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Troy A. Webber
University of South Florida, webbert@mail.usf.edu

Heather E. Soder
University of South Florida, soderh@mail.usf.edu

Geoffrey Potts
University of South Florida, gfpotts@usf.edu

Marina A Bornovalova
University of South Florida, bornovalova@usf.edu

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Preliminary Evidence that Digit Length Ratio (2D:4D) Predicts Neural Response to Delivery of Motivational Stimuli

Troy A. Webber[1], **Heather E. Soder**[1], **Geoffrey F. Potts**[1], and **Marina A. Bornovalova**[1]

[1]Department of Psychology, University of South Florida, 4202 East Fowler Ave., PCD4118G, Tampa, FL 33620, United States of America

Abstract

Reduced relative length of the 2nd to 4th digits (2D:4D) is thought to partially reflect fetal testosterone (FT) exposure, a process suspected to promote relatively permanent effects on the brain and behavior via structural and functional neuroadaptations. We examined the effect of 2D:4D on neural response – assessed by P2a and feedback-related negativity (FRN) event-related potentials (ERPs) – to motivational stimuli (reward or punishment) using two counterbalanced conditions of a passive S1/S2 outcome prediction design. P2a to expected and unexpected delivered rewards or punishments ($1 or white noise burst, respectively) and FRN to withheld rewards or punishments ($0 or silence, respectively) were observed in undergraduates. Lower left 2D:4D and greater 2D:$4D_{R-L}$ predicted amplified P2a to the delivery (but not FRN to the omission) of motivationally salient stimuli, regardless of valence and probability. These preliminary findings suggest that FT may organize dopamine neurons to respond more strongly to the delivery of motivational stimuli.

Introduction

The ratio of the second (index, 2D) to fourth (ring, 4D) digits (2D:4D) is a hypothesized anthropometric index of fetal testosterone (FT) exposure (Manning, Scutt, Wilson, & Lewis-Jones, 1998; Zheng & Cohn, 2001), particularly in human adults (Knickmeyer, Woolson, Hamer, Konneker, & Gilmore, 2011). The 2D:4D-FT relationship partially reflects the shared influence of the *Hox* genes on postnatal growth and patterning of digits and differentiation of the genital bud (Kondo, Zákány, Innis, & Duboule, 1997), as well as allelic variation in androgen receptor sensitivity (Manning, Bundred, Newton, & Flanagan, 2003). Several findings suggest that 2D:4D partially reflects FT exposure in humans, including 1) 2D:4D is negatively correlated with radioimmunoassays of FT (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004), 2) 2D:4D is lower in females with congenital

Correspondence: Address correspondence to Troy A. Webber, Department of Psychology, University of South Florida, 4202 East Fowler Ave, PCD4118G, Tampa, FL 33620. Electronic mail may be sent to webbert@mail.usf.edu. Phone number is (+01) (813) 974-0495. Fax is (813) 974-4617.

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adrenal hyperplasia – a condition associated with elevated FT exposure (Brown, Hines, Fane, & Breedlove, 2002), and 3) 2D:4D is lower in female opposite-sex twins thought to experience elevated FT exposure secondary to intrauterine transfer (van Anders, Vernon, & Wilbur, 2006).

In experimental animals, FT exposure promotes organizational hormonal effects on postnatal behavior via relatively permanent effects on brain structure and function (Schulz, Molenda-Figueira, & Sisk, 2009), particularly dopamine activity in the neural reward system (Lenz et al., 2012). Exogenous tesosterone administration in human adults modulates motivation toward lowered punishment sensitivity and heightened reward sensitivity (van Honk et al., 2004), likely reflecting increased dopamine metabolism in the medial frontal cortex (MFC) and other mesolimbic neural reward system structures (Alderson & Baum, 1981; de Souza Silva, Mattern, Topic, Buddenberg, & Huston, 2009). Lombardo et al., (2012) recently found that increased FT exposure, measured via amniotic fluid testosterone, positively predicted reward (but not punishment) sensitivity in male children via enhanced responsiveness of the neural reward system to positively valenced facial cues. It follows that potential anthropometric measures of FT exposure may similarly predict variability in neural response to motivational stimuli, yet no study has linked 2D:4D with neural response to reward or punishment.

Current Study

We tested the effect of 2D:4D on neural sensitivity to motivational stimuli in college students. Participants were monitored via electroencephalogram (EEG) while completing a reward and punishment prediction task that elicited two MFC-localized event-related potentials (ERPs) to reward and outcome predictability: the P2a (Potts et al., 2006) and the feedback-related negativity (FRN; Holroyd & Coles, 2002). These tasks allowed us to directly manipulate the delivery and omission of general, rather than socially relevant, reward and punishment. Given evidence that postnatal testosterone selectively enhances dopamine metabolism (de Souza Silva et al., 2009) and the influence of FT on neural reward (but not punishment) sensitivity (Lombardo et al., 2012), we expected a negative relationship between 2D:4D and neural response to rewards.

Materials and Methods

Participants

58 undergraduates were recruited via the Department of Psychology subject pool. Eligible participants provided written informed consent, were English-speaking, reported intact hearing/no hearing correction device, and denied psychotropic drug use and current treatment or past hospitalization for psychiatric disorders. Compensation included course credit and a portion of monetary winnings from the reward-motivated task (≤$10). All procedures were in compliance with the Declaration of Helsinki and approved by the Institutional Review Board.

Measures[1]

2D:4D—Two independent, trained research assistants physically measured the lengths of 2D and 4D for each hand. Intraclass correlation coefficients (ICCs) indicated excellent inter-rater reliability for individual digits (right 2D ICC = .96, right 4D ICC = .96, left 2D ICC = .94, left 4D ICC = .97). Each pair of digit measurements was averaged and ratios were calculated by dividing average 2D by average 4D for the right (R2D:4D) and left (L2D:4D) hand. ICC for R2D:4D was poor (.46) and good for L2D:4D (.80). Given evidence that the difference between R2D:4D and L2D:4D ($2D{:}4D_{R\text{-}L}$) is a positive, though weaker, correlate of FT exposure (Benderlioglu & Nelson, 2004), $2D{:}4D_{R\text{-}L}$ was included in exploratory analyses.

Reward and Punishment Sensitivity—Participants completed the Reward Prediction Task (RPT), an S1/S2 passive task that presented participants with predicted and unpredicted delivered and withheld monetary rewards (Potts et al., 2006). S1/S2 either reflected a lemon (withheld/non-reward) or a gold bar (delivered reward), with S1 predicting S2 80% of the time and S2 predicting the outcome ($0 for lemon, $1 gold bar) 100% of the time. Each trial cost $.25, reflecting a -$.25 net for non-rewards and $.75 for rewards. Of 480 total trials, 192 were predicted delivered rewards, 192 predicted withheld rewards, 48 unpredicted delivered rewards, and 48 unpredicted withheld rewards. An adapted version of the RPT – the Punishment Prediction Task (PPT) – used the delivery and withholding of aversive white noise bursts instead of monetary outcomes to measure neural punishment sensitivity (Soder & Potts, 2017). The PPT was identical to the RPT except participants were either presented with a cloud or lightning bolt. A cloud (withheld/non-punishment) and lightning bolt (delivered punishment) on S2 was followed by silence and white noise burst, respectively.

Manipulation Check—Subjective pleasantness/arousal ratings of the auditory cash rewards and white noise bursts were rated after each block on a 5-point Likert scale (valence: 1 = sad, 5 = happy) using the Self Assessment Mannequin (SAM; Bradley & Lang, 1994).

Equipment

EEG Acquisition/Analysis—EEG data was acquired through 128-electrode Geodesic Sensor Nets (EGI, Eugene) at a sampling rate of 250 Hz referenced to the vertex with .1–100 Hz analog filtering. The EEG was digitally filtered offline using a 20 Hz low-pass filter and segmented into 1000-ms epochs from 200-ms before to 800-ms after S2 onset. Epochs were screened for artifacts using EGI's Netstation artifact detection tool. EEG data for 2 participants were excluded due to excessive EEG artifact (minimum of 20 artifact free trials). 6 participants with average SAM ratings ≥4 (positive valence) across the two blocks were excluded. 6 remaining participants had incomplete 2D:4D or maternal age at birth (MAB) data, leaving 44 participants with complete data.

[1]Several other variables were collected and are described in the Supplementary Materials. We discuss previous links with 2D:4D, P2a, and FRN, and provide correlation matrixes to test convergent validity (see Supplementary Materials).

The remaining artifact free epochs were sorted by condition and averaged to create ERPs that were subsequently baseline corrected over the 200ms pre-stimulus period and re-referenced to the average reference. For the RPT, the average number of artifact free trials for unpredicted reward (UR) was 31.89, 34.33 for unpredicted non-reward (UNR), 129.24 for predicted reward (PR), and 129.15 for predicted non-reward (PNR). The PPT yielded an average of 32.15 artifact free trials for unpredicted punishment (UP), 29.95 for unpredicted non-punishment (UNP), 121.47 for predicted punishment (PP), and 127.00 for predicted non-punishment (PNP).[2] While P2a and FRN in the Potts et al., (2006) RPT validation study were relatively less distinct, visual inspection of the current data revealed two distinguishable components: 1) an earlier (170–220ms) P2a to delivered outcomes, and 2) a later (245–295ms) FRN to withheld outcomes (see Figure 1a–b).[3] While localized to the same neural generator and regulated by the DA reward system, the P2a and FRN are also differentially responsive to delivered and withheld motivational stimuli, with the P2a representing a positive deflection to delivered outcomes and the FRN a negative deflection to withheld outcomes (Potts et al., 2006). P2a and FRN data were analyzed separately by time window to best represent these unique relationships.[4]

Analyses

Outliers were replaced using Winsorization (2.5*IQR; Dixon & Yuen, 1974; Reifman & Keyton, 2010). Multilevel models in SAS 9.4 (PROC MIXED) modeled task (RPT, PPT), window (P2a, FRN), prediction (predicted, unpredicted), and delivery (delivered, withheld) as within-subjects random effects and tested fixed effects of each mean-centered 2D:4D index. Consistent with previous methodology (Kothari, Gafton, Treasure, & Micali, 2014) and evidence that MAB is a covariate of FT exposure (Ventura, Gomes, Pita, Neto, & Taylor, 2013), MAB was included as a mean-centered fixed effect covariate. *Post hoc* paired-samples t-tests identified whether, similar to results for the RPT (Potts et al., 2006), P2a and FRN were most positive and negative to UP and UNR, respectively. For significant overall 2D:4D effects, *post hoc* multiple regressions tested individual effects on the most positive P2a and negative FRN responses for the RPT and PPT conditions, as well as the ERPs from conditions significantly correlated with the 2D:4D indices. The false discovery rate (FDR) procedure was implemented using a 0.05 maximum FDR to enhance power while correcting for multiple 2D:4D comparisons (Benjamini & Hochberg, 1995; Glickman, Rao, & Schultz, 2014). Incremental effect sizes of 2D:4D over maternal age at birth are provided with change (Δ) in r^2. Δr^2 is meaningful if >.025 and medium in magnitude if ≥ .09 (Hunsley & Meyer, 2003).

[2]Proportion of predicted and unpredicted available trials for these averages was not significantly different from task parameters (all ps > .05).
[3]With the exception of P2a to UP, split-half reliabilities for the P2a/FRN were adequate (see Supplementary Materials).
[4]Data analyzed using the original Potts et al., (2006) time window were largely consistent with results below but weaker in magnitude (see Supplementary Materials).

Results

Reward/Punishment Sensitivity

The final sample was 94.0% right hand dominant and 78.0% female. Mean age was 20.94 (SD = 4.73). Figure 1a and 1b present grand average ERPs for the RPT and PPT, respectively. All results reflect FDR corrected p-values. Window [$F(43) = 27.54$, $p < .001$, $d = .1.58$] and delivery [$F(43) = 39.03$, $p < .001$, $d = 1.88$] significantly predicted ERP response. Task [$F(43) = 1.17$, $p = .40$, $d = .33$] and prediction [$F(43) = 0.11$, $p = .77$, $d = .10$] were non-significant, suggesting that ERPs varied as a function of window (P2a/FRN) and presence/absence of stimuli but not task (reward/punishment) or prediction (expected/ unexpected). Similar to established findings for the RPT (Potts et al., 2006), *post hoc* t-tests found that P2a to UP was more positive than PP [$t(43) = 5.19$, $p < .001$, $d = .78$], UNP [$t(43) = 2.94$, $p = .02$, $d = .44$], and PNP [$t(43) = 4.93$, $p < .001$, $d = .74$] in the earlier window. The FRN to UNP was more negative than PNP [$t(43) = 4.09$, $p < .001$, $d = .62$], UP [$t(43) = 5.60$, $p < .001$, $d = .84$], and PP [$t(43) = 5.55$, $p < .001$, $d = .84$] in the later window.

2D:4D Effects

Table 1 presents correlations between ERP responses to RPT/PPT conditions and 2D:4D indices. Multilevel models identified significant overall effects of L2D:4D [$F(41) = 6.44$, $p = .03$, $d = .77$] and 2D:4D$_{R-L}$ [$F(41) = 6.80$, $p = .03$, $d = .79$] on ERP amplitude, but not R2D:4D [$F(41) = 0.01$, $p = .93$, $d = .03$][5]. In *post-hoc* regressions, L2D:4D negatively predicted P2a to UR ($b = -.37$, $p = .01$, $\Delta r^2 = .133$; Figure 1c) but not UP ($b = -.29$, $p = .06$; Figure 1d), though a meaningful effect was observed ($\Delta r^2 = .082$). L2D:4D also negatively predicted P2a to PR ($b = -.35$, $p = .02$, $\Delta r^2 = .121$; Figure 1e) and PP ($b = -.32$, $p = .03$, $\Delta r^2 = .103$; Figure 1f). L2D:4D did not predict FRN to UNR ($b = -.13$, $p = .48$, $\Delta r^2 = .017$) or UNP ($b = -.11$, $p = .50$, $\Delta r^2 = .012$). 2D:4D$_{R-L}$ positively predicted P2a to UR ($b = .32$, $p = .03$, $\Delta r^2 = .100$) but not UP ($b = .12$, $p = .50$, $\Delta r^2 = .014$), PR ($b = .27$, $p = .07$), or PP ($b = .29$, $p = .06$), though PR ($\Delta r^2 = .072$) and PP ($\Delta r^2 = .086$) had meaningful effects. 2D:4D$_{R-L}$ did not predict FRN to UNR ($b = .11$, $p = .50$, $\Delta r^2 = .013$) or UNP ($b = .13$, $p = .48$, $\Delta r^2 = .017$).[6]

Conclusions

We document preliminary evidence that 2D:4D is related to neural sensitivity – measured by the P2a ERP component – to motivational stimuli. L2D:4D was a consistent, negative predictor of P2a amplitude to the delivery (but not FRN to the omission) of motivational stimuli, regardless of probability and, to a lesser extent, valence. 2D:4D$_{R-L}$ (left<right) exhibited a nearly identical but weaker pattern. Considering that midbrain dopamine neurons fire in response to the delivery (not omission) of both positive and negative motivational stimuli (Matsumoto & Hikosaka, 2009), findings are consistent with the notion that – in addition to the modulatory effects of postnatal testosterone on dopamine neuron excitability

[5]Results were identical in multilevel models that did not include MAB (see Supplementary Materials).

[6]Given our predominantly female sample and evidence for larger 2D:4D among females (Manning et al., 1998), we tested the same models using only female participants and found nearly identical results (see Supplementary Materials).

(Zheng, 2009) – FT exposure may organize midbrain dopamine neurons to be more easily excited by motivational stimuli.

Importantly, these preliminary findings are based on a small, predominantly female undergraduate sample. Small samples are typically characterized by lower power, reduced detection of true effects, and identification of significant or otherwise large effects that are inauthentic (Button et al., 2013). The current study took several measures to reduce the likelihood of false-positives (e.g., correction for multiple comparisons, convergent validity of target variables) and observed a consistent pattern of effects supported by existing data (for both the total and female only sample), though findings may still reflect the influence of reduced statistical power and should be interpreted with caution.

Another limitation concerns the limited inter-rater reliability for R2D:4D and L2D:4D-specific findings. Sex differences in 2D:4D are larger for R2D:4D (Hönekopp & Watson, 2010), though several studies have found significant effects for L2D:4D alone (Brown et al., 2002; Putz, Gaulin, Sporter, & McBurney, 2004; van Anders et al., 2006) and meta-analytic results show no difference in the predictive power of R2D:4D and L2D:4D (Hönekopp & Schuster, 2010). While differences in R2D:4D and L2D:4D are commonly studied – including two recent meta-analyses (Hönekopp & Schuster, 2010; Hönekopp & Watson, 2010) – there is currently no clear understanding of why these differences emerge. While variance unique to L2D:4D may be particularly relevant to neural reward processing, limited inter-rater reliability for R2D:4D was most likely contributory.

A final limitation is that we use a new task with limited reliability for the UP condition – possibly contributing to weaker effects for P2a to UP and 2D:4D – to examine punishment sensitivity. Although several studies observed the most negative FRN to UP (Sambrook & Goslin, 2015; Walsh & Anderson, 2012) and we observed the most negative FRN to UNP, previous research has almost exclusively examined these findings in the context of delivered negative punishment – the removal of appetitive stimuli (i.e., money). The PPT uses positive punishment – the application of an aversive stimulus (i.e., white noise) – and identified effects highly consistent with two recent studies using positive punishment (Hird, El-Deredy, Jones, & Talmi, 2017; Talmi, Atkinson, & El-Deredy, 2013). While these methodological issues necessitate a cautious interpretation and replication in larger, more demographically diverse, independent samples, these preliminary data may meaningfully guide future research on the relationship between 2D:4D and brain functioning.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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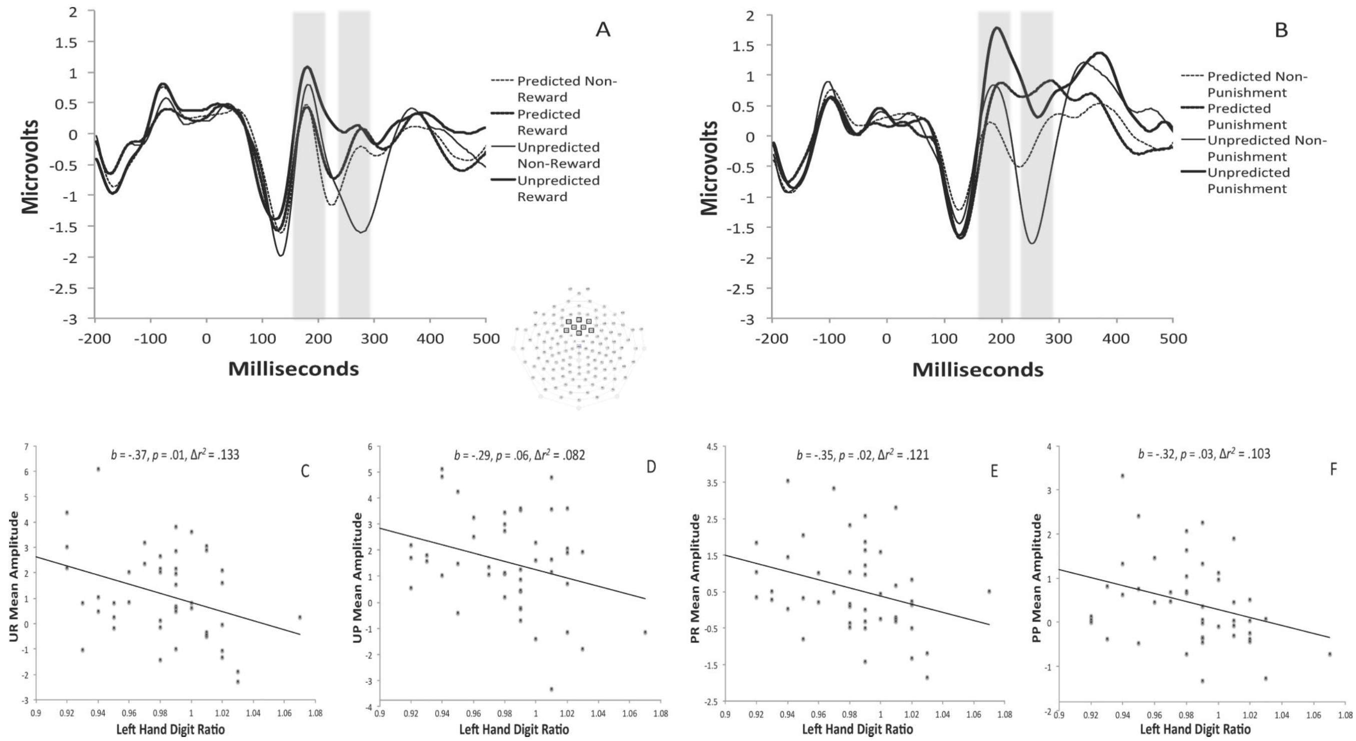

Figure 1.

(A) Grand average waveforms on the RPT, averaged over a region of interest indicated by the electrode map. Approximate analysis windows are highlighted in gray. (B) Grand average waveforms on the PPT. (C) Scatterplot of L2D:4D and mean amplitude for UR. (D) Scatterplot of L2D:4D and mean amplitude for UP. (E) Scatterplot of L2D:4D and mean amplitude for PR. (F) Scatterplot of L2D:4D and mean amplitude for PP. *p*-values for each regression coefficient reflect false discovery rate (FDR) corrections.

Table 1

Descriptive statistics and correlations among digit length ratios, ERP response to reward/punishment conditions, and maternal age at birth.

	L2D:4D	R2D:4D	2D:4D$_{R-L}$	UR	UNR	PR	PNR	UP	UNP	PP	PNP	MAB
L2D:4D	---											
R2D:4D	.41***	---										
2D:4D$_{R-L}$	−.66***	.42***	---									
UR	−.35**	−.07	.29*	---								
UNR	−.14	−.04	.11	.21	---							
PR	−.35*	−.10	.27	.65***	.13	---						
PNR	−.23	.08	.29*	.25	.55***	.15	---					
UP	−.29*	−.20	.12	.32*	.03	.48***	.24	---				
UNP	−.12	.02	.13	.32*	.61***	.08	.47***	−.20	---			
PP	−.31*	−.02	.29*	.16	.02	.35**	.36**	.63***	−.11	---		
PNP	−.16	−.07	.10	.16	.33*	−.14	.67***	.07	.57***	.20	---	
MAB	−.06	.02	.07	−.27	.04	−.22	.17	.09	.08	−.02	.06	---
Mean (SD)	.98 (.03)	.99 (.03)	.004 (.03)	1.02 (1.82)	−1.35 (2.35)	.41 (1.35)	−.54 (1.36)	1.34 (1.91)	−1.83 (2.97)	.40 (0.98)	−.25 (1.42)	27.48 (6.08)
Range	.15	.15	.17	8.36	11.33	7.09	7.18	8.43	16.89	4.65	7.70	33

Note:

* $p < .05$,

** $p < .01$,

*** $p < .001$;

L2D:4D = Left 2D:4D; R2D:4D = Right 2D:4D; 2D:4DR-L = Difference between R2D:4D and L2D:4D; UR = Unpredicted reward; UNR = Unpredicted non-reward; PR = Predicted reward; PNR = Predicted non-reward; UP = Unpredicted punishment; UNP = Unpredicted non-punishment; PP = Predicted punishment; PNP = Predicted non-punishment; MAB = Maternal age at birth; SD = Standard Deviation.