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Testosterone levels influence spatial ability: Further evidence for curvilinear relationship

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The aim of this study was to explore the influence of different testosterone levels on spatial ability. Four tests measuring various aspects of spatial ability were used. In the first part of the study tests were administered in three groups of subjects: two groups of healthy male volunteers - one tested in autumn (high-testosterone season) and the other one in spring (low-testosterone season), and a comparable group of females. In the second part of the study, a sub-sample of men was retested during a different season. The order of testing was counterbalanced. Spatial ability scores were compared both inter-individually (among groups with different presumed testosterone levels) and intra-individually (within subjects in different seasons). Between-subjects analyses showed that males in low-testosterone season have higher spatial ability scores than both females and males in high testosterone season. In the within-subjects part of the study, repeated measures ANOVA showed no significant main effect of testosterone, but the interaction *testosterone level* x *order of testing* was significant: there was a greater rise in males' spatial ability scores if the second trial occurred during low-testosterone season. Results are consistent with the hypothesis proposing curvilinear relationship between testosterone levels and spatial ability.

Key words: testosterone, spatial ability, spatial visualization, mental rotation, activational effects of sex hormones

Although men and women do not differ in general intelligence, as measured by standard IQ tests, sex differences in specific cognitive abilities have been identified. On average, females outperform males on tests of perceptual speed and accuracy, verbal fluency and certain memory functions, whereas males outperform females on certain tests of mathematical and visuo-spatial ability. Males excel especially in tasks requiring the formation of accurate mental representations of the positions or movements of objects in space (e.g., Collaer & Hines, 1995; Voyer, Voyer, & Bryden, 1995; Collins & Kimura, 1997; Crucian & Berenbaum, 1998; Karadi, Szabo, Szepesi, Kallai, & Kovacs, 1999; Neave, Menaged, & Weightman, 1999). Earlier explanations of males' better performance in spatial tests focused mainly on the socialization factors (Macoby & Jacklin, 1974), but the generality of the differences across populations, as well as their existence in subhuman species led to the inclusion of biological, mainly hormonal, factors (Linn & Petersen, 1985; Gaulin & Fitzgerald, 1988; Silverman, Phillips, & Silverman, 1996; Hampson, 2000) and development of models predicting the interaction of biological and environmental factors influencing the spatial abilities (Casey, Nuttall, & Pezaris, 1999).

Abundant research shows that sex hormones start influencing sexual differentiation of the brain during early prenatal development, and these organizational effects have lifelong irreversible consequences on behavioral and cognitive patterns (Williams & Meck, 1991; Breedlove, 1992; Berenbaum & Hines, 1992; Reinisch & Sanders, 1992; Hines & Sandberg, 1996; Fitch & Denenberg, 1998; Isgor & Sengelaub, 1998; De Vries & Simerly, 2002; Falter, Arroyo, & Davis, 2006). Later in life, behavior and cognition are further influenced by the activational effects of sex hormones, since their fluctuating levels activate prenatally defined behavioral or cognitive patterns.

Interestingly, it seems that the fluctuating levels of sex hormones influence performance only on sex-biased tests, i.e., those cognitive tests that show sex differences in general population, favoring either men or women (Hampson & Kimura, 1988; Silverman & Phillips, 1993; Kimura & Hampson, 1994; Hampson, 1995; Moody, 1997; O'Connor, Archer, Hair, & Wu, 2001). However, although research on the relationship between estrogen levels and cognition in healthy women gave relatively consistent results (higher

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scores in female-favoring tests and lower scores in male-favoring tests during periods of elevated estrogen, such as the late follicular and mid-luteal phase of the menstrual cycle (Hampson & Kimura, 1988; Hampson, 1990a, 1990b; Silverman & Phillips, 1993; Kimura & Hampson, 1994; Hampson, 1995; Moody, 1997), the research on the relationship between testosterone levels and cognition in healthy men gave inconclusive results. Specifically, for spatial cognition there are reports of both positive (Christiansen, 1993; Janowsky, Oviatt, & Orwoll, 1994; Silverman, Kastuk, Choi, & Philips, 1999; Hooven, Chabris, Ellison, & Kosslyn, 2004) and negative (Shute, Pellegrino, Hubert, & Reynolds, 1983; Gouchie & Kimura, 1991; Kimura & Hampson, 1994) relationships between testosterone levels and scores achieved in the spatial ability tests. It has been hypothesized that this apparent contradiction can be explained by the fact that studies finding a positive relationship have involved populations with relatively lower testosterone (e.g., older men, androgen-insensitive subjects, !Kung San of Namibia with constitutionally low levels of testosterone, or women), whereas studies finding a negative relationship generally involved healthy young men. This led some authors to propose a curvilinear relationship between androgen levels and spatial ability (Moffat & Hampson, 1996).

Testosterone can be either directly measured (using radioimmunoassay techniques) or indirectly assessed (using natural cyclic variations in testosterone levels). Many male mammals, including humans, show seasonal variations in testosterone levels -in the human male (at least in the northern hemisphere) they are higher in the autumn than in the spring, which is presumably an evolutionary remnant related to optimal mating and offspring production times (Kimura, 2000). Females, on the other hand, have consistently very low testosterone levels. A recent study (van Anders, Hampson, & Watson, 2006) showed that, although the testosterone level in women also peaked in the autumn, overall variations across seasons were still small compared to those in men: the testosterone levels in women ranged from approximately 20 pg/mL (in winter, spring and summer) to 30 pg/mL (in autumn), while the testosterone levels in male sample ranged from 45 pg/mL (in spring) to 100 pg/mL (in autumn).

In this study, we have used the seasonal variations as an indirect measure of the testosterone levels in males, in order to explore the influence of different testosterone levels on various aspects of spatial ability. More precisely, we have tested whether there were differences in performance on various spatial tests among groups with different presumed testosterone levels: women (the group with the lowest testosterone level), men tested in the low-testosterone season (spring), and men tested in the high-testosterone season (autumn). In the repeated measures part of the study, we have tested whether there were intraindividual variations in the spatial ability (same person – different testosterone levels), beyond the ones that could be expected due to the learning effect.

METHODS

Participants and procedure

A total of 320 subjects participated in the study (270 males and 50 females). They were all healthy volunteers (students of the Police Academy and Faculty of Kinesiology), between 18 and 31 years of age ($M = 21.3$, $SD = 1.7$). As our independent variable was the testosterone level, females were regarded as the group with the lowest level, males tested in spring as the group with the intermediate level ($n = 118$) and males tested in autumn ($n = 152$) as the group with the highest level of testosterone. A subsample of 77 men was seen twice, once during the low-testosterone season, and once during the high-testosterone season. The order of testing was counterbalanced, so that the influence of previous experience with the task would in the second trial be equally divided between groups with different testosterone levels. Since previous studies reported no seasonal variations in cognitive functions in women (Kimura & Hampson, 1994), and small seasonal variations in the testosterone levels (van Anders, Hampson, & Watson, 2006), the female subsample was tested in autumn only.

Instruments

We used four paper-pencil tests of spatial ability, which in previous studies proved to be sex-biased, favoring males (Linn & Petersen, 1985; Kimura, 2000):

Paper folding test (French, Ekstrom, & Price, 1963) - Subjects have to imagine the folding of pieces of paper, then imagine having a hole punched through the thickness of the paper in its folded position, and visualize where the holes would be when the paper is unfolded. The test consists of 20 items, and participants had 6 minutes to complete it.

Cube Comparison test (French, Ekstrom, & Price, 1963) - Each item presents two drawings of cubes, with letters and numbers printed on their sides. Participants must judge whether the two drawings could show the same cube from different orientations. The test consists of 42 items, and participants had 6 minutes to complete it.

Space relations test (Bennett, Seashore, & Wesman, 1947/1964) - This test measures the ability to visualize a three-dimensional object from a two-dimensional pattern, and to visualize how this object would look if rotated in space. Each problem shows one pattern, followed by five three-dimensional figures. Subjects have to choose all figures that can be made from the pattern. The test consists of 40 items, and participants had 10 minutes to complete it.

Figure rotation test (French, Ekstrom, & Price, 1963) - Each item consists of a target figure, and eight figures that are either a mirror image or the same figure rotated to a different orientation on the page. The subject must pick and choose all the figures that could be the same as the target figure. The test consists of 28 items, and participants had 8 minutes to complete it.

RESULTS

Preliminary analysis: The preliminary analysis was conducted to establish whether the tests we used fulfill the criterion of sex-biased spatial tasks, i.e. yield a significant difference between men and women. Significant sex differences were obtained for the Space relations test ($t(318) = 3.97, p < .001$) and the Figure rotation test ($t(316) = 2.74, p < .01$). Sex differences on the Cube comparison and Paper folding tests were not significant ($t_{CubeComp}(317) = 1.56$; $t_{PaperFold}(318) = 1.73$, n.s.), meaning that, at least in our sample, those tests did not prove to be sex-biased.

Between-subjects comparisons of testosterone effects: ANOVA with the testosterone level as a source of variance among groups showed significant main effects of testosterone level on the Space relations test ($F(317,2) = 12.28, p < .001$) and the Figure rotation test ($F(315,2) = 8.01, p < .001$) scores, but not on the Cube comparison ($F(316,2) = 1.43$, n.s.) and Paper folding ($F(317,2) = 1.83$, n.s.) tests. Post hoc Tukey test revealed significant differences among all three groups on the Space relations test. On the Figure rotation test post hoc Tukey showed that men with low testosterone level significantly differed from both women and men with high testosterone level, while the difference between women and men with high testosterone level did not reach statistical significance. Average performance in groups with different testosterone levels, expressed as z-values (to facilitate comparison across tests with different means and standard deviations), are shown in Figure 1.

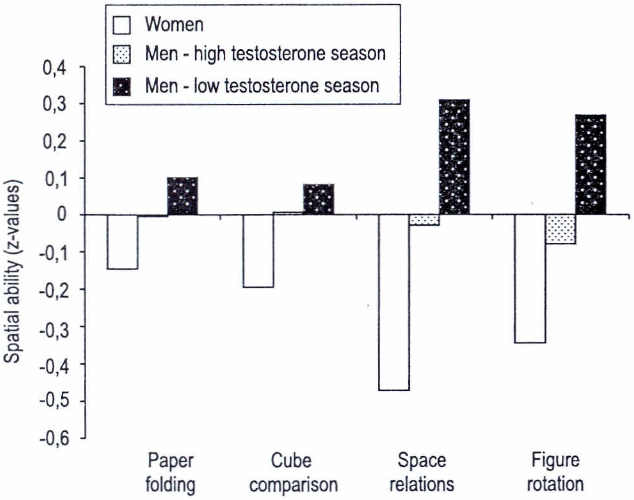

Figure 1. Average scores on four different spatial ability tests in groups with different presumed testosterone levels

Figure 2. Composite measure of spatial ability in groups with different presumed testosterone levels

In order to aggregate the scores on these four different tests and thus provide a basis for more comprehensive analysis, we computed a composite measure of spatial ability on the basis of z-scores. As can be seen in Figure 2, males tested in the low-testosterone season outperformed both males tested in the high-testosterone season and females ($F(315,2) = 7.23, p < .01$), while post hoc Tukey test showed that the difference between females and males in the high-testosterone condition was not significant.

Within-subjects comparisons of testosterone effects: The results of repeated measures ANOVA with level of testo-

Table 1

Results of repeated measures ANOVAs, with order of testing as between-subjects source of variance, and season of testing as within-subjects source of variance

		df	F
Paper folding	Season (high vs. low T)	75	1.24
	Order of testing	1	0.64
	Interaction	75	27.25***
Cube comparison	Season (high vs. low T)	75	0.51
	Order of testing	1	0.58
	Interaction	75	23.07***
Space relations	Season (high vs. low T)	73	3.25
	Order of testing	1	12.95***
	Interaction	73	55.74***
Figure rotation	Season (high vs. low T)	73	0.76
	Order of testing	1	0.38
	Interaction	73	31.39***

Note. Degrees of freedom are not the same for all the tests due to some missing cases.
***$p < .001$.

sterone as a source of variance within subjects, and order of testing as a source of variance between subjects, are shown in Table 1. The analysis showed no significant main effects of either the testosterone level or order of testing, with the exception of the Space relations test, where the main effect of testing order was significant. However, significant interactions were found for all four tests: participants "profited" more from the second trial if it was taken during low-testosterone season (Figures 3-6). Gains in the second trial were expressed by Cohen's δ index, which is a measure of effect

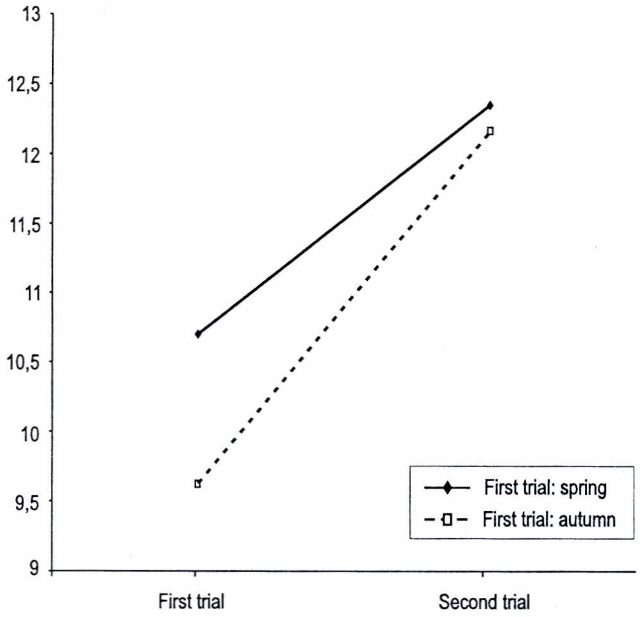

Figure 3. Scores on Paper folding test, depending on season and trial order

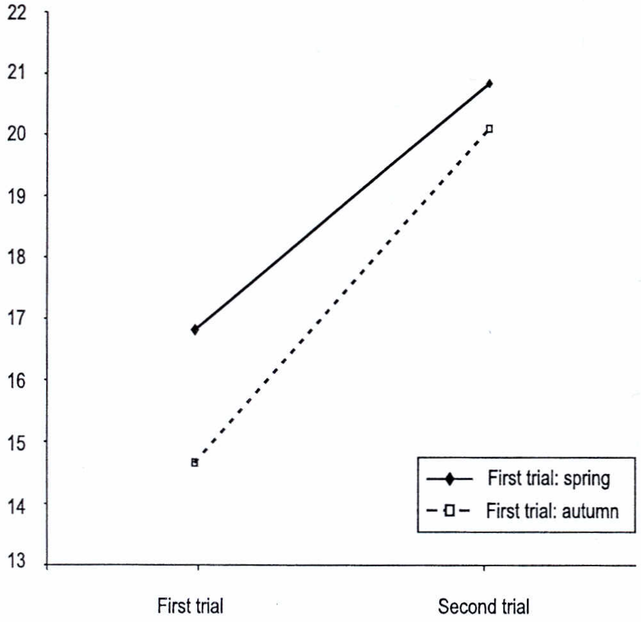

Figure 4. Scores on Cube comparison test, depending on season and trial order

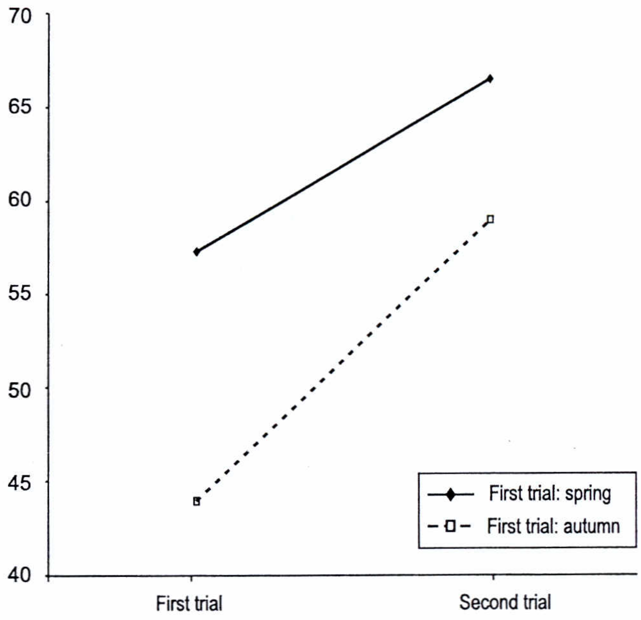

Figure 5. Scores on Space relations test, depending on season and trial order

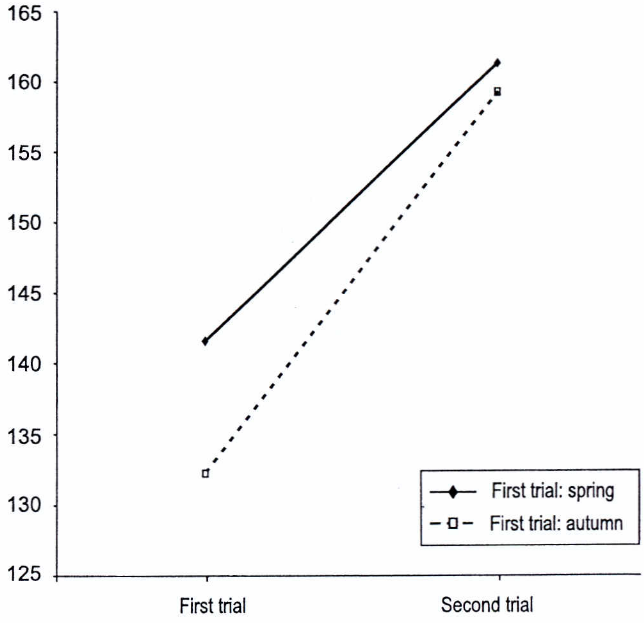

Figure 6. Scores on Figure rotation test, depending on season and trial order

size calculated as a difference between means, in terms of standard deviations: $(M_{\text{second trial}} - M_{\text{first trial}}) / SD_{\text{pooled}}$. If the second trial occurred during the high-testosterone season, the spatial ability scores improved by 0.41 - 0.56 standard deviation, while the improvement when the second trial occurred during low-testosterone season varied between 0.61 - 0.92 standard deviation.

DISCUSSION

In the between-subjects part of the study, we found significant differences on a composite measure of spatial ability among groups with different presumed levels of testosterone: the highest scores were obtained by men tested in spring (i.e. the group with the intermediate testosterone level), while the scores of both men tested in autumn (i.e. the group with the highest testosterone level) and women (i.e. the group with the lowest testosterone level) were significantly lower. These results are in accordance with the previously suggested curvilinear relationship between the testosterone level and performance on spatial ability tests (Moffat & Hampson, 1996; O'Connor et al., 2001), and consistent with an early theory by Petersen (Petersen, 1976), based on the observation that more physically androgynous individuals of both sexes tend to do best on spatial tests. As already mentioned, the analysis of participants tested in studies reporting contradictory results regarding the relationship between the testosterone level and spatial ability, revealed that a positive relationship was found in studies using populations with relatively lower testosterone (Christiansen, 1993; Janowsky, Oviatt, & Orwoll, 1994; Silverman et al., 1999; Aleman, Bronk, Kessels, Koppeschaar, & van Honk, 2004), whereas a negative relationship was obtained in studies using healthy young men (Gouchie & Kimura, 1991; Shute et al., 1983; Kimura & Hampson, 1994). This brought about the hypothesis that there might be an optimal level of testosterone, yielding maximum performance on spatial tests, while a further rise over that optimum leads to decrease in spatial abilities. As can be seen from Figure 2, showing the composite measure of spatial ability, our results support this notion.

Analyses of separate tests showed that testosterone level had a significant effect on scores in the Space relations test and the Figure rotation test, but not on the Cube comparisons and Paper folding tests. This is probably due to the fact that scores in the latter two tests showed no overall sex differences in our sample, as confirmed by the preliminary analysis, and activational effects of hormones can only be expected in sex-biased tasks. Men usually outperform women only on those tasks which require non-verbal strategies in order to be efficiently solved. Women usually excel in tasks which require analytical, serial approach, and can be efficiently solved with verbal strategies (Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002). There is a lack of agreement in literature with respect to the definition and classification of spatial abilities. The successful solving of a spatial task can involve different cognitive processes, and differentiation of spatial cognition in terms of mental processes is not an easy task. It has been shown that mean effect sizes of sex differences are not the same for various spatial tasks, which would also make them variously susceptible to activational hormonal effects.

Both the Cube comparisons and Paper folding tests have been categorized as spatial visualization tests (Voyer, Voyer, & Bryden, 1995; Linn & Petersen, 1985). Spatial visualization is defined as the ability to manipulate complex spatial information when several strategies are needed to produce the correct solution, and this type of spatial ability has a mean sex effects size of 0.13. It has already been shown (Voyer, Voyer, & Bryden, 1995) that for tests in this category sex differences were highly variable and frequently non-significant. It could be speculated that these tests might have a verbal component: cubes have letters and numbers written on them, so it could have facilitated the use of verbal strategies instead of/together with mental rotation or visualization. Similarly, Paper folding is a two-dimensional task, i.e., the paper is always folded in a single plain, and the participants could have easily verbalized the sequence of folding/unfolding the paper. If this strategy can be efficient in solving the kind of spatial visualization task presented in the Cube comparison and Paper folding tests, and given that women usually apply such a strategy (Casey, 1996), that could explain the lack of sex differences (and activational effects of testosterone) in scores on these tests.

On the other hand, men scored significantly higher than women in the Space relations and Figure rotation tests (by 0.9 and 0.7 standard deviations, respectively), and the activational effects of testosterone were also observed in these tests, with men tested in the low-testosterone season having the highest scores, followed by men tested in the high-testosterone season, and women (see Figure 1). If we go further in comparing effect sizes of sex differences with the effect sizes of activational effects of testosterone, it is evident that post hoc tests showed significant differences for all pair-wise combinations in the Space relation test, which proved to be more sex-biased, but only for two pair-wise combinations (women vs. low-testosterone men and low-testosterone men vs. high-testosterone men, but not women vs. high-testosterone men) for the Figure rotations test, which showed smaller effect size of sex differences. Mental rotation is the ability to quickly and accurately rotate two- or three-dimensional figures, in imagination. Mean effect size of sex differences in this group of tests is usually around 0.73, and mental rotation is one of the few cognitive abilities for which men have been shown to consistently outscore women (Voyer, Voyer, & Bryden, 1995; Jordan et al., 2002). Furthermore, it was found (Kovac & Rensselaer, 1989) that numerous invalid-processing strategies were least helpful in Space relations test, which might explain why women in our sample could not perform well on this test if they were using verbal problem solving strategies. The conclusion would be that various tests of spatial ability are not equally sex-biased, and the more biased a test is, the larger activational effect of sex hormones can be expected.

In the within-subjects part of the study, we compared the performance of the same group of men on spatial ability tests, during the low- and high-testosterone seasons. Knowing that some improvement is always expected when participants take the same test more than once, we tried to eliminate the influence of this effect on our results, using a counterbalanced order of testing (approximately half of the participants had their first trial in spring, and the other half in autumn). The fact that repeated measures ANOVAs showed no significant main effects of the order of testing (the only exception being the Space relations test) confirms that this manipulation was successful: if it was not, all participants - irrespective of season during which they were tested first - would have had much higher results in the second trial, and the main effect of season of testing would be significant. There was no significant main effect of season (i.e. testosterone level) either. Since testosterone-induced within-subjects shifts in scores are known to be minute (although statistically significant), and, at the same time, the effects of previous experience with the task can be substantial (probably due to the fact that participants acquire some new strategies and skills needed to successfully solve spatial problems) the lack of significant main effects in this study design is not surprising. However, repeated measures ANOVA showed significant season x order of testing interaction for all four tests, with men who had the second trial during low-testosterone season showing greater improvement in their scores (as can be seen from Figures 3-6). Generally, it seems that men are more able to efficiently use previous experience with the task during low-testosterone season, and this gain in test scores goes up to 0.92 in terms of Cohen's index, while the largest gain during high-testosterone season was 0.56. This result is also in line with the idea that high levels of testosterone impede performance on spatial tasks, while intermediate levels of testosterone facilitate spatial cognition.

Of course, there are some obvious methodological drawbacks of this study: presumed levels of testosterone, although probably correctly assessed, are still a rough measure, and we only had three categories of testosterone levels. In order to definitely confirm or dismiss the curvilinear relationship, it would be necessary to collect continuous measures of bioavailable testosterone in blood of both men and women, and correlate it with scores on spatial ability tests.

The methodological problems notwithstanding, the hypothesis predicting the curvilinear relationship between testosterone and spatial measures is the most plausible one, as it has also gained support in studies with direct manipulation of testosterone levels. If testosterone exhibits activational effects on spatial abilities, then experimental infusion or depletion of testosterone should elicit observable effects on spatial measures. In female-to-male transsexuals undergoing treatment preparatory for surgery for sex reassignment testosterone had an enhancing and not quickly reversible effect on spatial ability performance, while an opposite effect is reported from male-to–female transsexuals receiving androgen-ablation (Slabbekoorn, van Goozen, Megens, Gooren, & Cohen-Kettenis, 1999). In hypogonadal men, visuo-spatial abilities are impaired and most studies report improvement during androgen substitution (Janowsky, Oviatt, & Orwoll, 1994; Imperato-McGinley, Pichardo, Gautier, Voyer, & Bryden, 1991; Alexander, Swerdloff, Wang, Davidson, McDonald, Steiner, et al., 1998) and visuospatial abilities were also improved in women after the administration of testosterone (Aleman et al., 2004). Cerebral neuroimaging suggests that this improvement is due to an androgen-mediated activating effect on the cerebral structures involved in evaluating data of visuo-spatial content, such as the ventral visual processing stream (Zitzman, Weckesser, Shober & Nieschlag, 2001).

The relationship between testosterone and spatial cognition has been assessed on various levels of analysis. The proximate hormonal mechanisms discussed so far are probably not comprehensive enough to give answers about the function of such a relationship. Therefore, we shall conclude with a few final remarks regarding ultimate mechanisms that might have shaped these complex co-variations. The evolution of sex differences is often being discussed in terms of different pressures and adaptive problems that our evolutionary ancestors had to solve. It is hypothesized that better spatial ability in males evolved as a consequence of tens of thousands years humans spent as hunter-gatherers. Sexual dimorphism in body size led to a strong division of labor between men and women: men traveled larger territories in order to acquire food or mate, and there is a substantial body of evidence from comparative studies that larger territories are related to better spatial ability in the males of nonhuman mammals (Gaulin & Fitzgerald, 1988; Crawford & Krebs, 1998) Animal studies suggest that androgen and estrogen levels are the proximate mechanisms responsible for sex differences in spatial behavior (Hampson, 2000). It is possible to hypothesize that similar mechanisms operated in hominids at some point in our evolution (Kimura, 2000).

Some theories emphasize the importance of different activities men and women were dominantly engaged in during our evolutionary history (Silverman & Eals, 1992), while others emphasize different mating systems (Gaulin & Fitzgerald, 1988). Although they can be considered as mutually complementary (Crawford & Krebs, 1998), none of them provides satisfactory explanation of the possible function of activational effects of sex hormones on these evolved spatial sex differences. Could it be argued that this feature is also selected for, e.g., that it was useful for men's spatial ability to be enhanced in spring when the home camp might be relocated or hunting might be more intensive? Or is it more likely that hormone-related oscillations in human cognitive processes are just an accidental by-product of a function that served some other purpose, e.g., rise in testosterone levels in autumn, which enhanced the probability of conception and resulted in birth of offspring during warmer seasons, increasing their survival rate? There is no answer to that question as yet, and the nature of hormonal effects on spatial cognition will be fully explained only through combining various approaches on different levels of analyses.

REFERENCES

Aleman, A., Bronk, E., Kessels, R. P. C., Koppeschaar, H. P. F., & van Honk J. (2004). A single administration of testosterone improves visuospatial ability in young women. *Psychoneuroendocrinology, 29,* 612-617.

Alexander, G. M, Swerdloff, R. S, Wang, C., Davidson, T, McDonald, V., Steiner, B., et al. (1998). Androgen-behaviour correlations in hypogonadal men and eugonadal men. *Hormones and Behavior, 33,* 85-94.

Bennett, G. K., Seashore, H. G., & Wesman, A. G. (1964). *Baterija testova sposobnosti* [Differential Aptitude Tests](Centar za psihodijagnostična sredstva, Trans.). Ljubljana: Zavod SR Slovenije za produktivnost dela. (Original work published 1947)

Berenbaum, S. A, & Hines, M. (1992). Early androgens are related to childhood sex typed toy preferences. *Psychological Science, 3,* 203-206.

Breedlove, S. M. (1992). Sexual dimorphism in the vertebrate nervous system. *Journal of Neuroscience, 12,* 4133-4142.

Casey, M. B, Nuttall, R. L., & Pezaris, E. (1999). Evidence in support of a model that predicts how biological and environmental factors interact to influence spatial skills. *Developmental Psychology, 35,* 1237-1247.

Casey, M. B. (1996). Gender, sex and cognition: considering the interrelationship between biological and environmental factors. *Learning and Individual Differences, 8,* 39-53.

Christiansen, K. (1993). Sex hormone-related variations of cognitive performance in !Kung San hunter-gatherers of Namibia. *Neuropsychobiology, 27,* 97-107.

Collaer, M. L., & Hines, M. (1995). Human behavioral sex differences: A role for gonadal hormones during early development? *Psychological Bulletin, 118,* 55-107.

Collins, D. W., & Kimura, D. (1997). A large sex difference on a two-dimensional mental rotation task. *Behavioral Neuroscience, 111,* 845-849.

Crawford, C. B, & Krebs, D. L. (Eds.). (1998). *Handbook of evolutionary psychology: Ideas, issues, and applications.* Mahwah, NJ: Lawrence Erlbaum.

Crucian, G. P., & Berenbaum, S. A. (1998). Sex differences in right hemisphere tasks. *Brain and Cognition, 36,* 377-389.

De Vries, G. J, & Simerly, R. B. (2002). Anatomy, development, and function of sexually dimorphic neural circuits in the mammalian brain. *Hormones, Brain and Behavior, 4,* 137-191.

Falter, C. M, Arroyo, M., & Davis, G. J. (2006). Testosterone: Activation or organization of spatial cognition? *Biological Psychology,* 73, 132-140.

Fitch, R. H, & Denenberg, R. H. (1998). A role of ovarian hormones in sexual differentiation of the brain. *Behavioral and Brain Sciences, 21,* 311-352.

French, J. W., Ekstrom, R. B, & Price, L. A. (1963). *Kit of Reference Tests for Cognitive Factors.* Princetown, New Jersey: Educational Testing Service.

Gaulin, S. J. C., & Fitzgerald, R. W. (1988). Sex differences in spatial ability: An evolutionary hypothesis and test. *The American Naturalist, 127,* 74-88.

Gouchie, C., & Kimura, D. (1991). The relationship between testosterone levels and cognitive ability patterns. *Psychoneuroendocrinology, 16,* 323-334.

Hampson, E. (1990a). Estrogen-related variations in human spatial and articulatory motor skills. *Psychoneuroendocrinology, 15,* 97-111.

Hampson, E. (1990b). Variations in sex-related cognitive abilities across the menstrual cycle. *Brain and Cognition, 14,* 26-43.

Hampson, E. (1995). Spatial cognition in humans: possible modulation by androgens and estrogens. *Journal of Psychiatry and Neuroscience, 20,* 397-404.

Hampson, E. (2000). Sexual differentiation of spatial functions in humans. In: Matsumoto A (Ed.), *Sexual differentiation of the brain* (pp. 279-300). London: CRC Press.

Hampson, E., & Kimura, D. (1988). Reciprocal effects of hormonal fluctuations on human motor and perceptual-spatial skills. *Behavioral Neuroscience, 102,* 456-459.

Hines, M., & Sandberg, E. C. (1996). Sexual differentiation of cognitive abilities in women exposed to diethylstilbestrol (DES) prenatally. *Hormones and Behavior, 30,* 354-363.

Hooven, C. K, Chabris, C. F, Ellison, P. T, & Kosslyn, S. M. (2004). The relationship of male testosterone to components of mental rotation. *Neuropsychologia, 42,* 782-790.

Imperato-McGinley, J., Pichardo, M., Gautie, T., Voyer, D., & Bryden, M. P. (1991). Cognitive abilities in androgen-insensitive subjects: comparison with control males and females from the same kindred. *Clinical Endocrinology, 34,* 341-347.

Isgor, C., & Sengelaub, D. R. (1998). Prenatal gonadal steroids affect adult spatial behavior, CA1 and CA3 pyramidal cell morphology in rats. Hormones and Behavior, 34, 183-198.

Janowsky, J. S, Oviatt, S. K., & Orwoll E. S. (1994). Testosterone influences spatial cognition in older men. Behavioral Neuroscience, 108, 325-332.

Jordan, K., Wüstenberg, T., Heinze, J. H., Peters, M., & Jäncke, L. (2002). Women and men exhibit different cortical activation patterns during mental rotation tasks. Neuropsychologia, 40, 2397-2408.

Karadi, K., Szabo, I., Szepesi, T., Kallai, J., & Kovacs, B. (1999). Sex differences on the hand mental rotation task for 9-yr-old children and young adults. Perceptual and Motor Skills, 89, 969-872.

Kimura, D. (2000). Sex and cognition. Cambridge, MA: The MIT Press.

Kimura, D., & Hampson, E. (1994). Cognitive pattern in men and women is influenced by fluctuations in sex hormones. Current Directions in Psychological Science, 3, 57-61.

Kovac, R. J, & Rensselaer, B. (1989). The validation of selected spatial ability tests via correlational assessment and analysis of user-processing strategy. Educational Research Quarterly, 13, 26-34.

Linn, M. C, & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: a meta-analysis. Child Development, 56, 1479-1498.

Macoby, E. E, & Jacklin, C. N. (1974). The psychology of sex differences. Stanford, CA: Stanford University Press.

Moffat, S. D., & Hampson, E. (1996). A curvilinear relationship between testosterone and spatial cognition in humans: possible influence of hand preference. Psychoneuroendocrinology, 21, 323-337.

Moody, M. S. (1997). Changes in scores on the Mental Rotations Test during the menstrual cycle. Perceptual and Motor Skills, 84, 955-961.

Neave, N., Menaged, M., & Weightman, D. R. (1999). Sex differences in cognition: the role of testosterone and sexual orientation. Brain and Cognition, 41, 245-262.

O'Connor, D. B., Archer, J., Hair, W. M., & Wu, F. C. W. (2001). Activational effects of testosterone on cognitive function in men. Neuropsychologia, 39, 1385-1394.

Petersen, A. C. (1976). Physical androgyny and cognitive functioning in adolescence. Developmental Psychology, 12, 524-533.

Reinisch, J. M., & Sanders, S. A. (1992). Effects of prenatal exposure to diethylstilbestrol (DES) on hemispheric laterality and spatial ability in human males. *Hormones and Behavior, 26,* 62-75.

Shute, V. J, Pellegrino, J. W., Hubert, L., & Reynolds, R.W. (1983). The relationship between androgen levels and human spatial abilities. *Bulletin of the Psychonomic Society, 21*, 465-468.

Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In: J. H. Barkow, L. C. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 533-549). New York: Oxford University Press.

Silverman, I., & Phillips, K. (1993). Effects of estrogen changes during the menstrual cycle on spatial performance. *Ethology and Sociobiology, 14*, 257-270.

Silverman, I., Kastuk, D., Choi, J., & Philips, K. (1999). Testosterone levels and spatial ability in men. *Psychoneuroendocrinology, 24*, 813-822.

Silverman, I., Phillips, K., & Silverman, L. K. (1996). Homogeneity of effect sizes for sex across spatial tests and cultures: Implications for hormonal theories. *Brain and Cognition, 31*, 90-94.

Slabbekoorn, D., van Goozen S. H., Megens, J., Gooren, L. J., & Cohen-Kettenis, P. T. (1999). Activation effects of cross-sex hormones on cognitive functioning: a study of short-term and long-term hormone effects in transsexuals. *Psychoneuroendocrinology, 24*, 423-447.

van Anders, S. M., Hampson, E., Watson, N. V. (2006). Seasonality, waist-to-hip ratio, and salivary testosterone. *Psychoneuroendocrinology, 31,* 895-899.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychological Bulletin, 117*, 250-270.

Williams, C. L, & Meck, W. H. (1991). The organizational effects of gonadal steroids on sexually dimorphic spatial ability. *Psychoneuroendocrinology, 16,* 155-176.

Zitzman, M., Weckesser, M., Shober, O., & Nieschlag, E. (2001). Testosterone-induced changes in cerebral glucose metabolism: association with visuospatial capability. *Experimental and Clinical Endocrinology and Diabetes, 109*, 302-304.