despite differences in coder pairs. Evening out between-study motive differences through within-study standardization of scores may thus have eliminated valid between-study variance and somewhat restricted our ability to detect reliable results. Slight between-sample variations were also in evidence for 4D, but not 2D measurements, which suggests that these variations may represent genuine between-sample differences in ring finger length and not between-coder differences in finger length measurements, which should have led to comparable variations in 2D measurements.

Another limitation concerns the measurement of finger soft tissue instead of the bones, whose length reflects the influence of sex steroids on growth patterns. According to Manning (2002), digit ratio measurements from the soft tissue of the hands correlates with 2D:4D determined from x-rays only at $r = .45$. The issue is further complicated by the observation that indirect digit measurements from scans, relative to direct measurements from the fingers, are associated with lower 2D:4D scores, presumably due to the deforming effects of pressing one’s hand against a surface on finger soft tissue (Ribeiro, Neave, Morais, & Manning, 2016). These methodological constraints suggest that despite the high level of intercoder reliability we obtained for finger measurements, such measurements represent only rather coarse estimates of actual finger bone length and thus of the effect of sex steroids on digit ratios. This may also have attenuated observed associations between motive measures and 2D:4D or D_{R-L}.

A third limitation concerns the inferences that can be drawn from digit ratio measurements about specific motivational needs. Because 2D:4D appears to capture variance associated both with nAchievement and with the interplay of nPower and AI, it is impossible to use this measure for estimating the strength of either motive with any certainty.

Conclusion

The present research provides evidence for a link between digit ratio, a marker of prenatal sex steroid exposure, and nAchievement and nPower in adulthood. This suggests that the seeds for individual differences in motivational needs are sown even before birth and that the link between implicit motives and the endocrine system is more pervasive than previously assumed (e.g., Schultheiss, 2013). Our findings also hint at a lateralization of the effects of prenatal sex steroids on the body and on brain systems supporting motivational functions. We therefore suggest that this is a worthwhile area for further research on the neuronal basis of implicit motives.

Footnotes

[1] We opted for an overall analysis based on individual participant data rather than a meta-analysis of each study's interaction effect because the former method is deemed to be more flexible and to have better statistical power than the latter (Simmonds & Higgins, 2007).

[2] One reviewer suggested that our GLMs represent model misspecifications due to their "inherent causal assumptions about the relationships between the variables", predicting digit length from motive variables and gender. It was not our intention to suggest a causal relationship between the variables tested in these models, because we believe both sides of the GLM equations to have no direct influence on each other and instead to reflect causal effects of a third variable – that is, prenatal steroid levels. We chose the GLM models reported here because they allowed us to model relationships between within- and between-subject measures in a straightforward fashion.

[3] Handedness, as assessed by a single item inquiring about the preferred hand for writing (N = 610 non-missing data; 57 left-handed, coded 1, all others coded 0), was significantly associated with D_{R-L}, $r = -.147$, $p < .001$. We also observed, in a logistic regression, a Sex x nPower x AI effect on handedness at the trend level ($B = -0.498$, $SE = 0.281$, $Z = -1,77$, $p = .076$). Despite this, controlling for handedness did not substantially change the three-way interaction on D_{R-L}, $B = -.00647$, $SE = .00213$, $t(601) = -3.04$, $p = .0024$. Likewise, when we included handedness as an additional predictor, the resulting four-way interaction did not become significant, $B = -.00649$, $SE = .0076$, $t(594) = -0.83$, $p = .41$, while the Sex x nPower x AI interaction remained significant in the final model, $B = -.00605$, $SE = .00227$, $t(594) = -2.66$, $p = .0080$. We conclude from these findings that although D_{R-L} is associated with handedness, handedness does not account for the Sex x nPower x AI interaction on D_{R-L}.

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Table 1

Within-study attrition and measurement reliability (Pearson r) and between-study variability for PSE and digit (ratio) measures.

	Study 1	*Study 2*	*Study 3*	*Study 4*	
Initial *N*	164	162	162	160	
Removed					
missing/incomplete PSE	--	3	1	--	
missing/incomplete scan	4	9	3	2	
unresolved ID mismatches	2	6	--	--	
Final *N*	158	144	158	158	
♀/♂	80/78	73/71	79/79	80/78	
Age in years *M* (*SD*)	22.03 (2.54)	22.50 (3.22)	22.45 (3.00)	21.39 (2.15)	
nPower *M* (*SD*)	5.16_{acd} (2.83)	6.20_{bd} (3.35)	4.92_{ac} (2.68)	5.79_{abd} (2.63)	$F(3, 614) = 6.25, \eta^2 = .0296, p < .001$
Interrater reliability	.869	.852	.828	.782	
nAchievement *M* (*SD*)	4.56_{a} (2.09)	4.77_{a} (2.57)	4.36_{a} (2.53)	4.72_{a} (2.24)	$F(3, 614) = 0.92, \eta^2 = .0045, p = .4303$
Interrater reliability	.755	.855	.818	.805	
nAffiliation *M* (*SD*)	5.43_{a} (2.70)	6.22_{ab} (2.98)	6.39_{b} (2.72)	6.87_{b} (2.82)	$F(3, 614) = 7.26, \eta^2 = .0342, p < .001$
Interrater reliability	.860	.883	.883	.884	
AI *M* (*SD*)	4.79_{a} (3.84)	6.04_{b} (4.21)	4.99_{ab} (3.61)	4.75_{a} (2.92)	$F(3, 614) = 4.07, \eta^2 = .0195, p = .0070$
Word count *M* (*SD*)	572_{a} (164)	614_{a} (186)	603_{a} (180)	576_{a} (140)	$F(3, 614) = 2.28, \eta^2 = .0110, p = .0781$
Left 2D (mm)	72.15_{a} (5.22)	72.61_{a} (5.08)	71.69_{a} (4.59)	72.39_{a} (5.00)	$F(3, 614) = 0.96, \eta^2 = .0047, p = .4121$
Interrater reliability	.995	.975	.991	.996	
Left 4D (mm)	74.48_{abc} (5.91)	75.46_{ab} (5.34)	73.58_{ac} (5.29)	74.66_{abc} (5.46)	$F(3, 614) = 3.05, \eta^2 = .0147, p = .0281$

Table 1 (contd.)

Interrater reliability	.965	.964	.966	.990	
Right 2D (mm)	72.52_{a} (4.71)	72.56_{a} (5.06)	71.75_{a} (4.37)	72.33_{a} (4.98)	$F(3, 614) = 1.04$, $\eta^2 = .0051$, $p = .3736$
Interrater reliability	.995	.995	.981	.983	
Right 4D (mm)	74.99_{abc} (5.57)	75.60_{ab} (5.23)	73.77_{ac} (5.18)	74.77_{abc} (5.36)	$F(3, 614) = 3.10$, $\eta^2 = .0149$, $p = .0263$
Interrater reliability	.996	.980	.985	.993	
Left digit ratio	0.969_{ab} (0.034)	0.963_{a} (0.025)	0.976_{b} (0.036)	0.970_{ab} (0.030)	$F(3, 614) = 4.25$, $\eta^2 = .0203$, $p = .0055$
Interrater reliability	.915	.873	.899	.931	
Right digit ratio	0.969_{ab} (0.032)	0.960_{a} (0.029)	0.974_{b} (0.038)	0.968_{ab} (0.033)	$F(3, 614) = 4.23$, $\eta^2 = .0203$, $p = .0056$
Interrater reliability	.952	.877	.922	.895	
Average digit ratio	0.969_{ab} (0.030)	0.962_{a} (0.026)	0.975_{b} (0.033)	0.969_{ab} (0.027)	$F(3, 614) = 5.11$, $\eta^2 = .0244$, $p = .0017$
Interrater reliability	.952	.884	.951	.938	
R-L ratio difference	-0.001_{a} (0.027)	-0.002_{a} (0.018)	-0.002_{a} (0.033)	-0.002_{a} (0.027)	$F(3, 614) = 0.13$, $\eta^2 = .0006$, $p = .9422$
Interrater reliability	.696	.836	.523	.815	

Note. For Studies 1 through 4, digit measure reliability estimates were based on 16, 16, 32, and 30 duplicate measurements, respectively. Digit ratio and ratio difference reliability estimates were based on values calculated from digit length measurements. Means with different subscripts differ at $p < .05$ (Tukey's honestly-significant-difference test).

Table 2

Descriptive statistics and correlations of studied variables

	1.	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**	**9.**	**10.**	**11.**	**12.**
1. nPower (z)	(.825)											
2. nAchievement (z)	.117*	(.799)										
3. nAffiliation (z)	-.084	.085	(.873)									
4. Activity Inhibition (z)	.106*	-.128*	-.168***	--								
5. Left 2D (mm)	.084	.037	-.127*	.069	(.988)							
6. Left 4D (mm)	.060	.026	-.103	.061	.898***	(.968)						
7. Right 2D (mm)	.071	.036	-.100	.057	.955***	.879***	(.978)					
8. Right 4D (mm)	.060	.024	-.103	.043	.884***	.952***	.879***	(.981)				
9. Left digit ratio	.041	.025	-.037	.011	.092	-.355***	.038	-.278***	(.907)			
10. Right digit ratio	.014	.023	.021	.024	-.010	-.300***	.086	-.398***	.657***	(.909)		
11. Average digit ratio	.030	.026	-.008	.019	.044	-.359***	.069	-.373***	.906***	.915***	(.939)	
12. R-L ratio difference	-.032	-.002	.069	.017	-.120*	.048	.062	-.166***	-.364***	.462***	.065	(.726)
Women *M*	-0.114	-0.020	0.228	-0.029	69.461	71.289	69.791	71.549	0.975	0.976	0.976	0.001
Women *SD*	0.953	1.044	0.981	0.994	4.105	4.349	4.085	4.282	0.032	0.033	0.030	0.027
Men *M*	0.116	0.021	-0.233	0.029	74.996	77.821	74.858	78.045	0.964	0.960	0.962	-0.005
Men *SD*	1.030	0.949	0.962	1.001	4.164	4.382	4.031	4.258	0.030	0.031	0.028	0.027
p	.00424	.6088	< .001	.4723	< .001	< .001	< .001	< .001	< .001	< .001	< .001	.0101
d	-0.231	-0.041	0.474	-0.058	-1.339	-1.496	-1.249	-1.521	0.345	0.507	0.471	0.208
All *M*	0.000	0.000	0.000	0.000	72.201	74.523	72.300	74.766	0.970	0.968	0.969	-0.002
All *SD*	0.998	0.998	0.998	0.998	4.973	5.451	4.783	5.364	0.032	0.033	0.030	0.027

Note. Bracketed values on diagonal represent interrater reliability estimates (Pearson correlation). For PSE motive measures, it is based on raw scores. Reliability estimates for digit measures and calculated ratio and ratio difference scores based on 94 duplicate measurements.

* *p* < .01, ** *p* < .001, *** p < .0001

Table 3

Robustness of Sex x nPower x Activity Inhibition x Hand x Finger effect

		Study 1	*Study 2*	*Study 3*	*Study 4*
Overall effect without study	*F*	8.11	8.92	7.01	6.71
	df	1, 452	1, 466	1, 452	1, 452
	p	.0046	.0030	.0084	.0099
	partial η^2	.0176	.0188	.0153	.0146
Specific effect (only this study)	*F*	1.95	1.87	6.50	2.62
	df	1, 150	1, 136	1, 150	1, 150
	p	.165	.173	.012	.108
	partial η^2	.0128	.0136	.0415	.0172

Table 4

Robustness of Sex x nAchievement x Finger effect

		Study 1	*Study 2*	*Study 3*	*Study 4*
Overall effect without study	*F*	4.90	3.40	5.57	6.36
	df	1, 456	1, 470	1, 456	1, 456
	p	.0273	.0660	.0187	.0120
	partial η^2	.0106	.0072	.0121	.0138
Specific effect (only this study)	*F*	1.88	3.07	0.821	0.470
	df	1, 154	1, 140	1, 154	1, 154
	p	.172	.0817	.366	.494
	partial η^2	.0121	.0215	.0053	.0030

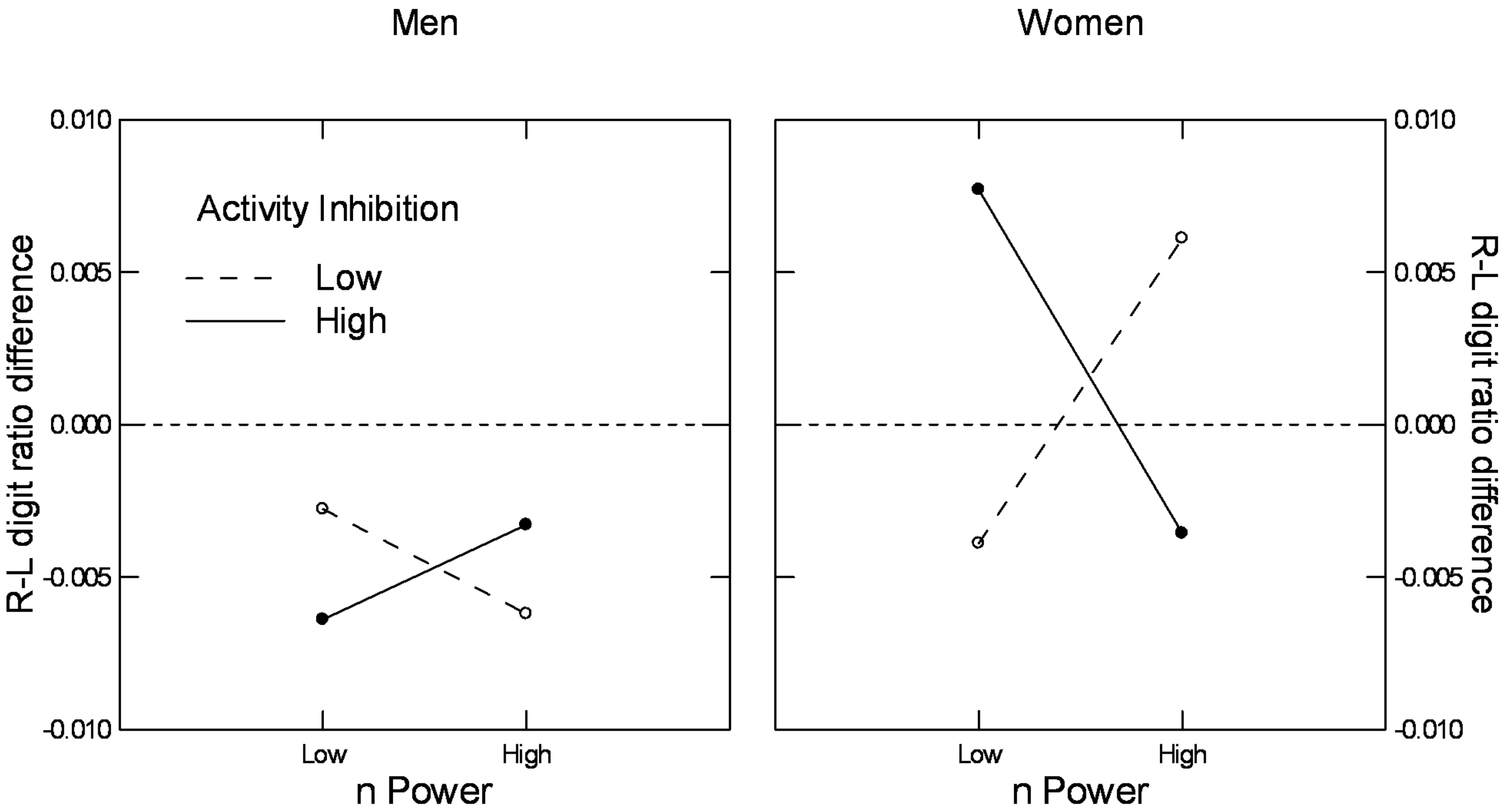

Figure 1. Interaction effect of nPower, activity inhibition (for both, low: -1 SD; high: +1 SD), and sex on D_{R-L} scores.

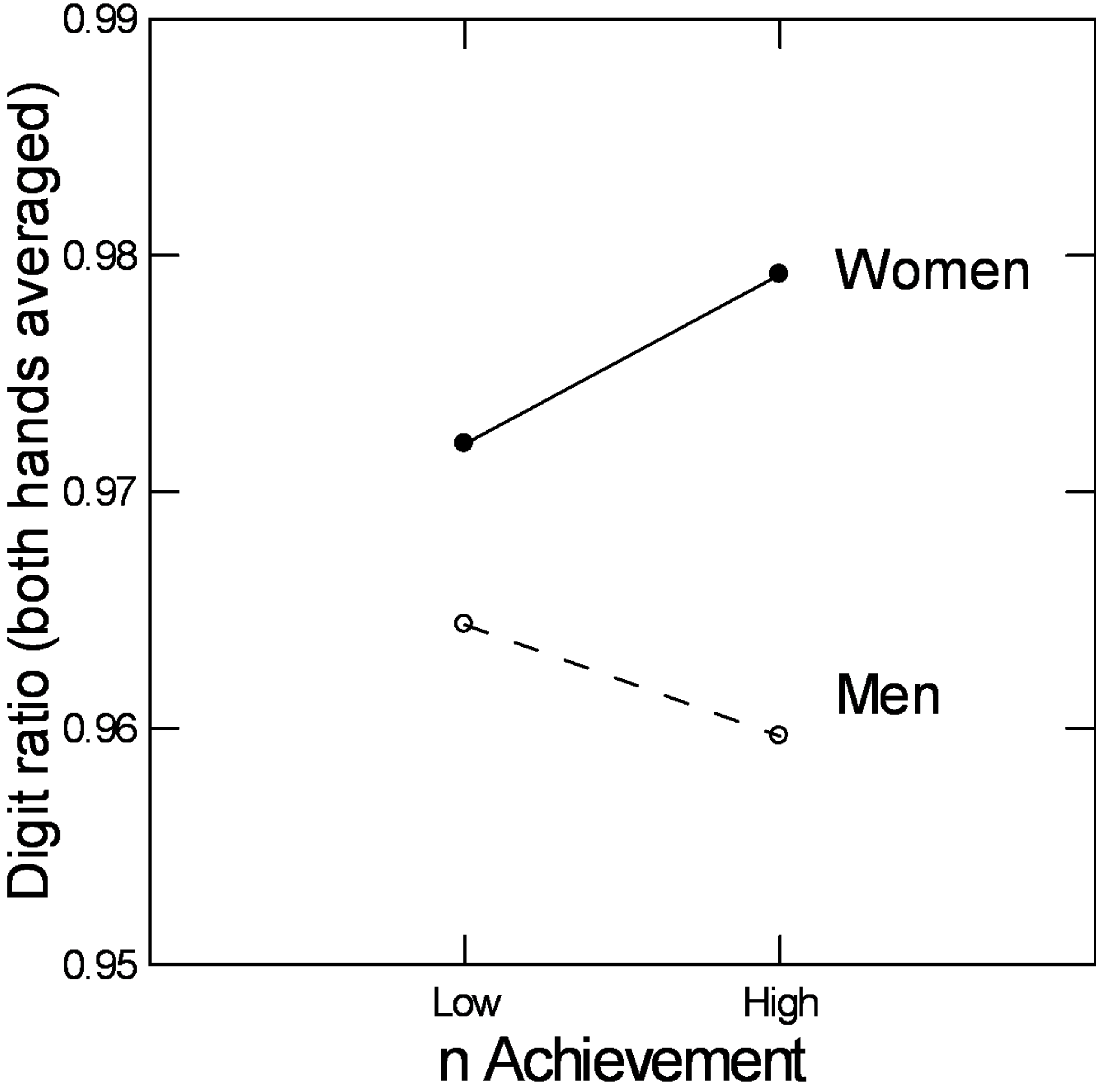

Figure 2. Interaction effect of nAchievement (low: -1 SD; high: +1 SD) and sex on digit ratio scores, averaged for both hands.