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Estradiol and mental rotation: Relation to dimensionality, difficulty, or angular disparity?

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ABSTRACT

Several studies have reported that performance on spatial rotation tests is better at menses than at high estradiol phases of the menstrual cycle in women. These effects are debated because nearly all reports of menstrual cycle variability have relied on a single test, the Mental Rotations Test (MRT, Vandenberg and Kuse, 1978). In the present study, we investigated key features of the MRT that might be responsible for its association with estradiol levels. We hypothesized that associations could be demonstrated for other tasks that share the same characteristics. Forty-four women ages 20–38 years, matched on education and general ability, were assessed at low ($n = 24$) or high ($n = 20$) estradiol stages of the menstrual cycle on a set of spatial tests that varied in dimensionality, plane of rotation, angular disparity, and effortfulness. Saliva was used to quantify estradiol and progesterone. Low estradiol was found to be associated with significantly better accuracy on the MRT and also on a mental rotation task that required large angles of rotation but employed only two-dimensional object representations and rotations limited to the picture plane. In contrast, a task using identical stimuli that required only small angles of rotation did not show an estradiol effect. A group difference also was seen on a test of perceptual closure. The results confirm that the estradiol effect is not limited to the MRT, and identify the rotational element, but also aspects of figural perception, as possible processes that may be responsive to estrogens. These findings advance our understanding by showing an association between estradiol and discrete spatial processes. Implications for understanding the origins of the robust sex difference commonly observed on the MRT are discussed.

Introduction

One of the largest cognitive sex differences found in humans is seen for mental rotation, the ability to visualize the rotation of an object around its axis. Mental rotation is one of several core types of spatial ability, identified through factor analytic studies, which require the formation of an accurate representation of the spatial configuration of objects or the movement of objects in space (for review see Carroll, 1993). Laboratory measures of mental rotation predict success at navigating in virtual and real environments (Moffat et al., 1998; Silverman et al., 2000), and mental rotation is a basic element of such everyday activities as tool use or object recognition. It is intrinsic to many technical occupations (e.g., Kass et al., 1998; Nguyen et al., 2012; Wai et al., 2009). The male advantage on mental rotation tasks averages ~0.56 standard deviations in size, but is larger in young adults than in adolescents or at middle age and beyond (Jansen and Heil, 2010; Voyer et al., 1995). The Mental Rotations Test (MRT) devised by Vandenberg and Kuse (1978) is used extensively to study spatial ability and displays one of the largest sex differences ($d = 0.70$–0.94; Voyer et al., 1995). Although both sexes can improve with extended practice, some studies suggest that a sex difference in mental rotation persists under well-practiced conditions (Terlecki et al., 2008; Uttal et al., 2012; but see Kass et al., 1998), implying that factors other than differential experience might also contribute to the sex difference in performance.

Neuroendocrine studies have investigated the possibility that sex steroids play a role, via their organizational or activational effects in the CNS. A body of evidence has reported variation in women's performance on mental rotation tasks in association with estradiol levels over the ovarian cycle. Nearly all of these studies used Vandenberg and Kuse's MRT or, in a few instances, the Shepard–Metzler figures, the source of the abstract figures depicted on the MRT (Shepard and Metzler, 1971). Better performance is found during menses, when estradiol levels are lowest, than during the midluteal or periovulatory phases of the cycle when estradiol levels are high (e.g., Hausmann et al., 2000; Maki et al., 2002; Mäntylä, 2013; McCormick and Teillon, 2001; Moody, 1997; Phillips and Silverman, 1997; Silverman and Phillips, 1993; Šimić and Santini, 2012). Although evidence is limited, the magnitude of the sex difference appears to be reduced if men are compared with women tested at menses (e.g., Mäntylä, 2013; McCormick and Teillon, 2001). A shortcoming of many menstrual

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cycle studies is the failure to measure hormones directly, but among studies that have used assays to quantify concentrations, inverse correlations have been observed between estradiol levels present at the time of testing and accuracy on the MRT (or a positive correlation with time required for a correct response) (Courvoisier et al., 2013; Hausmann et al., 2000; Maki et al., 2002; see also Hampson, 1990a). Correlations with progesterone have not been found, suggesting that estradiol not progesterone is the hormone responsible. It is informative theoretically that the effects of the ovarian cycle reported for mental rotation are *not* seen for many other types of cognitive functions, which exhibit either no relation to the cycle or, in a few cases, such as verbal fluency or certain memory-related functions (e.g., Hampson and Morley, 2013; Maki et al., 2002), show improvement at high not low levels of estradiol. It is likely that the effects are dependent on particular cognitive processes recruited during mental rotation tasks, but the features that elicit the 'estradiol effect' are not understood.

Under most conditions, administering estradiol to young women for research purposes is not ethically permitted. As a result, nearly all studies investigating the influence of estradiol levels on mental rotation have utilized the menstrual cycle as a convenient and ecologically valid method to investigate performance at high or low levels of natural estrogens. Oral contraceptives do contain ethinyl estradiol, but only in conjunction with a variety of progestogens derived from 19-nortestosterone, which are active at the androgen receptor, have androgenic properties (Speroff and Darney, 2011) or anti-androgenic properties (Fuhrmann et al., 1996), and which exert their own effects on mental rotation tasks (Wharton et al., 2008). Therefore, capitalizing on natural variations in estradiol that occur over the menstrual cycle remains the dominant method of investigating the associations between estradiol and spatial cognition.

Even though many studies have found variation in performance on mental rotation tasks over the menstrual cycle, not all studies have detected significant variation (e.g., Epting and Overman, 1998; Kozaki and Yasukouchi, 2009). It is possible that nonsignificant findings reflect other methodological variables, such as the use of females too young to have achieved full adult levels of ovarian steroid production (see Lipson and Ellison, 1992). Alternatively, it is possible that mental rotation tasks *other than the MRT* do not elicit menstrual cycle effects, even if appropriate samples are used. If effects were found to be limited to the MRT, it would significantly change our understanding of the importance of estrogen for spatial sex differences. Indeed, the MRT is a complex task that evokes several distinct cognitive processes (e.g., forming an accurate representation of the object to be rotated, rotating it, etc.) and some have argued that the sex difference arises not from its rotation (spatial) component, but from other features of the MRT such as having to encode and maintain an image of a target object whose shape is structurally complex (Kaufman, 2007; Parsons et al., 2004). Though it is widely assumed that menstrual cycle effects observed on the MRT reflect effects of steroids on the spatial component, this is not the only possible underlying process that could be influenced by hormones and manifest as a change in accuracy on the task.

The present study speaks to the larger question of which features of the MRT are responsible for its association with estradiol levels. It is not currently known why the MRT evokes such a large sex difference, so identifying which processes are hormone-sensitive may ultimately shed new light on the sex difference that is so reliably found. This question is also important from a neuroendocrine point of view—identification of relevant features may provide useful insight into latent cognitive processes that are influenced by steroids, extend our understanding of other types of tasks that may likewise be hormone-sensitive, help to identify candidate brain regions subject to modulation by estradiol, and lead to better informed theories regarding the adaptive significance of the hormonal modulation observed. In humans, the locations of estrogen receptors (ER) in the brain remain largely unknown, especially in neocortical regions relevant to cognition (cf. Perlman et al., 2005). Species differences are acknowledged (Österlund et al., 2000). An association between estradiol and the MRT suggests that receptors may be expressed in one or more cortical regions important for MRT performance. By beginning to define which processes are sensitive to estradiol, we can lay the groundwork for future behavioral or neuroimaging studies where specific cognitive processes can be targeted and systematically varied for investigation.

The present study employed a set of mental rotation tasks selected so as to vary in key features, in order to explore which features were important to elicit the estradiol effect in a well-characterized group of healthy women. The MRT was used to confirm the estradiol effect that has been reported in previous studies (e.g., Hausmann et al., 2000; Maki et al., 2002). We expected that women who had low estradiol, consistent with menses, would perform better on the MRT than women tested at high estradiol levels. Nearly all previous studies that identified a menstrual cycle effect have used the MRT task specifically. Several features of the MRT are argued to be the source of the particularly robust sex difference it elicits including: the fact that it involves two-dimensional (2D) depictions of three-dimensional (3D) objects; the fact that the objects are structurally complex and difficult to encode; that the rotations required are in the 'depth' plane relative to an observer (i.e., around the *y*-axis); that the rotations required are large; or that in some items parts of the objects are occluded by other parts and must be inferred (Kaufman, 2007; McWilliams et al., 1997; Parsons et al., 2004; Phillips and Silverman, 1997; Voyer and Hou, 2006). Basic figure perception is a significant source of individual variation on the MRT, and reportedly accounts for ~50% of the variance in scores (Caissie et al., 2009). Both the difficulty of the figural encoding and the large-angle rotations required are attributes that contribute to the difficulty level of the MRT, which is judged by respondents to be very high. Effortfulness in itself could be a potential source of a menstrual cycle effect if the effect were secondary to cycle-related mood changes, such as changes in depressive affect or fatigue.

To date, only one study has asked which feature of the MRT underlies its variation over the menstrual cycle. Phillips and Silverman (1997) suggested that an effect may be evident only on spatial tasks that involve images of 3D objects, because the visual system evolved to function in a 3D natural environment and therefore, 3D objects carry greater ecological validity. In support of this idea, Phillips and Silverman found that a set of *2D* rotation tasks, where the 'objects' to be rotated were checkerboard patterns or abstract line drawings (e.g., scalene triangle), did *not* show a menstrual cycle effect, whereas the MRT did show an effect in the same group of women. Unfortunately the 2D tasks used differed from the MRT not just in the dimensionality of the stimuli to be rotated, but also in other features that were uncontrolled (e.g., complexity of the figures, larger vs. smaller angular disparities, perceived difficulty). Any of these features might be a basis for the menstrual cycle effect observed on the MRT but not on the 2D rotation tests.

We hypothesized that the association with estradiol levels is not specific to the MRT, but rather can also be seen on other spatial tasks that share key features with the MRT. Following Phillips and Silverman (1997), we investigated if stimulus dimensionality is important. As an alternative hypothesis, we investigated whether the key feature is angular disparity, i.e., whether, as for the MRT, an estradiol effect can be found on other tasks where there are large angular disparities between the targets and choice stimuli so that rotation must be sustained through a large visual angle. Thirdly, as there is evidence that occluded items on the MRT show a larger sex difference than non-occluded items (Voyer and Hou, 2006), we examined whether perceptual closure might be a source of the estradiol effect. Perceptual closure has been identified by Carroll (1993) and others as a distinct form of spatial ability, defined as "the ability to unify an apparently disparate perceptual field into a single percept" (Ekstrom et al., 1976). It plays a role in object identification (Grützner et al., 2010) and may participate in deriving accurate 3D representations from the 2D depictions on the MRT, especially for items where arms of the figures are partly occluded or concealed. Finally, we evaluated if task difficulty