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Spatial navigation related to the ratio of second to fourth digit length in women

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Abstract

Prenatal gonadal hormones have been implicated as important factors in the development of different spatial abilities, including spatial navigation. The aim of the study reported here was to examine the relationship between navigational abilities and the second-to-fourth digit ratio (2D:4D ratio) in healthy women. There is evidence that the ratio of the length of second and fourth digits is negatively related to prenatal testosterone and positively positively related to prenatal estrogen. In this study, the 2D:4D ratio was measured in a sample of 46 female university students. The subjects' place learning ability was tested in a real arena maze (RAM). Our results tend to support an association between prenatal gonadal hormone concentration and some aspects of spatial navigation. The subjects with lower 2D:4D ratio had significantly longer hidden platform-finding latency, better spatial recall, and selected significantly more navigation cues in a posttest of the arena maze learning.

Keywords: Second-to-fourth digit ratio; Spatial navigation; Prenatal steroids

1. Introduction

The aim of the present study was to investigate the influence of prenatal gonadal hormones on human spatial navigation in women. The hormonal level of the perinatal environment was

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estimated indirectly using a recently introduced indicator of prenatal hormone levels: the second-to-fourth digit ratio (2D:4D ratio).

The generalization that prenatal hormones secreted by the gonads are critical for differentiation of the central nervous system and the development of certain spatial functions has been indicated by several nonhuman and human studies. In rats, for example, strong evidence has been provided regarding the perinatal influence of androgens on adult spatial abilities (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991). It has been shown that the administration of testosterone (or its metabolites) to neonatal female rats improved their performance in a maze task, whereas neonatal castration decreases the accuracy of males to varying degrees. However, there appears to be no data on the maze behavior of neonatal females treated with estrogen (Williams & Meck, 1991).

In humans, the early presence of sex hormones also appears to be an important proximate developmental cause of spatial abilities and in the differentiation of underlying brain structures. Some of the best evidence for this is provided by studies of people with congenital adrenal hyperplasia (CAH). The women with this endocrine abnormality outperformed their normal relatives in some spatial tasks (Collaer & Hines, 1995; Resnick, Berenbaum, Gottesman, & Bouchard, 1986). In normal subjects, the results of Cole-Harding, Morstad, and Finegan (1988) on members of opposite-sex twin pairs showed similar association between prenatal testosterone concentration and spatial performance. More direct evidence is provided by Grimshaw, Sitarenios, and Finegan's (1995) study. They observed a positive relationship between spatial abilities (the rate of object mental rotation) of 7-year-old children and their prenatal testosterone, measuring it directly in the second trimester of normal pregnancies. On the other hand, indirect evidence of developmental studies of spatial cognition in children and adolescents has shown that sex differences emerge early, rather than late, indicating a strong dependency of spatial abilities on perinatal gonadal hormone concentration (Kimura, 1996; Sherry & Hampson, 1997). Taken together, research both in human and nonhuman subjects strongly suggests that a prenatal environment that has androgen is associated with better spatial abilities later in life.

In humans, the prenatal hormone-dependent spatial abilities are typically examined in abstract paper-and-pencil spatial tasks, such as mental rotation, water level test, spatial relation test, etc. (Voyer, Voyer, & Bryden, 1995). However, there is relatively only tentative evidence for prenatal hormone-related differences in human place-learning and way-finding in a three-dimensional (3D) real environment. The experimental data on adult subjects usually show reliable sex differences lending support to the hypotheses of gonadal hormone influences in these spatial abilities. In real environments, for example, Lawton (1994, 1996) revealed that women are more likely to use a route strategy of way-finding (attending to instructions on how to get from place to place), whereas men are more likely report using an orientation strategy (maintaining a sense of their position in relation to environmental reference points). The characteristic of performance by men and women in virtual space can also be different. Moffat, Hampson, and Hatzpantelis (1998) obtained robust sex differences, favoring males, in the efficiency of spatial route learning in a virtual maze. Another study demonstrated similar sex differences in topographic learning and memory in a virtual Morris water task (Astur, Ortiz, & Sutherland, 1998). Given this gender-related difference in adult place-learning and way-finding strategies, one might also expect a relation between prenatal hormone concentration and these spatial abilities.

One problem of investigating the influence of prenatal steroids on spatial abilities is the difficulty of directly testing hormonal concentrations in utero. However, prenatal exposure to testosterone and estrogen may leave morphological markers, which could be used to test these relationships indirectly (e.g., Manning, Trivers, Thornhill, & Singh, 2000). A fetus is exposed to prenatal testosterone from two sources: the fetal testes and fetal adrenal glands. The main source of prenatal estrogen comes from the adrenal glands and the placenta through the aromatase conversion of testosterone (George, Griffin, Leshin, & Wilson, 1981). These fetal sources of steroids are highly dependent on the differentiation process of fetal gonads (Lording & De Kretser, 1972). It has been known for some time that differentiation of the fetal gonads is controlled by Homeobox or *Hox* genes (Zákány & Duboule, 1999). In particular, the posterior-most *Hoxd* and *Hoxa* genes are strongly expressed in the urogenital system, including gonads. However, these genes are also required for the growth and differentiation of digits and toes (Kondo, Zákány, Innis, & Duboule, 1997). This common control and similar developmental mechanism of distal limbs and genital eminence can be illustrated by the progressive removal of the posterior *Hox* gene function: It results in a concomitant loss of digits and genital bud derivatives (Kondo et al., 1997). The hand–foot–genital syndrome (which typically involves several anomalies on distal limbs and genital buds) is also caused by *hox* gene mutation (Manning & Bunder, 2000). Manning, Scutt, Wilson, and Lewis-Jones (1998) suggested that this sharing of causal factors in digit and gonad differentiation raises the possibility that patterns of digit formation can reflect spermatogenesis and prenatal sex hormone concentration. In accordance with this relationship, in the human hand, the 2D:4D ratio is a sexually dimorphic trait because in males the fourth digits tends to be longer than the second (2D:4D $\leq$ 1), but in females both digits tend to be of equal length (2D:4D $\geq$ 1) (Manning, Barley, et al., 2000). In addition, there is evidence that digit length is fixed in utero by about the 14 week of pregnancy (Garn, Burdi, & Babler, 1975). A negative correlation between 2D:4D ratio and prenatal testosterone is supported by the following observations: (a) the waist/hip ratio of mothers (a positive correlate of testosterone) is negatively related to the 2D:4D ratio of their male and female children (Manning, Trivers, Singh, & Thornhill, 1999); (b) the 2D:4D ratio of mothers is negatively correlated with the concentration of testosterone in the amniotic fluid of their fetuses (Manning, 2002), and (c) boys and girls with CAH (a trait which is associated with high prenatal androgen) have lower 2D:4D ratios than sex-matched controls (Brown, Hines, Fane, & Breedlove, 2001).

Given that the differentiation of the central nervous system is affected by prenatal hormonal concentration, the 2D:4D ratio may also be a predictor of sex-dependent cognitive processes and the underlying differentiation of the central nervous system. To support this view, it has been shown that lower 2D:4D ratios are associated with left-hand preference (Manning, Trivers, et al., 2000), autism (Manning, Baron-Cohen, Wheelwright, & Sanders, 2001), and depression (Martin, Manning, & Dowrick, 1999). A negative relationship was also found between female and male homosexuality and digit ratio (Williams et al., 2000; Robinson & Manning, 2000). In addition, testing physical competitiveness and visual–spatial abilities, men with lower ratios reported higher attainment in a range of sports and had higher object mental rotation scores (Manning & Taylor, 2001).

In summary, the purpose of the study reported was to examine the relationship between human spatial navigation and 2D:4D ratio in a real place-learning task. This research was carried out within a larger study, which is concerned with different visual–spatial abilities in women. Our prediction was that a low 2D:4D ratio would be related to a male-like performance in spatial navigation.

2. Method

2.1. Participants

Forty-six female participants were recruited from the University of Pécs, Hungary. All subjects were undergraduate or postgraduate students and were paid for their participation. They were aged between 19 and 26 with a mean of 21.24 years. Subjects' height (mean = 166.67 cm) and weight (mean = 60.06 kg) were also recorded.

Volunteers were interviewed to ensure that they had no psychiatric, neurological illness, or disordered menstrual rhythm. Their psychiatric symptom status was screened by the Symptom Checklists (SCL-90-R; Derogatis, 1977). The subjects were within normal range on symptoms factor of SCL-90-R. All participants were right handed as indicated by Chapman and Chapman's (1987) Handedness Scale.

2.2. Measurement of 2D:4D ratio

The length of the second and fourth digits was measured directly on the ventral surface of the right and left hand from the basal crease of the digit to the tip. Where there was a band of creases at the base of the digits, the digit length was measured from the most proximal of these creases (Manning et al., 1998). The digits were measured twice, using a Vernier caliper, measuring to the nearest 0.01 mm. The digit ratio was calculated by dividing the length of the second digit by that of the fourth. Repeatabilities of similar measurements made directly on digit length have been high in several previous studies (e.g., Manning, Trivers, et al., 2000; Martin et al., 1999). Participants with injuries to the second and/or fourth digits were excluded from the study.

We calculated the repeatability of our measurement in the form of intraclass correlation coefficients (r_1). The r_1 values of the 2D:4D ratios were high both for right (2D: r_1=.99, 4D: r_1=.99, 2D:4D: r_1=.95) and left hand (2D: r_1=.98, 4D: r_1=.97, 2D:4D: r_1=.81). In addition, repeated measures of ANOVA showed a nonsignificant main effect of first and second measurements [left hand: 2D: $F(1,45) = 1.11$, P=.3; 4D: $F(1,45) = 0.5$, P=.48; 2D:4D: $F(1,45) = 1.27$, P=.34; right hand: 2D: $F(1,45) = 1.47$, P=.23; 4D: $F(1,45) = 0.27$, P=.6, 2D:4D: $F(1,45) = 1.74$, P=.19]. We concluded that our measurements of second and fourth digits' length and 2D:4D ratio represented real differences between subjects.

2.3. Measurement of spatial navigation and place-learning

2.3.1. Description of real arena maze (RAM)

The basic configuration and the theoretic line of the RAM originated from the Morris circular water maze training protocol that has been described by Morris (1981) and Morris, Garrud, Rawlins, and O'Keefe (1982). The main features of this apparatus, the circular arena with an invisible platform to learn a place controlled by an allocentric framework, was kept and adapted for humans whose vision was occluded by nontransparent goggles. Our apparatus consisted of a large circular timber wall dray arena (6.5 m in diameter, 2 m in height, 33.2 m^2 in floor space, ear temperature 20 ± 5 °C). On the floor of the arena maze were located eight navigation objects, shafts with different fixed geometric cues that were unique in shape but same in size and surface (1 m in height, 400 cm^2) in basic areas in fixed order (see Fig. 1). Three starting positions were located equidistantly around the edge of the west and south wall of arena. For training, the allocentric spatial knowledge in the arena maze a platform disc (50 cm in diameter) was located at a fixed place of the east and north area of the maze floor at equal distance from the three starting positions. The locations of the navigation cues and the platform disc were fixed across trials. The disc was equipped with pressure-sensitive detectors which, when stepped on by the subject, elicited an electrically

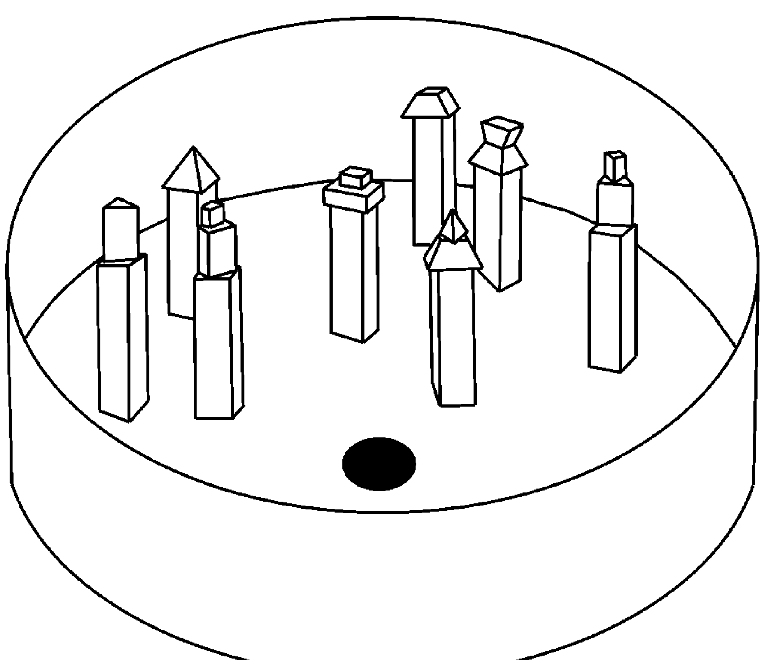

Fig. 1. A view from above of the RAM showing the navigation objects and the escape target (black circle) on the floor.

generated voice (60 dB) over the center of the maze (4 m in height). The subjects received no other feedback on their performances.

Before entering the RAM laboratory, participants were fitted with nontransparent swimming glasses, so that the subjects had no proximal and distal information on the order of arena maze to help locate visually the landmarks and the target escape platform. The laboratory was divided into two parts. One was the waiting room where the vision-obscured subject waited for instructions, trials, and physiological measurements. The other part was used as the arena maze, with two doors (an entrance and an exit) on the wall of the west and south sides of arena. The functions of the doors varied randomly between the two positions. In consequence, the subjects were deprived of the utilization of egocentric references-based navigation. The subjects were guided into the RAM by an assistant and started in front of the arena wall in A, B, or C randomly varied positions. They were instructed to find the place of the escape platform disc using navigational cues to find and to learn the shortest route toward the platform. When after trial and error they stepped on the platform and the reward signal was elicited, the subjects were instructed to pay particular attention to the spatial relations among the landmarks around the platform and to record the spatial relations among the navigation cues. Every subject was allowed to spend 300 s in a trial to explore the arena maze and find the place of the nonvisible platform. After finding the hidden escape target disc lying on the surface of the floor, the subject was allowed a fixed time to explore the environment of the platform (15 s). The escape platform-finding procedure contained seven consecutive trials with 2-min intertrial intervals, except for the third and seventh trial cases, in which 10 min were allowed for rest. After the completed trial, the blindfolded subjects were guided by an assistant out of the maze to the rest room via the A or B exit and afterwards guided into the maze for start next trial via the A or B entrance door. Intertrials and intersubjects in fixed random order were used to control the order of the door and the trial start positions.

When the subject left the RAM, after removing the equipment, as a posttest, the subject was asked to construct a scaled-down model of the RAM on a round table using miniature navigation cues similar to those applied in original size in the RAM task. The subject was provided with 16 like-shape miniaturized navigation cues used in RAM. The subject was asked to select the adequate cues and construct the real spatial order of the RAM by drawing the place of the escape platform and locating the navigation cues in the round table arena. The round table and the landmarks were scaled down in the original size of the RAM. The scale of the reduction was 3:1.

2.3.2. RAM data collection

The variables included the following: (a) the first RAM platform-finding latency (RPL1); (b) the second RAM (recall probe) platform-finding latency (PRL2); (c) navigation cue identification and cue learning (RCU) that contained the number of the correctly selected and utilized navigation cues in the posttest that was considered as the score of cue learning effectiveness during route finding toward the escape platform in the first RAM task.

3. Results

3.1. Relationship between subjects' performance in RAM and 2D:4D ratio

The sum of the platform-finding latencies across the trials of the first and second RAM (RPL1 and RPL2, respectively) was used to test the relationship between subjects' performance and 2D:4D ratio.

For the first RAM, the 2D:4D ratio negatively related both to platform-finding latency (RPL1) and navigation cue identification (RCU). The subjects with lower ratios used longer exploratory time to find the escape target and selected more navigation cues correctly in the posttest. The relationship between RPL1 and 2D:4D was significant for the right hand but not for the left hand and the mean 2D:4D ratio. The relationship between RCU and 2D:4D was significant for right hand and mean 2D:4D ratio but not for the left hand (see Table 1).

For the second RAM, we did not find any significant association between RPL2 and digit ratio variables (see Table 1).

The difference between RPL1 and RPL2 (RPL1−2) was considered as a score of subjects' spatial recall effectiveness. The relationship between RPL1−2 and 2D:4D ratio was analyzed. We found that subjects with lower digit ratio had more positive scores of RPL1−2. This relationship was significant for right hand but not for left hand and mean digit ratio.

Table 1

Results of linear regression analyses of platform-finding latency (RPL1, RPL2, and RPL1−2; dependent variables), navigation cue identification (RCU; dependent variable), and 2D:4D ratio (independent variable) ($n = 46$)

	Coefficient (b)	R^2	F
RPL1−2D:4D			
Right hand	−.36	.13	6.49 *
Left hand	−.11	.01	0.49
Mean ratio	−.26	.06	3.13
RCU−2D:4D			
Right hand	−.32	.11	5.15 *
Left hand	−.27	.07	3.51
Mean ratio	−.33	.11	5.46 *
RPL2−2D:4D			
Right hand	.07	< .01	0.22
Left hand	< .01	< .01	< 0.01
Mean ratio	.04	< .01	0.06
RPL1−2−2D:4D			
Right hand	−.34	.12	5.7 *
Left hand	−.08	< .01	0.32
Mean ratio	−.24	.06	2.57

* $P < .05$.

3.2. Influence of relative digit length

As indicated by earlier studies, the second and fourth digits can influence the relationship of 2D:4D ratios to different degrees (Robinson & Manning, 2000). Therefore, we also investigated the influence of digit length on spatial navigation. The length of the digits was controlled by the height (cm) of the subjects (relative digit length). We have the following descriptive statistics for relative digit length: mean 2D/height: min = 0.36, max = 0.46, S.D. =0.002, mean = 0.41; mean 4D/height: min = 0.37, max = 0.47, S.D. = 0.002, mean = 0.42. More significant results were obtained in the association of relative digit length and place-learning variables. We found that the mean of the fourth digit was most strongly related to these variables. It significantly and positively related to platform-finding latency (RPL1: b=.31, r^2=.09, F = 4.46, P=.04) and navigation cue identification (RCU: b = 0.34, r^2=.12, F = 6.08, P=.02) in the first RAM. The length of the second digit showed also a positive but nonsignificant relationship with these variables (RPL1: b=.16, r^2=.02, F = 1.22, P=.27; RCU: b=.13, r^2=.02, F = 0.79, P=.37). There was not a significant association between relative digit lengths and platform-finding latency in the second RAM (2D: b=.04, $r^2 < .01$, F = 0.07, P=.78; 4D: b=.02, r^2=.01, F = 0.02, P>.05).

4. Discussion

We have found that a putative indirect measure of prenatal gonadal hormone concentration (2D:4D digit ratio) can be a predictor of spatial navigation abilities in women.

In particular, we found that 2D:4D ratio related negatively to platform-finding latency and navigation cue identification but positively to delayed spatial recall. These findings indicate first that subjects with male-type 2D:4D ratio (2D:4D < 1) tended to use an exploratory bias navigation strategy compared to the subjects with female-type 2D:4D ratio (2D:4D $\geq$ 1) in a strange situation, in an unfamiliar RAM. Second, the advantage of subjects with male-type digit ratio in cue learning effectiveness could be a direct consequence of their longer exploration time. Third, the significant improvement in time required to solve the second maze by subjects with male-type 2D:4D ratio indicates their better ability to construct a long-term spatial map after the negotiating of an unfamiliar maze.

In previous studies, there is a general consensus that gonadal steroids cause organizational effects during perinatal development, which has multiple effects on the associational–perceptual–motor abilities that can guide the spatial navigation (e.g., Williams et al., 1990; Williams & Meck, 1991; Collaer & Hines, 1995; Hampson, 1995). In support of this, animal and human studies in which subjects' prenatal steroid exposure was abnormally excessive because of an experimental manipulation or an endocrine syndrome (e.g., CAH women) reported an advantage of subjects with higher androgen level in spatial navigation. This generally refers to their better ability to navigate accurately in 3D space and to learn routes to reach a visible or a hidden target. We have argued earlier that the differentiation of digits and neural structures subserving spatial functions are under similar control of prenatal steroids. Thus, the finding of the significant relationship of 2D:4D ratio and platform-finding latency can reinforce the view of prenatal steroid modulation in spatial navigation. Furthermore, the negative direction of this relationship suggests a more active spatial exploratory strategy in women' adult navigation whose perinatal development were proceeded in higher androgen level environment.

The cue learning effectiveness is one of the basic spatial skills that may contribute to spatial navigation. Our results suggest that subjects with higher prenatal androgen exposure, using an active spatial exploration strategy, showed an advantage in remembering of cues in the posttest. It also suggests that the exploratory strategy can promote the cue learning effectiveness during route finding toward a target.

The precision in the positioning of perfectly selected cues was not estimated in the present work. The results of a recent study (Postma et al., 2000), however, give rise to the possibility of a common activational effect of testosterone in integration of information on object-to-position identification and precise metric location of objects. Postma et al. (2000) found this testosterone-affected integration only in a delayed recall condition indicating the hormonal sensitivity of long-term spatial memory. In the present study, the difference between platform-finding latency of the first and the second RAM (RPL1–2) can also be considered as a score of long-term memory and the subjects' effectiveness to recall spatial map constructed in the first maze. Subsequently, our results on the positive relationship between RPL1–2 and 2D:4D ratio suggest that the organizational effects of prenatal steroids can also influence spatial recall. Regarding the underlying neural formations, earlier studies (O'Keefe & Nadel, 1978; Smith & Milner, 1981) suggest that hippocampal formation could be one of the important factors for the characteristic of long-term spatial representation. The link between hippocampal formation and prenatal steroids also appears to be supported on significant associations between 2D:4D ratio and certain regions of human hippocampus (Kallai et al., in preparation).

In summary, we can conclude that the 2D:4D ratio predicts that females with male-type 2D:4D ratio (2D:4D $\leq$ 1) use longer exploration time with a better cue learning effectiveness and better spatial recall during negotiating of a real maze task. Given the high probability that 2D:4D ratio is a correlate of prenatal steroid concentrations, our findings further indicate that gonadal hormone levels in utero can modify some aspects of spatial abilities in adulthood. Nevertheless, in light of the present results, the contribution of prenatal steroids to within sex variation of spatial navigation also appears to be supported.

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