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Review

The influence of steroid sex hormones on the cognitive and emotional processing of visual stimuli in humans

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ABSTRACT

Steroid sex hormones are responsible for some of the differences between men and women. In this article, I review evidence that steroid sex hormones impact on visual processing. Given prominent sex-differences, I focus on three topics for sex hormone effects for which there is most research available: 1. Preference and mate choice, 2. Emotion and recognition, and 3. Cerebral/perceptual asymmetries and visual–spatial abilities. For each topic, researchers have examined sex hormones and visual processing using various methods. I review indirect evidence addressing variation according to: menstrual cycle phase, pregnancy, puberty, and menopause. I further address studies of variation in testosterone and a measure of prenatal testosterone, 2D:4D, on visual processing. The most conclusive evidence, however, comes from experiments. Studies in which hormones are administrated are discussed. Overall, many studies demonstrate that sex steroids are associated with visual processing. However, findings are sometimes inconsistent, differences in methodology make strong comparisons between studies difficult, and we generally know more about activational than organizational effects.

1. Introduction

In the following review I will discuss the evidence that steroid sex hormones impact on visual processing. The main areas of research examining these effects relate to how steroid sex hormones may impact on the structural organization of the visual processing areas of the brain and activational effects of steroid hormones leading to variation in how individuals process what they see. In terms of activational effects, one of the key arenas where steroid sex hormones may affect perceptual processing is in the processing and interpretation of visual social stimuli. There are several types of steroid hormones which may impact on visual processing. While these can be classified into distinct groups based on the specific receptors to which they bind, in terms of how they may affect visual processing it will be useful here to cluster them into three main functional groups: Steroid hormones related to sexual differentiation (androgens, estrogens, and progestagens), which I will collectively call ‘‘sex hormones’’, are the focus of this review. Steroid hormones related to metabolic control, immune function, and stress (glucocorticoids) and steroid hormones related to the more functional body mechanisms of salt and water balance (mineralocorticoids) are not discussed here.

This classification in relation to the general role of these steroid hormones is useful because it highlights the domains in which these hormones may impact on visual perception. Specifically, sex hormones relate to the development of sexual characteristics, leading to the differentiation of male and female. We may then expect sex hormones to relate to sex differences in visual processing. Such sex differences may arise via organizational effects, activational effects, and interactions between the two. Organizational effects reflect the early influence of hormones during development and represent stable, potentially permanent, effects. For example, sex hormones early in development can result in organizing neural architecture of the brain. Activational effects reflect that, once mature, circulating sex hormones can serve to activate brain architecture, influencing behavior. In fact, particular brain tissue may be organized by sex hormones early in development and this same tissue become activated by circulating sex hormones in maturity (see e.g., Arnold, 2009 for a review).

In this review I focus on three topics which have received the most attention in terms of research. Two prominent sex differences linked to the visual domain lie in visual–spatial abilities and brain lateralization, both of which are potentially tied to sex hormones (Kimura, 1996). Alongside these differences, sex hormones are related to sexual orientation (Collaer and Hines, 1995) and relative attention to same-sex and opposite-sex images (Alexander and Charles, 2009). We can then consequently expect that sex hormones will be tied to visual preferences related to mate choice. The other two groups of steroid hormones are not related to sexual differentiation and so we can expect their impact on visual processing to be somewhat distinct. Given glucocorticoids are related to the body’s ability to withstand illness and are sensitive to stress, we might expect that these steroid hormones may relate to visual perception of disgusting stimuli, as these relate to contagion risk,

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and also to visual cues to social support and/or stressors. Because of limited space and the prediction that these steroid hormones may have somewhat distinct effects on visual processing, I focus here on sex hormones. Some aspects of how sex hormones may relate to the processing of emotional stimuli are discussed later. I will discuss the impact of steroid sex hormones on visual perception in accordance with three major domains that have received most research attention: 1. Preferences and Mate Choice, 2. Expression and Recognition, and 3. Cerebral/perceptual Asymmetries and Visual–spatial Abilities. There is reason to expect sex hormones to impact on all three of these domains.

1.1. Sources of evidence for the effects of steroid hormones on visual processing

In reviewing the effects of steroid sex hormones on visual processing, it would be possible to highlight each group of steroid hormones in turn. Here, I present an alternative structure in which evidence for the impact of steroid sex hormones on visual processing is presented according to the source of the evidence. This is useful because of the nature of much of the research on steroid hormonal effects: it is difficult to isolate the specific impact of individual hormones in many studies presented in the literature. For example, many studies rely on examining the effects of natural fluctuations of hormones, such as across the female menstrual cycle or across puberty/menopause. In these studies, specific hormones may be implicated, and indeed measured, but hormonal profiles of all of the sex hormones likely change which means that the observed effects may reflect the action of multiple hormones. Even in experimental studies, such as in natural experiments comparing women using and not using hormonal contraception, steroid hormones interact and so researchers are unlikely to be able to conclude that administration of a specific hormone has a direct effect on visual perception. In the case of hormonal contraception users, for example, administered doses of estrogens leads to a decrease in the androgen testosterone (e.g., Alexander et al., 1990). These examples also highlight that studies variously address the impact of naturally occurring steroid hormones that are produced by the body and artificially produced hormones designed to duplicate the action of naturally occurring steroid hormones. The former is most relevant for studies which measure hormones from individuals or assess other factors related to hormonal profiles (Section 2), which provide indirect measures of influence, whereas the latter is most relevant for administration of particular hormones, which provide more direct experimental evidence for influence (Section 3). In the following two sub-sections I discuss the methods used in indirect and direct sources of evidence for the impact of steroid hormones on visual perception.

1.1.1. Indirect evidence

Most studies of the impact of steroid sex hormones on visual processing are indirect because they take either a correlational approach or rely on natural variations in hormonal profiles. For example, studies may measure particular hormones, like testosterone, and correlate scores generated from visual processing tasks with hormones levels. While this type of study can implicate the particular hormones in visual processes, the correlation does not determine causation and the effects observed may be mediated by an unmeasured factor correlating with score and hormone level. Other studies rely on measures of hormonal change according to natural fluctuations or life events such as cycle stage or puberty. There has been much research using these variations as they form natural quasi-experiments for researchers. However, these fluctuations are seldom for individual hormones and usually reflect several hormones simultaneously changing. So while these studies can indicate that steroid hormones influence visual preference, it is difficult to know which hormone is responsible for the action. Indirect evidence is discussed in Section 2 below.

1.1.2. Direct experimental evidence

Direct evidence of steroid sex hormones impacting on visual processing generally involves administering specific hormones to individuals and measuring their responses on visual tasks. This is comparatively rare in human participants because of the ethical problems of administering such hormones, particularly if one was interested in conducting a randomized control trial. In this instance most research has been conducted on non-human animals, although, possibly reflecting researcher interests and specific factors relating to certain animal model species, there is relatively little work that directly assesses impacts on visual processing. Some data on humans is available from certain groups. For example, hormonal contraception represents a self-administered hormonal dose and studies have usefully compared users and non-users. Rarely, but importantly, some researchers have been able to study human participants being administered sex hormones, for example, as part of gender reassignment procedures. These direct sources of evidence for the impact of steroid hormones on visual processing are discussed in Section 3 below.

2. Within-person and between-person variation in hormonal profile

There are many studies of within- and between-person variation of sex hormones that relate to visual processing. In this section I review studies examining variation in visual processing in relation to steroid sex hormones according to female menstrual cycle (Section 2.1), pregnancy (Section 2.2), and changes across the lifespan, highlighting puberty and menopause (Section 2.3). I additionally discuss extra studies on testosterone as distinct from other sex hormones because much research focuses on variation in testosterone (Section 2.4).

2.1. Female menstrual cycle

The menstrual cycle represents a natural variation in women's hormones relating to the probability of conception. Women's cycles are approximately 28–29 days, although there is variability around this average (Chiazze et al., 1968). The cycle can be divided into three phases: the follicular phase, ovulation, and the luteal phase. Menstruation marks the end of one cycle and the beginning of the next. Each of the phases represents different levels of sex hormones (Pauerstein et al., 1978). During the follicular phase (days 6–14) in which the ovarian follicles mature, estrogen levels rise and are highest just prior to ovulation (around day 14/15), when conception is most likely (Wilcox et al., 2001). After ovulation, during the luteal phase, estrogen levels drop and progesterone levels rise as the body prepares for pregnancy. Progesterone levels drop towards the end of the luteal phase until menstruation when the cycle beings again if the woman has not conceived. Given the link between becoming pregnant and evolutionary pressures to become pregnant by high quality men, researchers in this area have studied visual mate preferences quite intensively. These shifts in sex hormones means that researchers interested in the steroid hormones affecting sex differences have also used the natural variation in hormonal levels in cycling women to test their ideas. I note here that researchers differ in how they recruit women to these studies. The clearest data involves hormonal data collected at two points in the cycle, however, cross-sectional studies and studies that use self-reports of menstruation to mark cycle phase are common. Likewise, the actual comparison of times can differ. For example, some authors have compared the follicular phase to the luteal phase and

others the early and late follicular phases. Since conception risk is higher in the late follicular phase than luteal phase, and the late follicular phase and highest progesterone test session from the luteal phase should also differ markedly in progesterone level, this comparison captures differences in both fertility and progesterone level (Gilbert, 2000). By contrast, comparing the early and late follicular phases (Koehler et al., 2002, 2006) will capture differences in fertility but not progesterone level. Given researchers have argued progesterone may be an important component of cyclic preferences shifts (Jones et al., 2005a; Puts, 2005), it may be unlikely that cyclic shifts would be seen in studies testing women during the early and late follicular phases. It should also be noted that annovulatory phases in some women could add noise to data from studies that do not use hormone levels to confirm cycle phase, although such noise is unlikely to skew the results of such studies.

2.1.1. Preferences and mate choice

Multiple studies have demonstrated that women's preferences for various traits in various domains including smell, sound, and vision, shift across the menstrual cycle (Rikowski and Grammer, 1999; Puts, 2005; Feinberg et al., 2006; Little et al., 2011). In terms of visual preferences, one of the best documented phenomena in studies examining cyclical preference shifts is a greater attraction to masculine male faces at peak fertility in the menstrual cycle (Penton-Voak et al., 1999; Johnston et al., 2001; Little et al., 2007a,b; Jones et al., 2008; Little and Jones, 2012), a within-individual shift presumably driven by variation in hormone levels across the cycle. Examples of masculinized and feminized male faces can be seen in Fig. 1. Preferences have generally been addressed by presenting two images side by side and asking participants to select the most attractive of the pair, a two alternative forced choice test. Other studies have presented stimuli to individuals and had them rated on a scale (often 7- or 9-points) for attractiveness. This shift in preferences for masculinity has been proposed to be adaptive in changing the preferences of women when they are most likely to become pregnant towards high quality males or in leading to attraction to more cooperative men when not likely to become pregnant (Penton-Voak et al., 1999; Johnston et al., 2001; Little et al., 2007a,b; Jones et al., 2008; Little and Jones, 2012). Alongside masculinity of face shape, preferences for other indices of masculinity also change across the cycle. Increased preferences for darker facial skin color (Frost, 1994), visual cues to dominant behavior (Gangestad et al., 2004), and for masculine body shapes (Little et al., 2007a,b) that coincide with the late follicular (i.e. fertile) menstrual cycle phase have been reported. Cyclic shifts are also seen for other mate choice relevant traits whereby fertile women are quicker to categorize men's faces as male (Macrae et al., 2002) and generally rate men as more attractive (Danel and Pawlowski, 2006). Shifts are also seen for other face traits, such as self-resemblance (DeBruine et al., 2005), health (Jones et al., 2005a), and symmetry (Little et al., 2007a,b), and are also evident in increases in pupil diameter when viewing potential sexual partners during the fertile phase (Laeng and Falkenberg, 2007). These cyclic shifts are thought to reflect the underlying effects of female hormones on preferences for male traits. Several hormones change across the cycle and shifts have been linked to variation in estrogen (Roney and Simmons, 2008), progesterone (Jones et al., 2005a; Puts, 2005), and testosterone (Welling et al., 2007), although such shifts are potentially best explained by complex interactions among multiple hormones (Feinberg et al., 2006; Welling et al., 2007).

Fig. 1. Examples of manipulated feminized (left) and masculinized (right) female and male faces used in studies of preferences across the cycle (Little and Jones, 2012) and other studies. Preferences for masculine male faces are generally found to be higher in the follicular phase when estrogens are high (e.g., Little and Jones, 2012).

As a different, but potentially complementary, explanation for shifting preferences, alterations in progesterone level have been associated with increased commitment to a partner, and increased preferences for less masculinized male faces during the luteal phase of the cycle (Jones et al., 2005a). Similar findings for the link with progesterone are seen for preferences for masculine voices (Puts, 2006). This link with progesterone may reflect an increase in the care and support that is sought during times when a woman's hormonal profile is similar to that characterized in pregnancy (Jones et al., 2005a). In this way, rather than acquiring direct benefits for offspring from masculine men, women may instead maximize investment from feminine men when raised progesterone prepares the body for pregnancy (Jones et al., 2005a).

Another factor that influences preferences for facial masculinity is the type of relationship being looked for. Studies have shown that women tend to prefer more masculine faces when judging for a short-term than for a long-term relationship (Little et al., 2002). Indeed, in a variety of studies, cycle effects are often more likely seen when women judge for short-term relations (reviewed in Gangestad and Thornhill, 2008; Jones et al., 2008). In a similar way to already having an investing partner, short-term relations minimize the need to value investment from partners. While studies have focused on male masculinity, symmetry is another putative cue to male health (Thornhill and Gangestad, 2006) and has also been found to vary across the cycle with studies showing both within- and between-subject shifts in preferences towards more symmetric faces at high fertility (Little et al., 2007b). Relationship status and relationship context appear to be important for cyclic shifts in preferences. Cyclic shifts in women's preferences for masculine characteristics in men's faces are generally greatest among women who already have romantic partners and when women judge men's attractiveness for short-term, extra-pair relationships (Penton-Voak et al., 1999; Little et al., 2007a,b; Gangestad and Thornhill, 2008; Jones et al., 2008). In particular, preferences appear to shift mainly for short-term contexts, when context has been examined, and indeed no study that has distinguished between short- and long-term contexts has shown a cycle shift for long-term judgments (reviewed in Gangestad and Thornhill, 2008; Jones et al., 2008).

While there is indeed a growing body of evidence that shifts in preferences for masculine traits do occur across the cycle, some studies have not demonstrated these effects. There have been unsuccessful replications of cyclic variation in women's masculine face preferences. For example, two recent studies observed no evidence for cyclic variations in women's preferences for masculine versus feminine male faces (Peters et al., 2009; Harris, 2011). Additionally, a recent study found that women preferred the faces of men with high testosterone levels at high fertility during the menstrual cycle, but observed no effect of cycle phase on women's preferences for male faces that were perceived to be masculine (Roney et al., 2011).

Despite these null findings, studies demonstrating cyclic shifts have also been supported by brain imaging studies. Women have been found to show increased medial orbitofrontal cortex, an area involved in reward, activation in response to male faces in the follicular phase of the cycle compared to the luteal phase (Rupp et al., 2009a,b) and women show increased activation in several brain regions toward masculine versus feminine faces in the follicular phase that are suggestive that women find masculinized faces more rewarding. (Rupp et al., 2009a,b).

Although many studies have now demonstrated that women's preferences for the body odours of symmetric men are enhanced around ovulation (reviewed in Gangestad and Thornhill, 2008), evidence for cyclic shifts in women's preferences for symmetry in men's faces is equivocal. As noted, one paper presenting two studies, one between- and one within-subject, has found that women's preferences for symmetric male faces were stronger around ovulation than during other phases of the menstrual cycle, at least among partnered women who were instructed to judge men's attractiveness as short-term mates (Little et al., 2007b). By contrast, several other studies have observed no evidence for cyclic shifts in women's preferences for symmetric men's faces (Koehler et al., 2002; Cardenas and Harris, 2007; Oinonen and Mamanian, 2007; Peters et al., 2009), although one of the studies with a null finding for preference did find that women's ability to detect asymmetries in men's faces varied over the menstrual cycle in the predicted manner (Oinonen and Mamanian, 2007).

There are significant methodological differences between studies examining cycle effects making direct comparisons between those reporting null and positive effects difficult. Studies differ, for example, in stimuli number, stimuli type, and how fertility is defined. One key difference appears to be the issue of relationship context. Most studies reporting null results for preferences for masculine (Peters et al., 2009; Harris, 2011; Roney et al., 2011) and symmetric faces (Cardenas and Harris, 2007; Oinonen and Mamanian, 2007; Peters et al., 2009) have examined general attractiveness ratings and have not distinguished between short- and long-term contexts. Given larger cyclic shifts for short-term judgments and the general absence of effects for long-term judgments in some studies of facial masculinity and symmetry preferences, general attractiveness judgments may be less likely to show effects of cycle phase than judgments of men's attractiveness for short-term relationships, specifically. While several studies suggest that cycle effects are most prominent for short-term ratings, one recent study has found that preferences for both facial symmetry and masculinity change only for short-term and not long-term judgments (Little and Jones, 2012). It may be then that term of relationship sought is critical to observing cycle effects on preferences in some types of studies (Little and Jones, 2012).

2.1.2. Expression and recognition

As noted earlier, the luteal phase represents a time in which progesterone is raised, and so reflects a similar change during pregnancy. Absolute levels of progesterone in pregnancy are higher than levels during the luteal phase and so changes may be smaller but potentially in the same direction. It may be expected that at this time women should be more attentive to visual cues to threat and danger that could pose a risk to the developing fetus during pregnancy (Conway et al., 2007). Following this logic, several studies have examined cyclic shifts in recognition of emotional expressions, focusing on progesterone. Studies have shown that changes in progesterone level are associated with changes in the strength of aversion to cues of contagion (Flaxman and Sherman, 2000; Fessler, 2002). As noted in Section 2.2.1, for example, women are more attracted to healthy appearing faces when progesterone is high in the luteal phase (Jones et al., 2005a).

This has led researchers to examine women's sensitivity to potential cues to nearby sources of contagion and physical threat by using images of disgusted and fearful facial expressions (Conway et al., 2007). When rating intensity of expressions, women in the mid-luteal phase, when progesterone level is high, perceived fearful and disgusted expressions with averted gaze as more intense than those with direct gaze compared to when at a time when progesterone is lower (Conway et al., 2007). Other studies examining accuracy and not intensity have revealed a somewhat different pattern. For example, emotion recognition has been found to be more accurate in the follicular than luteal phase which appears to be related to a negative correlation between progesterone level and emotion recognition accuracy (Derntl et al., 2008a). Examples of images used to test emotional expression recognition can be seen in Fig. 2. Another study has tied these shifts to changes in amygdala activity. Using an emotion recognition task, stronger amygdala activation was found in women during their follicular phase compared to the luteal phase (Derntl et al., 2008b). In line with some previous studies, emotion recognition accuracy was highest in the follicular phase. Additionally, negative correlations were found between progesterone levels and amygdala response to fearful, sad and neutral faces, providing more support that progesterone changes reactions to visual emotional stimuli across the menstrual cycle. (Derntl et al., 2008b).

Alongside progesterone, estrogen has also been associated with shifts in emotional recognition across the cycle. One study, for

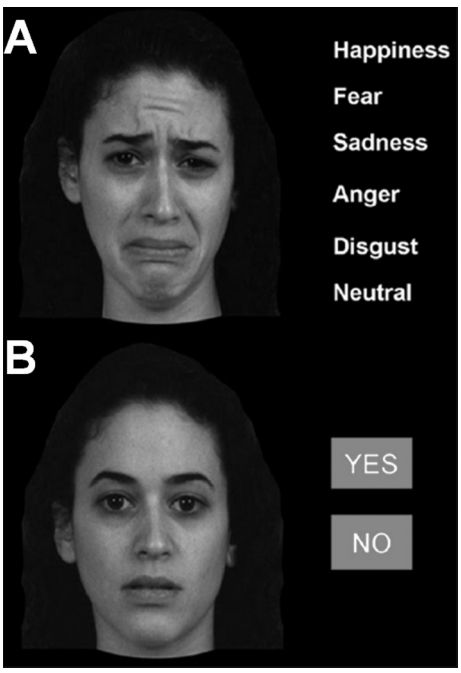

Fig. 2. Expression recognition tasks used in some studies (Gur et al., 2002a,b; Derntl et al., 2008a). (A) Classification of emotion task in which correct answers are a score of expression recognition ability and (B) recognition memory task in which participants are asked if the saw (yes) or did not see (no) the face in a prior learning phase.

example, has demonstrated a relatively specific association between cycle phase and fear recognition, in which the accuracy of recognizing emotional expressions was compared across different stages of the menstrual cycle. For the emotional expression of fear only, women were significantly more accurate at the late follicular stage prior to ovulation when estrogen levels are high than at menstruation when estrogen levels are low (Pearson and Lewis, 2005). Other studies which measured hormonal concentrations at different cycle stages have revealed similar patterns of results. For example, comparing follicular and luteal stages and measuring hormones, it as been shown that fear, anger, and sadness are more accurately recognized in the follicular phase (Guapo et al., 2009) and the study also showed that estrogen levels were negatively correlated to accuracy in perception of angry faces.

2.1.3. Cerebral/perceptual asymmetries and visual–spatial abilities

Several studies have assessed how functional cerebral asymmetries in visual processing fluctuate across the menstrual cycle. These asymmetries relate to sex differences in hemispheric specialization, with men being more lateralized than women as shown in line bisection tasks (Bourne, 2005). Consequently, these processing asymmetries appear to be related to varying levels of sex hormone over the menstrual cycle (Hausmann and Gunturkun, 2000; Hausmann et al., 2002). While studies have generally demonstrated a role of sex hormones in processing asymmetries, the pattern is not consistent across all studies. Some studies suggest that processing asymmetries, such as those seen in line bisection tasks or identification tasks in which different information is presented to left and right visual fields via a tachistoscope, are greatest in the luteal phase, when progesterone and estrogen are relatively high (Bibawi et al., 1995; McCourt et al., 1997) compared to other studies, which show stronger lateralization during menses, when concentrations of both of these sex hormones are lower (Heister et al., 1989). Regardless of direction, these effects suggest a role of sex hormones although there is also disagreement regarding which sex hormone is most responsible for the shift and the mechanism by which it occurs. Some researchers have suggested that progesterone produces the observed shifts by diminishing hemispheric communication (Hausmann and Gunturkun, 2000; Hausmann et al., 2002) while other researchers suggest that estrogens suppress right hemisphere function while enhancing left hemisphere function (Hampson, 1990a,b). While Hausmann and colleagues presented evidence more consistent with the former explanation, some of their more recent work supports the latter. For example, using a rapid serial visual presentation task, with one stream in each visual field, estrogens were found to reduce cerebral asymmetries by decreasing right hemisphere function (Hollander et al., 2005). It is possible that the two explanations are not mutually exclusive and work in tandem to shift visual processing asymmetries across the cycle.

Alongside processing asymmetries, one relatively stable sex difference is found in visual–spatial tasks, such as mental rotation ability, in which men outperform women. Indeed, the Mental Rotation Test, in which participants imagine cube stimuli revolving in 3D space, produces reliable sex differences (Voyer et al., 1995) and comparable sex differences in mental rotation abilities are found in more recent studies (Halari et al., 2005; Schoening et al., 2007). Examples of images used to test mental rotation ability can be seen in Fig. 3. Several studies have demonstrated that menstrual cycle phase impacts on performance in visual–spatial spatial tests. These studies show a pattern of lower performance scores during the follicular or mid-luteal phase, when estradiol or and progesterone levels are higher, and better performance scores during menses, when steroid hormone levels are generally low (Hampson and Kimura, 1988; Hampson, 1990a,b; Phillips and Silverman, 1997). Measuring sex hormones across the cycle,

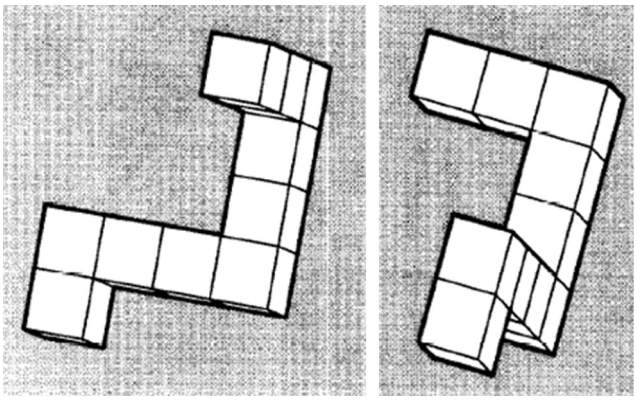

Fig. 3. Example of mental rotation task (from Kimura, 1996). Participants are asked if the image on right is the same as the image on the left.

one study has further noted that higher estradiol concentrations are associated with a decrease while higher testosterone concentrations are associated with an increase spatial abilities (Hausmann et al., 2000). Additionally, Stroop task performance has also been found to differ across the cycle, particularly associated with levels of estradiol (Hatta and Nagaya, 2009). These studies together suggest that sex-differences in visual–spatial abilities are affected by steroid hormones, perhaps particularly estradiol and testosterone. As in previous sections, however, not all studies have found cyclic shifts in visual–spatial ability. Some researchers have found no evidence that performances changed according to cycle phase (Epting and Overman, 1998), despite demonstrating significant sex differences in various tasks. Other studies have found no fluctuations across the cycle for other visual–spatial tasks (Gordon et al., 1986) and no correlation between estrogen and visual–spatial abilities, such as mental rotation (Gordon and Lee, 1993).

2.2. Pregnancy

Like cycle phase, pregnancy reflects a time of hormonal change in women and consequently has been studied by researchers in this context. Estradiol, progesterone and cortisol levels all rise during pregnancy (Lauritzen and Klopper, 1983; Peterson, 1983). While cycle phase research, at least on preferences, has generally followed the view that attention to high quality male partners is likely to be highest when conception is most likely, researchers of shifts in pregnancy have understandably been more focused on abilities related to the protection and care of offspring. Indeed, researchers have often noted that investment and protection of vulnerable young is critical and so we might expect that pregnant women may be particularly sensitive to visual emotional or other cues to threat or support as well as sensitive to cues to contagion and pathogens.

2.2.1. Preferences and mate choice

Because the hormonal profile of the mid-luteal phase is relatively more similar to that during pregnancy than other cycle phases, many researchers have focused on cycle effects rather than comparisons of pregnant and non-pregnant women. Another factor that may have led to a paucity of research on this group concerning preferences is that pregnant women are unlikely to be seeking a current partner for reproduction. There has been then only one study examining attractiveness judgments in pregnant and non-pregnant women. Following the logic that women who are pregnant will be sensitive to disease and hence select social partners who are healthy and disease free, this study has demonstrated that pregnant women prefer healthy appearing faces more than their non-pregnant counterparts (Jones et al., 2005b).

2.2.2. Expression and recognition

Comparisons of pregnant and non-pregnant women are also rarer in the emotion recognition domain than studies of cycle shifts. There are, however, studies that suggest visual emotion processing differ during pregnancy. One study has shown that the ability to encode facial expressions of emotion differ between early and late pregnancy using a within-participant design. Women scored more highly for accuracy for remembering fearful, angry and disgusted facial expressions (expression associated with threat or harm) and also sadness during late pregnancy (Pearson et al., 2009). This finding is in line with similar results at the mid-luteal stage of the cycle when progesterone is high and also in line with the logic that it may be useful to recognize emotional faces during late pregnancy as an adaptation to increasing vigilance towards emotional signals of threat, aggression and contagion (Pearson et al., 2009). Another study has assessed attention to emotional face expressions in pregnant and non-pregnant women. Pregnant women were found to be more attentive to fearful faces compared to controls and this attention to fear was associated with increased levels of estradiol and progesterone at least in trimester 2 (Roos et al., 2012). Again, the findings are in line with the prediction that heightened sensitivity to danger cues may reflect the importance of recognizing and responding to sources of danger during late pregnancy.

2.2.3. Cerebral/perceptual asymmetries and visual–spatial abilities

There are studies that have examined changes in visual–spatial ability across pregnant and non-pregnant women. One proposed area of difference lies in memory and, while studies have shown that women think their memory is impaired during pregnancy, when tested, women's recognition memory does not differ between pregnant women and non-pregnant controls in some studies (Sharp et al., 1993), although this same study does show that pregnant women performed worse at recall of words. In terms of spatial tests, one study has examined the impact of carrying male or female fetuses on test performance. Interestingly, following women from early pregnancy to after they had given birth, women who were pregnant with boys performed better than women who were pregnant with girls on some tests of spatial ability (Vanston and Watson, 2005). This study suggests that beyond any hormonal changes associated with all pregnancies, some aspect of carrying male or female foetuses could impact on the mothers' cognition (Vanston and Watson, 2005). The pattern of results is consistent with the notion than women carrying boys experience higher levels of testosterone and/or lowers levels of estrogen than women carrying girls.

2.3. Changes across the lifespan: puberty and menopause

Both puberty and menopause are associated with shifts in hormonal profile in women. At puberty, sex hormones generally increase to adult-like levels and at menopause female sex hormones, most notably estradiol decreases. There are also good reasons to predict that women's perceptions in relation to preference and emotion may change during the transitions between different phases of a woman's reproductive lifespan. Because women are not able to reproduce either pre-puberty or post-menopause, we might see a shift away from mating psychology at these times. Similarly, attention to cues important in choosing partners that may benefit offspring via genetic inheritance may be diminished relative to women within their reproductive years (Hawkes et al., 1998; Vukovic et al., 2009).

2.3.1. Preferences and mate choice

The transition through puberty represents the move from a juvenile to an adult state and involves significant changes in behavior as well as hormonal profile particularly regarding changes to an adult-like pattern of sex hormones. Puberty is known to affect many types of psychological processes (Buchanan et al., 1992), although broad similarities between judgments of facial attractiveness by children and by adults are generally found (Cross and Cross, 1971; Cavior and Lombardi, 1973; Dion, 1973; for review see Langlois et al., 2000). Several studies have demonstrated interesting differences in ratings that might reflect pubertal development. For example, young children, both male and female, do not show preferences for the waist-to-hip ratio that is found most attractive by adults, but teenagers do (Connolly et al., 2004). Saxton et al. (2009) have demonstrated that pubertal development is related to preferences for several important face traits. Saxton et al. (2009) found that in a cross-sectional sample of male and female children aged 11–15, while both the younger and older groups of children preferred more average, symmetric and feminine faces, older children were significantly more likely than younger children to select the average, symmetric and, when judged by girls but not boys, feminine male faces as more attractive (Saxton et al., 2009). Another study has demonstrated significant differences in female preferences for male facial masculinity comparing pre-puberty and post-puberty groups. Girls aged 11 and 12 had lower preferences for masculinity compared to the preferences of young adult women (Little et al., 2010).

Another point in women's lives where face preferences may change is during menopause. Again, as in puberty, changes in hormonal profile that occur at menopause influence many aspects of behavior. Menopause in humans has been held up as an evolutionary puzzle but many modern theories suggest that the end of ones' own reproduction can be adaptive if it provides post-reproductive grandmothers who enhance their inclusive fitness by helping to care and provide for their daughters' children (Hawkes et al., 1998; Shanley et al., 2007). Indeed, having maternal grandmothers improves the nutritional status and enhances the survival chances of children in rural Gambia (Sear et al., 2000). After menopause, we might then expect that women's psychological mechanisms would no longer be geared towards mating themselves and instead would be geared towards promoting investment in family and cooperation in their community (e.g., Hawkes et al., 1998). One study has investigated circum-menopausal women's preferences for masculinity and femininity in the faces of young adult men and women. It was found that post-menopausal women demonstrated stronger preferences for femininity in other women's faces than pre-menopausal women did (Vukovic et al., 2009). While no significant difference between pre- and post-menopausal women was seen for judgments of men's faces, the data were in the predicted direction; pre-menopausal women reported marginally higher preferences for masculinity than post-menopausal women did. The authors suggest that dislike of feminine (i.e. attractive) same-sex competitors may decrease as fertility decreases in line with the idea that post-menopausal women are no longer as concerned by attractive potential mating rivals as are women within their reproductive range (Vukovic et al., 2009). Similar effects are seen across the cycle where more fertile women also demonstrate a decrease in preferences for femininity in female faces (Jones et al., 2005a; Welling et al., 2007). Another two studies have demonstrated that women's preferences for masculinity in male faces decrease after menopause using both young (Little et al., 2010) and older (Jones et al., 2011) face stimuli. Together, these more recent studies support the idea that preferences for masculinity are highest among women at ages when they are reproductively active and when they producing hormones relevant for reproduction.

2.3.2. Cerebral/perceptual asymmetries and visual–spatial abilities

There are limited studies that address changes across puberty and into adulthood in this domain. There is, however, evidence that puberty does impact on visual spatial abilities. For example,

comparing 8 year olds and young adults on a mental rotation task, men were quicker at the mental rotation task than women, but there were no differences between boys and girls (Roberts and Bell, 2000). This emergence of a sex difference in mental rotation ability across puberty suggests that pubertal hormones play a role in generating such effects. This study also established that these differences were apparent in brain processing mechanisms. Men showed more brain activation than women during the task but this difference was absent for boys and girls (Roberts and Bell, 2000). There is also evidence that menopause in women is related to a less lateralized performance on visual–spatial tasks (Hausmann and Gunturkun, 1995). Most research on post-menopausal women and these variables concerns the impact of hormone replacement therapy and these studies are discussed in more detail in section 3.2. Men have no equivalent to menopause but testosterone generally decreased with age in men (Moffat et al., 2002). Examining testosterone in a longitudinal sample of men aged 50–91 for around 10 years, men with lower testosterone levels performed worse on visuo-spatial tests and showed a faster rate of decline in their visual memory (Moffat et al., 2002).

2.4. Testosterone: activational and organizational effects

While testosterone may vary according to cycle, pregnancy, and other factors, I address further studies on testosterone here. This is because testosterone demonstrates additional fluctuations, varying both diurnally and seasonally and because there are also other interesting data available for testosterone in human participants that are absent for other sex hormones. For other sex hormones most evidence exists for activational rather than organizational effects. This is because demonstrating such organizational effects in human participants is difficult. For example, such studies would require measurement of hormones before birth, when brain organization begins, followed by long-term follow-up studies of visual processing into adulthood. Testosterone is an interesting exception here because of a putative marker of prenatal testosterone is available to researchers: a well-studied digit length ratio, 2D:4D, related to concentrations of prenatal testosterone (Manning et al., 1998; Lutchmaya et al., 2004). An explanation of how to measure 2D:4D ratio can be seen in Fig. 4. In this section I highlight some specific syndromes that are relevant to the early impact of testosterone on perception before moving on to discuss the same three areas as for previous sections.

2.4.1. Organizational effects and specific syndromes

As well as 2D:4D ratio, other cases highlight organizational roles for testosterone and androgens. Sex differences in interest in social versus more mechanical visual stimuli appear present from an early age. For example, young infants demonstrate a sex difference in looking time at different stimuli, with girls looking longer at a face while boys look relatively longer at a mobile (Connellan et al., 2000) and girls attending more to a video of a moving face while boys are relatively more attentive to a video of a moving car (Lutchmaya and Baron-Cohen, 2002). These early differences in interest in social stimuli may potentially be underpinned by prenatal testosterone level. One study examining fetal testosterone levels and subsequently testing infants at 12 months of age found that girls made significantly more eye-contact with their parent than boys in video recordings of interaction and that eye contact was associated with fetal testosterone level (Lutchmaya et al., 2002). These early differences highlight that while testosterone may have activational effects in adults, prenatal organizational effects may be apparent at early stages in development.

Further evidence for the early impact of testosterone on organising tissue influencing behavior comes from clinical groups that show deviation from the usual pattern of androgen exposure. Some researchers have noted that autism, and the associated Asperger syndrome, may in part be associated with high levels of prenatal testosterone and there is evidence both that 2D:4D is negatively associated with prenatal testosterone (Lutchmaya et al., 2004) and that the 2D:4D ratios of children with autism is below the mean value of the population they were drawn from (Manning et al., 2001). Given that autism is associated with marked deficits associated with sociality and has been proposed as representing an extreme 'male' brain (Baron-Cohen et al., 2005), these associations are consistent with testosterone having an early organising effect, masculinising the brain.

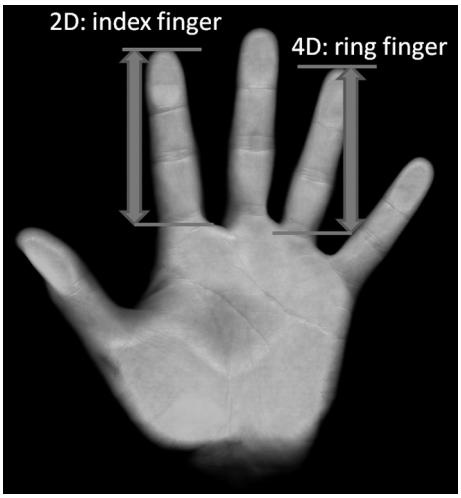

Fig. 4. Measuring 2D:4D ratio from hands. Measurements are generally taken from the mid-point of the bottom crease of the two digits to the tip of each digit. 2D score divided by the 4D score produces the ratio. Men tend to have a longer 4th digit relative to 2nd digit than women meaning that men have lower 2D:4D ratios than women (Manning et al., 1998).

Another example comes from individuals with congenital adrenal hyperplasia (CAH), a condition caused by mutations in genes coding for enzymes linked to hormone production pathways, often resulting in exposure to high concentrations of androgens in utero. Indeed, girls and women with CAH appear more interested in male typical behaviors than their non-CAH siblings (Berenbaum, 1999). Consistent with an organizing effect of testosterone masculinising the brain, female adolescents and young adults score higher on mental rotation tests compared to their non-CAH sisters (Berenbaum et al., 2012). Other studies comparing men and women with CAH to non-CAH siblings on tasks of mental rotation and targeting have shown increased targeting ability but not mental rotation in CAH women and decreased mental rotation but not targeting ability in CAH men (Hines et al., 2003). There may also be a link between CAH and 2D:4D, as may be expected. Females and males with CAH have a significantly lower 2D:4D than non-CAH controls, although this was true for the right hand in females and the left hand for males (Brown et al., 2002). Not all studies are consistent with CAH impacting on male-like abilities, with some studies showing equivalent performance between females with CAH and those without on spatial or verbal abilities (Malouf et al., 2006). Meta-analysis, however, suggests that, overall, studies show that females with CAH perform better on spatial tasks, while CAH males perform worse compared to controls (Puts et al., 2008).

Turner syndrome presents the opposite pattern to CAH, in which females are exposed to lower than average androgen levels due to the absence of part or all of one X chromosome. Impaired visual–spatial and perceptual abilities appear to be characteristic of children and adults with Turner syndrome (Nijhuis-van der Sanden et al., 2003; Ross et al., 2006). For example, adults with Turner syndrome have been found to have lower performance on spatial/

perceptual skills compared to matched controls (Ross et al., 2002). While the data provide a somewhat complex pattern, individuals with complete androgen insensitivity syndrome, in which cells do not respond to androgen, have been shown, relative to controls, to perform less well on visuo-spatial tests (Imperatomcginley et al., 1991).

2.4.2. Preferences and mate choice

At a very broad level, testosterone has been related to sexual orientation, then influencing the attractiveness of same-sex and opposite-sex stimuli (Alexander and Charles, 2009). In men, testosterone is positively related to their interest in sexual stimuli (Rupp and Wallen, 2008). Further, men report greater attraction to feminine women's faces what their saliva testosterone as is high (Welling et al., 2008). Women's testosterone levels vary according to cycle stage, generally rising between menstruation and ovulation and then declining (Alexander et al., 1990; VanGoozen et al., 1997). Testosterone may effect visual interest in certain stimuli because it is positively related to measures of women's sex drive (Riley and Riley, 2000). This has also led some authors to suggest that testosterone could be related to cyclic shifts in women's preferences for masculine faces. Measuring testosterone across the cycle in women (examining times when salivary progesterone or estrogen were equivalent), it has been shown that masculine faces are most preferred by women when salivary testosterone was highest (Welling et al., 2007). This study then suggests testosterone may play a role in driving women's attraction to masculine men more generally. In related work, 2D:4D ratio has also been related to women's preferences for men's facial masculinity, with women with more masculine ratios preferring more masculine men (Scarbrough and Johnston, 2005). Taken together, these studies highlight both activational and organizational effects of testosterone at least on women's preferences.

2.4.3. Expression and recognition

There is evidence that testosterone influences the social reward value of emotional expressions on faces. For example, testing the degree to which subjects find anger faces reinforcing, higher levels of saliva testosterone have been found to be related to more reinforcement for angry appearing faces, as measured in a learning task (Wirth and Schultheiss, 2007). Further studies also suggested that, measuring diurnal testosterone within-participant, testosterone at peak levels (in the morning) best predicted responses (Wirth and Schultheiss, 2007). These findings may reflect that testosterone decreases aversions to angry or threatening stimuli, or even indicate a tendency to increase interest in cues to dominance. Other studies have also indicated that current circulating testosterone is associated with abilities to process other's emotions (Bos et al., 2012). Prenatal testosterone has also been found to relate to measures relating to social perception skills. For example, face perception abilities, as measured by a face inversion task, has revealed correlations between 2D:4D and face processing skills (Leow and Davis, 2012). There is, however, more limited evidence for 2D:4D to be related to emotion related tasks. For example, as tested in the reading the mind in the eyes task in which participants judge emotional and mental states from images of eyes, no differences have been found according to 2D:4D ratio (Voracek and Dressler, 2006).

2.4.4. Cerebral/perceptual asymmetries and visual–spatial abilities

Testosterone has been found to be associated with a variety of visual tasks. For example, in older men, using tasks addressing visual-processing speed and mental rotation abilities, testosterone was positively associated with faster visual-processing speed and faster mental rotation (Van Strien et al., 2009). In other studies, more limited effects of testosterone on mental rotation ability are seen. Using measures of saliva testosterone and a diurnal shift in a large sample of men and women, mental rotation task performance was not found to be related to testosterone concentrations in either sex (Puts et al., 2010). The authors suggest that organizational effects may then be more important in generating sex differences in spatial abilities. In line with the idea that early effects may be important, there is evidence for organizational effects of testosterone on hemispheric lateralization from studies of 2D:4D. For example, in lateralised face tests, lower, masculine or high testosterone, 2D:4D ratios, were associated with greater lateralization as shown by stronger right hemisphere dominance (Bourne and Gray, 2009).

Other studies also support the early role of testosterone. For example, in utero, sex of sibling can change the hormonal environment. In female twins, presence of a male twin versus a female twin is associated with better performance on mental rotation tasks, supporting the idea that having a male co-twin in utero results in a greater exposure to testosterone and early impacts of testosterone on mental rotation abilities (Heil et al., 2011). Fetal testosterone has been found to have measurable effects in children 7–10 years old, with both boys and girls with higher levels of fetal testosterone performing better on the embedded figures test, which measures attention to detail and piecemeal versus holistic processing, but not targeting and mental rotation tests (Auyeung et al., 2012). As well as in utero, organization may take place at puberty, although changes have been less well studied (Berenbaum and Beltz, 2011). Given that sex differences in mental-rotation tasks are seen in infants, with males reacting more to visual stimuli requiring mental rotation (Moore and Johnson, 2008; Quinn and Liben, 2008), if testosterone underpins this sex difference, the effects of testosterone appear to be present before puberty. Lastly, 2D:4D has been related to judgments of line angle as a measure of visuospatial ability with men and women with lower male-typical digit ratios performing better (Collaer et al., 2007). Comparing 2D:4D, as a marker of in utero testosterone, and current levels of testosterone as predictors of abilities of targeting, and other visual tasks has suggested that 2D:4D is perhaps a stronger predictor of these abilities than current testosterone (Falter et al., 2006), although the overall pattern does not uniformly support 2D:4D as a predictor of all of these abilities. Further research on the relative contributions of in utero, pubertal and current levels of testosterone would likely prove important in this area.

3. Experimental administration of steroid hormones

For ethical reasons, direct administration of sex hormones to determine their relationship to visual processing is relatively uncommon. Some researchers have examined the direct effects of administering, for example, testosterone in laboratory settings. More commonly, however, researchers have taken advantage of natural experiments in which participants are individuals who have elected to self-administer sex hormones for other reasons. For example, one type of hormone administration related to contraception, "the pill", is taken by millions of women worldwide. Other notable examples come from hormones taken post-menopause in women, hormone replacement therapy, and hormonal administration as part of gender reassignment in trans-gender men and women. These sources of evidence are discussed below.

3.1. "The pill" and hormonal contraception

Hormonal contraceptives work by altering hormonal fluctuations that occur during the natural menstrual cycle, through negative feedback effects on the hypothalamus and anterior pituitary gland, which suppress gonadotropin release and inhibit follicular

development and ovulation (Rivera et al., 1999). They consist of synthetic formulations of either a progestagen (e.g., the "minipill", or progestin-only pill) or a dose of both an estrogen and a progestagen (e.g., the "combined pill"). The oral contraceptive pill, and other hormone-based contraceptives (e.g., patch or implant) work by suppressing ovarian hormones, which alters the hormonal profile of the woman, and results in a leveling effect in concentrations of estrogen and progesterone (Rivera et al., 1999; Benagiano et al., 2006). This in turn works to prevent follicular development and subsequent hormonal shifts associated with ovulation (Frye, 2006). Women's levels of circulating testosterone are also suppressed during hormonal contraceptive use (e.g., Alexander et al., 1990).

3.1.1. Preferences and mate choice

Because of the hormonal differences between users and non-users of hormonal contraception, we might expect hormonal contraceptive use to impact on cyclic shifts seen in preferences noted earlier and even have general effects on preferences. Indeed, several studies of cycle effects on preferences have demonstrated a lack of (or weaker) shifts in women using hormonal contraceptives (Penton-Voak et al., 1999; Alvergne and Lummaa, 2010). Much research on the effects of the pill on preferences has generally examined only between-group comparisons, comparing different groups of pill users and non-users. This means that there may exist other differences between users and non-users that account for variation in preference beyond hormonal changes associated with the pill (Roberts et al., 2008), such as differences in sexual behavior (Little et al., 2002). As noted earlier, the menstrual cycle is associated with various shifts in visual preferences. Given that these preference shifts are likely governed by natural variation in hormone levels (e.g., Welling et al., 2007; Jones et al., 2008; Little et al., 2008), it is perhaps unsurprising that many such effects are absent in those reporting hormonal contraceptive use (Penton-Voak et al., 1999; Johnston et al., 2001; Jones et al., 2005b; Pawłowski and Jasienska, 2005; Puts, 2005, 2006; Haselton and Miller, 2006; Gangestad et al., 2007; Little et al., 2007a,b; Rosen and Lopez, 2009). More recently, one study has examined within-participant changes in preferences for facial masculinity demonstrating that women who initiate pill use decrease their preferences for face masculinity compared to controls (Little et al., 2013). Further, this study demonstrated a potential downstream effect of this shift in preferences whereby women who met their partner while using the pill had less masculine partners than women who met their partner while not using the pill (Little et al., 2013).

3.1.2. Expression and recognition

In contrast to preferences, there have been few studies of oral contraceptive use and expression and face recognition. One study, examining neural responses to faces, has demonstrated more brain activation to faces in the right fusiform face area, an area of the brain proposed to be relatively specialized for face perception (Gauthier and Tarr, 1997; Kanwisher et al., 1997), in women taking oral contraceptives than non-users (Marecková et al., in press). This study suggests enhanced processing of social cues in women taking oral contraceptive. Of course a general interest in faces is somewhat unqualified and we do not know from this study if this simply reflects interest in same-sex or opposite-sex faces. Intriguingly, this study also demonstrated that activation in oral contraception users was most similar to non-users at mid-cycle, when estrogen is high, than at menstruation when estrogen and progesterone is lower, suggesting similarities between oral contraception action and the high fertility phase of the cycle (Marecková et al., in press), a finding at odds with other results in the face preference domain.

3.1.3. Cerebral/perceptual asymmetries and visual–spatial abilities

Studies have generally supported the notion that hormones administered in oral contraceptives impact on both perceptual asymmetries and visual–spatial abilities. For example, comparing oral contraception users to non-users within-participant on a visual line-bisection, users demonstrate less lateralization than non-users suggesting greater interhemispheric interaction (Cicinelli et al., 2011). Some studies have also demonstrated effects of oral contractive on mental rotation abilities, comparing oral contraceptive users and non-users and demonstrating that mental rotation reaction times were longer in users than non-users (Griksiene and Ruksenas, 2011).

3.2. Other studies of steroid hormone administration in humans

Studies of the experimental administration of sex hormones and the subsequent impact on visual preferences or social perception are relatively rare in humans. Although not assessing visual stimuli, relevant to mate-choice and preferences, administration of testosterone has been associated with changes in sex drive and desire. For example, testosterone administration has been found to increase sexual desire in postmenopausal hysterectomized women (El-Hage et al., 2007). This effect is also seen in men, with men showing increases in sex drive/interest in sex with testosterone administration (Bancroft, 2005). Administration of testosterone has also been found to change men's heart rate response to angry faces, potentially reflecting a response reflecting increased potential for an aggressive response from the viewer (van Honk, et al., 2001). More commonly, experiments in humans have generally addressed sex differences in function rather than reaction to visual social stimuli. For example, administration of testosterone to women can improve visual–spatial ability (Vangoozen et al., 1995) and a single administration can increase mental rotation abilities (Aleman et al., 2004). Similarly, testosterone administration also enhances spatial abilities in elderly men (Janowsky et al., 1994) and is associated with better spatial memory and spatial ability (Cherrier et al., 2001). These effects, however, have not been seen for hemispheric asymmetries in visual tasks. For example, hormone replacement therapy (HRT) in post-menopausal women has been found to not influence lateralization measures associated with emotion processing and visual–spatial attention (Bourne and Gray, 2009). Similarly, another study, while finding that HRT impacted on lateralization on a language task, found no evidence for HRT to effect lateralization on a face task (Bayer and Erdmann, 2008). These later studies are then suggestive that hormone administration may impact visual–spatial skills but not hemispheric lateralization, which is puzzling given evidence for shifts in lateralization according to cycle phase and oral contraception use. One further study on emotion processing may help explain why the effects of administering hormones may be reliant on some organizational effects of hormones on the brain. There is evidence that administering sex hormones changes reactions to visual social stimuli, although the effect appears to interact with early testosterone exposure. For example, using the reading the mind in the eyes task, a measure of empathy and emotion sensitivity, van Honka and colleagues have demonstrated that a single administration of testosterone to women can impair abilities to infer emotions, intentions, and other mental states from the eye region of faces (van Honka et al., 2011). Further, this effect was only seen in women with more masculine 2D:4D ratios (van Honka et al., 2011), demonstrating that testosterone has short-term effects on visual processing of social stimuli and also that this may interact with organizational effects of testosterone early in life. Indeed, we could generally expect that hormonal influences on visual perception reflect interactions between organizational and activational effects (Arnold, 2009). It should be noted, however, that

participants were oral-contraceptive users and so it would be useful to establish if the findings generalize to women with natural hormonal profiles. An interesting case occurs in women who undergo gender reassignment involving the administering of testosterone. One study examining the cognitive abilities of female-to-male transsexuals with 6 months of testosterone treatment showed improved performance on a visual memory task over this time (Gomez-Gil et al., 2009).

4. Non-human animal comparisons and the mechanism of action for steroid hormones on processing visual stimuli

Given the evidence in previous sections that sex hormones impact on visual processing, there is a question of how steroid sex hormones impact on visual processing. A full discussion is beyond the scope of this review but in this section I briefly discuss comparisons with research on non-human animals and also highlight two types of mechanism: how sex hormones may impact on the brain and how they may relate to motivation.

4.1. Non-human animal comparisons

Having reviewed varied evidence for the association between sex hormones and visual perception in humans, it is worth briefly examining some similarities seen in studies of non-human animals. Often, the effects of hormones can be measured more directly, a more detailed analysis of actual changes in the brain can be conducted, and more controlled administration of hormones can take place in studies of non-human animals.

In terms of general sex-typical behavior, non-human animal studies have revealed that administering sex hormones during the time that sexual differentiation of the brain occurs can impact on behavior in such a way that the animal exhibits sexual behavior more typical of the opposite-sex (Goy and McEwen, 1980). Likewise, studies of non-human animals demonstrate clear effects of sex hormones such as testosterone on sexual behavior. For example, androgens are involved in the maintenance of sexual arousal in rats and blocking of androgen receptors in the amygdala results in lower sexual arousal in males as measured by the instances of erection when presented with females (Bialy et al., 2011). Analogous effects are seen in male fish whereby injections of testosterone increase approach responses towards females, but not males (Lord et al., 2009). Further, examining preferences for faces in monkeys, during the peri-ovulatory phase female rhesus macaques looked longer at the faces of male conspecifics than at female faces, suggestive that female macaques have heightened preferences for male visual stimuli when most likely to become pregnant (Lacreuse et al., 2007), an effect similar to one seen in human females.

Studies on how sex hormones influence recognition and particularly expression processing, are more limited in non-human animals. There is, however, evidence that sex hormones have a variety of effects on reactions to social stimuli in non-human animals (Eisenegger et al., 2011). For example, social recognition in female rats appears to be associated with hormonal profile. Examining the recognition of a juvenile male by female rats at three stages, after ovariectomy, after estradiol treatment, and after termination of estradiol treatment, only females tested during the estradiol treatment demonstrated recognition of the male on second encounter indicating an important role of estradiol in recognition in female rats (Hlinak, 1993). Sex hormones are also related to the regulation of factors such as oxytocin which in turn are related to social learning, learning from conspecifics (see Choleris et al., 2009for review). In terms of attention to emotional stimuli, rhesus macaque monkeys who were administered with testosterone spent a longer time watching video clips containing fights between unfamiliar conspecifics than they did at base line, suggesting an increased interest in visual cues to conflict at higher testosterone and potentially tied to processing of social threat (Lacreuse et al., 2010).

Several specific effects are observed in non-human species that are related to findings seen in humans for spatial ability. For example, pregnancy appears to influence spatial abilities in rats as in humans, with pregnant rats performing better on maze tasks than non-pregnant rats and with lower levels of estradiol/higher levels of progesterone positively predicting better performance (Galea et al., 2000). Similarly, there appears to be cycle effects on spatial learning in rat with females in estrous performing worse than non-estrous females (Frye, 1995). As noted earlier, there are changes across the cycle in humans in terms of spatial ability. Female rhesus macaques perform better on spatial task in the follicular compared to the peri-ovulatory phase of the menstrual cycle, suggesting that when estradiol levels are higher, visual–spatial abilities are impaired (Lacreuse et al., 2001). Sex difference in spatial ability in rats may also reflect organizational effects. Male and female rats show anatomical sex differences in the hippocampus, a brain region which is related to spatial ability, and when females are treated neonatally with testosterone this results in the growth of a more male-like hippocampus as well as better performance on spatial tasks compared to untreated females (Roof and Havens, 1992). Additionally, as in humans, where puberty represents time when at least preferences are seen to change, in rats there are sex differences in cell growth in sexually dimorphic regions of the brain while preventing the production of gonadal hormones prepuberty prevents such sex differences in growth (Ahmed et al., 2008), highlighting a mechanism by which behavior may change in puberty in humans according to sex hormone concentrations.

4.2. Changes in the brain

While sex hormones may cause structural organization effects on the brain during development, the question arises about how activational effects of sex hormones impact on visual processing. It is possible that levels of sex hormones influence cortical networks associated with specific cognitive functions. One study, for example, has examined 3D mental rotation in humans and brain function using fMRI comparing follicular and mid-luteal phases of the cycle and found that brain activation in frontal and parietal areas was correlated with estrogen and that activation during the follicular phase was correlated with testosterone (Schoening et al., 2007). In non-human animals, increasing sex hormone concentrations have been associated with increased activity in neural activity in the amygdala (Goldstein et al., 2005; Jasnow et al., 2006) and the prefrontal cortex (Keenan et al., 2001), as well changing aspects of neurotransmitter systems such as the serotonin system (Rubinow et al., 1998). These relationships are suggestive that neuronal activity can be directly related to hormone concentrations. Such relationships may come about via sex hormones changing neuronal activity in specific brain regions by acting on the chemical properties and structural aspects of cells. In the case of estrogen, for example, estrogens can change the neurochemical and physical structures of cells (McEwen et al., 1997) with estrus hormones in the female rat being shown to remodel hippocampal cells (Gould et al., 1990) and change dendritic spine density in the amygdala and hippocampus (Kinsley and Lambert, 2006). These short-term changes in certain brain regions may underpin changing visual processing according to hormonal profiles.

4.3. Motivation

Motivation is not a distinct mechanism from changes in the brain, as the mechanism for motivational change likely lies in such changes. Motivation is, however, a different level of explanation to account for general differences in visual processing. There are, for

example, general effects of sex hormones on mood with positive affect being associated with high estrogen and progesterone levels (Wang and Johnston, 1993). Using fMRI, one study has shown that brain activity differs in the ovulatory phase of the menstrual cycle compared to other phases in responses to erotic films (Zhu et al., 2010). This links sex hormone profile to the processing of sexual arousal in the brain. (Zhu et al., 2010) and it is possible that differences in sexual arousal mediate some of the responses I have discussed concerning attraction to particular types of men during the follicular phase of the cycle. For example, estrogens may generally promote the processing of sexual stimuli and so we might predict that many traits associated with sexual attraction, such as face and body masculinity and symmetry may be relatively more rewarding during this time. Such motivational explanations are likely most applicable to studies of preferences and emotion processing.

5. Summary and conclusions

In this article, I have reviewed the evidence that steroid sex hormones impact on visual processing. Given sex-differences in certain arenas, I highlighted the best studied topics in sex hormone effects: 1. Preference and mate choice, 2. Emotion and recognition, and 3. Cerebral/perceptual asymmetries and visual–spatial abilities. There are various methods to address the impact of sex hormones in these areas, but it is clear that researchers have focused differentially on type of evidence and topic. For example, there is much research on preferences varying across women's menstrual cycle, presumably because researchers in this area are particularly interested in the adaptive value of mate preferences at peak fertility. In contrast, research on hormone administration in post-menopausal women is more focused on more mechanistic sex differences in lateralization and visual–spatial abilities, presumably because preference and mate-choice are of less interest in this group. Similarly, the majority of studies discussed deal with activational and not organizational effects. This is because in humans, such studies are difficult. One exception is testosterone and this is because there is physical measure (2D:4D) that can be used as a proxy for prenatal testosterone exposure. This means that we have much more evidence for the activational impact of most sex hormones than we do for organizational effects. It should be noted, however, that 2D:4D is only an indirect measure of testosterone's organizational effects and is likely noisy. Evidence for early effects can also be seen, however, in various conditions that are characterized by deviations from normal androgen exposure, such as those shown in CAH and Turner syndrome.

Across type of studies and topics of studies, many studies have demonstrated significant associations or effects of steroid sex hormones on visual processing. However, the story is by no means clear-cut as there a number of inconsistencies in the direction of effects and several studies do not show effects that are seen in other studies. Perhaps the best evidence comes from experimental administration of hormones and in these studies the directions of effects appear most consistent. This highlights some of the problems with a reliance on indirect estimations of the impact of steroid sex hormones. Firstly, hormones co-vary, and so such studies are often tapping multiple hormones. Secondly, there are many contextual factors that appear to influence at least the social reactions to visual stimuli that are proposed to be related to sex hormones. For example, in examining cyclic shifts in preferences three studies have shown no evidence for cyclic variations in women's preferences for masculine versus feminine male faces (Peters et al., 2009; Harris, 2011; Roney et al., 2011), but these studies addressed general attractiveness judgments and did not distinguish between short- and long-tem contexts. These null effects may have occurred because of larger cyclic shifts for short-term judgments and a general absence of effects for long-term judgments (Little et al., 2007a,b; Gangestad and Thornhill, 2008). Thirdly, there may be interactions between activational and organizational effects that obscure effects in studies where both are not addressed. For example, although evidence suggests that activational effects of testosterone on spatial abilities may be limited, one study has suggested, at least for social judgements, there is an interaction between 2D:4D and current levels of testosterone (van Honka et al., 2011). This is suggestive that perhaps inconsistent results may result from specific sampling strategies and the interaction between organizational and activational effects is important to consider. Fourthly, different tasks are often used between studies which may be more or less sensitive to detect certain effects. For example, sex differences in visual–spatial ability appear to be most consistently seen in mental rotation tasks (Voyer et al., 1995) and so studies using these tasks may be most sensitive to detecting associations with sex hormones, although the limited activational effects seen in some studies (Puts et al., 2010) may point to stronger organizational effects. As another example, research on facial attractiveness has used both real and computer graphic manipulated faces but studies on cyclic shifts have generally used manipulated faces. Computer graphic studies which manipulate masculinity have tended to suggest that feminine male faces are attractive while studies of real faces using rated masculinity have usually demonstrated preferences for masculinity (see Rhodes, 2006). This has led Rhodes (2006) to suggest that real faces may reveal a truer picture of women's preferences than computer manipulated images. Following this claim, in one study presenting a null results for cycle shift for both perceived masculinity and symmetry in unmanipulated images, researchers have suggested that cyclic shifts in women's masculinity preferences may be an artifact of the computer graphic methods (Peters et al., 2009). Such a claim is, however, difficult to reconcile with earlier findings from a study that demonstrated cyclic shifts in women's preferences for masculinity in real (i.e., unmanipulated) face images (Little et al., 2008). This claim is also problematic given the converging evidence for cyclic shifts in women's preferences for masculinity from studies that have assessed preferences for masculinity in other domains (e.g., behavior, personality descriptions, body odor). Indeed, we might expect other effects to be seen across different stimuli types. For example, hormonal contraception also has the potential to change preferences across several different domains (Wedekind et al., 1995; Alvergne and Lummaa, 2010) and preferences for masculinity in male vocal traits also appear to be weaker in pill users than non-users (Feinberg et al., 2008) while other research has shown pill-use influences preferences for the odor of genetically similar and dissimilar men (Wedekind et al., 1995; Roberts et al., 2008).

Lastly, there are substantial differences in methods of hormone measurement between studies. For example, some studies of the cycle rely on self-report to classify women while others measure hormones in women. The latter should be more reliable than the former. Likewise, studies of pregnancy and other factors may or may not measure hormones, with those that measure hormones likely to generate more reliable results. Having noted that this may be problematic for comparisons across studies, it seems unlikely that noise would bias studies to find positive results and so we should not discount studies using more indirect estimation of hormone levels as significant effects appear less likely to be found under such conditions. Of course, even among studies that rely on self-reported stages of the cycle, for example, studies differ in how they classify women as high and low conception risk, and so compare women of different hormonal profile. In a related way, studies vary in how they measure hormones (e.g. saliva versus blood measures) and in studies administrating varying hormones the dose administered may be an important variable.

In conclusion, this review highlights that many studies demonstrate, both indirectly and directly, that sex steroids are associated

with visual processing. The review, however, also highlights that findings are sometimes inconsistent and that differences in methodology make strong comparisons between studies difficult. We generally know more about activational than organizational effects of sex hormones on visual processing in humans. Overall, future research can usefully focus on comparing different methods and tests to address the reliability of the effects of sex hormone on visual processing in humans.

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