Contrast sensitivity and emotion recognition across the menstrual cycle

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> "All the variety, all the charm, all the beauty of life is made up of light and shadow."
>
> — Leo Tolstoy

Abstract

Findings within the current literature demonstrate that certain aspects of female perception may be influenced by fluctuation in reproductive hormones associated with the menstrual cycle. Cyclic shifts in female mate preferences, facial recognition and low-level visual processing have been attributed to such hormonal variations. The cycle shift hypothesis posits that such systematic shifts in female perception provide an evolutionarily valuable function, selected by nature to harness females' inclusive fitness. However, there are a number of limitations facing this evolutionary account, one of which is the lack of a mechanistic explanation of such changes in female perception. In a novel approach to investigating candidate mechanisms of this cyclic variation, experiment 1 measured contrast sensitivity across the menstrual cycles of naturally cycling women and women using combined-oral contraception, and also in males. Findings showed no difference in contrast sensitivity between male and female participants, where no differences were observed across the menstrual cycles in either female group. The second experiment was an extension of this, based on a growing body of evidence suggesting that higher-level perceptual processes such as facial emotion perception are driven wholly by low-level processing of basic visual properties. The second experiment investigates the role of low-level visual processing in emotion detection both between and within men and women. It also measures these low-level processes between ovulating and menstruating women as an investigation of the role that variation in female fertility may play in such basic processes. Findings from experiment 2 were consistent with current evidence of low-level visual processes accounting for aspects of facial emotion perception, however revealed no differences between or within sexes. Together these results are discussed within context to current evolutionary theories of facial processing in women.

Chapter 1: Introduction

1.1 Sex differences in visual perception

This section provides a basic overview of the proposed primary sex differences in perception such as the male advantage in spatial perception and female advantage in face perception. These shall be discussed in relation to accounts of their associated biological mechanisms and evolutionarily adaptive functions. Insight into the cognitive mechanisms and processes that govern these sex differences will provide a basic understanding of some of the unique characteristics that are purportedly proposed for female perception. These characteristics, such as advantages in face perception, form a basis for understating the aspects of female perception in which this thesis investigates. This includes cyclic variation in aspects of female perception occurring relative to hormonal fluctuations associated with the menstrual cycle.

Evidence of sex differences in perceptual abilities

Spatial perception

A frequently reported finding among studies of sex differences in cognitive abilities is a male advantage for visuo-spatial processing (see Voyer, Voyer & Bryden, 1995 for review). Mental rotation tasks are a commonly used group of measures for investigating perceptual spatial performance. A standard mental rotation task involves a target black and white drawing of a three dimensional shape, which is presented against a uniform background and from a particular angle or perspective. Participants must select from a series of novel shapes that that matches a given target, regardless of the perspective that this novel shape is presented form (see Figure 1)(Vandenberg & Kuse, 1978). Tasks such as these rely upon observers' spatial skills; the ability to construct a mental representation of the prototypical shapes and to spatially manipulate these in an attempt to identify those that match a target shape (Linn & Petersen, 1986). One body of research claims to consistently demonstrate that men tend to outperform women on spatial tasks such as these. This often appears as a general consensus, where a sex difference in spatial performance has been reported as males outperforming females by around 15%, where 75% of male scores will exceed the average female score (Collins & Kimura, 1997; Voyer, Voyer & Bryden, 1995; Silvermann & Eals 1992). A meta-analysis of these sex differences in visuo-spatial performance suggested that for tasks of spatial perception and mental rotation, the occurrence of better male performance is a robust and consistent finding across studies spanning several decades (Linn & Petersen, 1986; Voyer, Voyer & Bryden, 1995). Findings such as these together postulate the notion that males, in general, are more likely to outperform women on tasks that require the mental visualisation and spatial manipulation of objects (Linn & Petersen, 1986; Voyer, Voyer & Bryden, 1995; Herlitz, Nordstrom & Airaksinen, 1999; Herlitz, Nilsson & Backman, 1997; Lewin, Wolgers & Herlitz, 2001). This male advantage for spatial ability has often been attributed to a proposed male propensity for gestalt processing (Hugdahl, Thomsen & Ersland, 2006; Thomsen et al., 2000; Jordan et al., 2002); a perceptual process that enables the mental representation and transformation of an object in a way that is analogous to the physical equivalent (Shepard & Cooper, 1986; Shepard & Metzler, 1971). However, it is important to acknowledge that despite such assumptions of a consistent male-advantage for visuo-spatial processing, further research argues that this effect is not necessarily robust (see Voyer, Voyer & Bryden, 1995 for review). In such cases, the size of the sex difference reported in studies of spatial perception is argued to be a very small and inconsistent finding (Caplan, MacPherson & Tobin, 1985; Hyde, 1981). It has instead been argued that these sex differences may account for only a very small percentage of variance in the general population (1-5%)(Hyde, 1981), where it could be that they are more likely accounted for by socially constructed confounds such as gender differences in enrolment to mathematics courses (Caplan, MacPherson & Tobin, 1985; Jacklin, 1979; Fennema & Sherman, 1977). Additional factors such as discrepancies in the definition of spatial ability (Voyer, Voyer & Bryden, 1995) and the lack of published research reporting no sex differences (otherwise recognised as the "file drawer problem") may also exaggerate the appearance of such sex differences existing in spatial processing (Voyer, Voyer & Bryden, 1995; Caplan, Macpherson & Tobin, 1985; Rosenthal, 1979). However, it is equally important to consider that support for a male advantage in spatial cognition comes from cross cultural and non-human animal studies. Here, the effect has been replicated by studies conducted in Japan (Silverman, Philips & Silverman, 1999), India, South Africa and Australia (Porteus, 1965), and in studies of other mammalian species including non-human primates (Roof & Havens, 1992; Lacreuse et al., 1999; Jones, Braithwaite & Healy, 2003). Therefore, for the purpose of the present research, it is important to recognise that the consensus on an association between sex and visuo-spatial processing is somewhat equivocal. This lack of clarity on the matter demonstrates a necessity for further investigation of phenomena that may or may not be more subtle and complex than current views suggest.

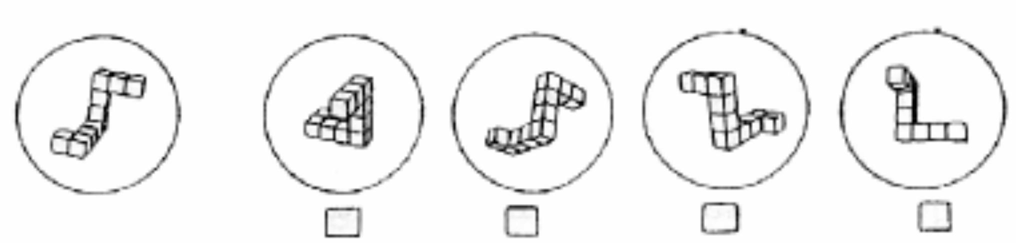

Figure 1. A sample from the Vandenberg Mental Rotations test (Vandenberg & Kuse, 1978). Here, the target shape appears next to 4 novel shapes, where the task is to select from these that which is the same as the target (correct shapes are 1 and 3, from left).

Face Perception

Conversely, findings from research concerned with face perception reveal that females appear to display a propensity greater than average for facial processing (Kanwisher, McDermott & Chun, 1997). An extensive study measuring differences in male and female episodic memory performance found that face recognition in women may operate differently to that in men. Participants were presented with a series of photographs of faces that were composed of either a whole face, or consisted of featural information only (such as eyes, mouth, nose). These were presented for a short (1 second) or long (3 second) period of time, and later shown again to the participant amidst an array of novel faces. When asked to identify faces that had previously been seen, women were more likely to recognise familiar faces regardless of both their presentation time or whether the face was presented with whole or only featural information. Interestingly, while both men's and women's recognition of male faces was similar, overall greater performance in women was accounted for by their better recognition of other female faces. This greater female tendency for recognising same sex faces was not associated with their performance on other tasks of episodic memory. While men's recognition of faces was related to their scores of verbal ability, this measure was not a reliable predictor of women's recognition of faces. The absence of a relationship between female's recognition of faces and verbal ability suggest that for women, face recognition may operate differently from other facets of episodic memory (Lewin & Hertliz, 2002). Similar studies also investigating the female advantage in face perception have generated similar results. Women's facial recognition of both Swedish and Bangladeshi faces belonging to adults and children was significantly better than that of male participants'. Facial recognition in female participants was significantly greater compared to males' for all types of faces, regardless of the age, sex or ethnicity of the faces. These results suggest that face perception in women is better overall in women, independent of the ethnicity, age or sex of the face presented (Rehnman & Herlitz, 2007). Similarly, when presented with an array of faces belonging to young children, women were more likely to successfully remember the associated names belonging to these faces than were men (Herlitz, Nilsson & Backman, 1997; Yonker et al., 2003), and also more likely to notice subtle gradations in the structure of faces belonging to babies (Sprengelmeyer et al., 2009). A study measuring recognition of an array of familiar and novel patterns also revealed that women were more likely to be better at recognising facial stimuli (Goldstein & Chance, 1970). This female advantage for face perception appears consistent across findings, and gains further support from research suggesting that it has a long developmental trajectory. Here, a female advantage in face perception appears to be present at some of the earliest stages of development. From as early as twenty-four hours after birth, female neonates dedicate more attention to facial stimuli (Connellan et al., 2000), and this interest persists into later childhood (Rehnman & Herlitz, 2006). Similarly, recognition of faces of both Swedish and Bangladeshi adults and children is greater in 9 year old girls compared to their male counterparts (Rehnman & Herlitz, 2006). However, findings that demonstrate a female advantage for perceiving faces have often been attributed not to an overall advantage for recognising all faces, but to a female bias for recognising same-sex (other female) faces. A consistent finding on tests of facial recognition is that female participants are more likely to recognise faces of other females, as opposed to better overall recognition for faces regardless of sex (Lewin & Herlitz, 2002; Rehnman & Herlitz, 2006; McKelvis, 1987; McKelvie, Standing, St. Jean & Law, 1993; Cross, 1971; Shaw & Skolnick, 1994; Shaw & Skolnick, 1999). Interpretations of this same-sex recognition bias in females refer to the influence of experiential factors on such aspects of face perception. These interpretations posit that women consistently encounter and experience female faces as a result of environmental factors such as female-directed media exposure (Wright & Sladden, 2003) and a greater female interest in socialising (Kaplan, 1978). This familiarity with the female face creates a tendency for recognising such facial cues, allowing for better recognition of them by female participants (McKelvie, 1981; Wright & Sladden, 2003). However, these findings do not necessarily invalidate evolutionarily functional accounts of this female advantage (Wright & Sladden, 2003). The extent to which these theories necessitate that females may be more susceptible to such experiential factors shall be discussed later in this chapter susceptibility.

Mechanisms of sex differences in perception

Neural correlates of sex differences

Studies investigating the neuro-circuitry underpinning spatial abilities have revealed sex differences in cortical activation and processing strategies for solving visuo-spatial tasks. Independently of the above findings of a male superiority in spatial abilities, there are also robust differences in the brain regions and processing channels that men and women rely on for spatial perception. In a recent neuroimaging study, where performance on tasks of mental rotation was equal, functional magnetic resonance imaging (fMRI) revealed different patterns of cortical activation across different regions in the brains of male and female participants (Jordan et al., 2002). While these findings replicated a consistently found activation of the parietal region of the brain, sex differences in activations of other regions were also found. Experimental and clinical studies show that the parietal cortex plays an important role in spatial processing (Vallar & Perani, 1986; Mesulam, 1999; Corbetta et al., 1995; Yantis et al., 2002; De Schotten et al., 2005; Anderson, 1985; Jordan et al., 2002), and this region is considered to be one of the primary brain centres for establishing spatial awareness in relation to ones body (Patestas & Gartner, 2013). This ability is paramount to interaction with, and manipulation of the physical world (Robinson, 1973). It is therefore unsurprising that both sexes display significant activation in these regions during tasks of spatial perception. However, sex-specific activation patterns showed that for women, the inferior parietal cortex and temporal regions, such as the intrapartietal sulcus and inferior temporal gyrus, received greater activation during the mental rotation task. Women also showed a small, but present activation in frontal regions of the brain, such as the inferior frontal gyrus. Activations in these frontal and temporal regions were not observed in the brains of male participants. Instead, males displayed activation in the areas connecting regions of the brain associated with the parietal and occipital lobes. This included greater activation in areas such as the right parieto occipital sulcus (Jordan et al., 2002). These findings of different male and female activation patterns of parietal-occipital and frontal-temporal regions (respectively) are consistently found. Often, they are considered to show evidence of a disparity in male-female processing strategies during mental rotation tasks; reflecting an inherent sex bias for accessing different neuro-circuitry during spatial perception (Jordan et al., 2002; Hugdahl, Thomsen & Ersland, 2006; Weiss, 2003).

These sex differences in processing strategies reveal some interesting differences in the functionality of male and female brains. Sex-specific preferences for different information processing streams have been suggested as some of the primary mechanisms underpinning sex differences in perception (Jordan et al, 2002; Hugdahl, Thomsen & Ersland, 2006). Males are considered to have a distinct bias for processing certain visual information via the dorsal stream; a route associated with an object's "where" information such as spatial location and motion. Information here is processed rapidly, with little amounts required to undergo higher-level cognitive processing (Deubel, Schneider & Paprotta, 1998). A male bias for dorsal processing may be the underlying process that governs their predisposition for gestalt analysis of a visual scene. This way, identifying spatial properties of an object in relation to one another occurs in a very quick, and holistic manner. Equally, a female bias for processing visual information via the ventral processing stream will likely benefit from regions implicated in visual identification and recognition. Here, the visual properties of an object are analysed in a more detailed manner (Jordan et al., 2002; Hugdahl, Thomsen & Ersland, 2006). An example of this is the way in which the ventral stream processes the high-frequency properties of an object; information that translates to the finer details of a visual scene (Thomsen et al., 2000; Jordan et al., 2002). Dedication to processing these intricate visual characteristics naturally requires a degree of access to higher-level processing, and establishes cues that will aid object identification and recognition. A female bias for ventral processing during spatial tasks is demonstrated by greater activation in identification regions of the brain located in frontal and temporal lobes (Jordan et al., 2002; Cabeza & Nyberg, 2000; Carpenter et al., 1999). Findings from neuroimaging studies such as these suggest a female preference for accessing neuroanatomy that underpins higher perceptual processes such as visual identification and memory. This female bias for ventral processing may account for better female performance on cognitive tasks that require a capacity for visual identification and recognition. For example, women have been shown to outperform men on visual memory tests (Ghi et al., 1999), readiness to recognise and identify objects (Neave et al., 2005), memory of object identity (Levy, Frick & Astur 2005) and the ability to discriminate among an array of colour shades (Abramov, 2012; McIntyre, 2002; Pardo, Perez & Suero, 2007).

Further evidence of such sex differences for visual processing comes from studies concerned with lateralisation of information processing. These studies investigate the extent to which a particular cognitive process is a specialised function that is confined to one particular hemisphere of the brain. Studies such as these provide insight into the way that each half of the brain is implicated in certain cognitive functioning. While performing tasks of mental rotation, male participants display a strong hemispheric dominance, where this kind of visuo-spatial processing takes place primarily in the right parietal regions of the brain. Females, however, demonstrate bilateral visuo-spatial processing as they adopt the use of both left and right parietal regions during mental rotation tasks (Johnson, McKenzie & Hamm, 2002; Rasmjou, Hausmann & Güntürkün, 1999). These results further suggest that for women, spatial perception may be more globally organised in the brain. Studies of lateralisation processing of facial stimuli have also revealed similar sex differences suggesting that men and women rely differently on each hemisphere during face perception. When presented with a range of positive facial emotions, males demonstrate stronger lateralisation for this facial processing than females (Bourne, 2004; Bourne & Todd, 2004; Rasmjou, Hausmann & Güntürkün, 1999). This means that in general males' processing of facial information is dominated by a single hemisphere (particularly the right hemisphere) (Bourne, 2005; Proverbio et al., 2010). Although female participants also rely on this same right hemisphere processing, they show bilaterally distributed facial processing where their perception of faces relies on inputs from both hemispheres of the brain (Bourne, 2005; Proverbio et al., 2010). It has been proposed that bilateral facial processing adopts separate and unique inputs from each hemisphere of the brain, such that each hemisphere plays an important yet different role in face perception. For example, while the right hemisphere is considered to be the primary locus for configural processing, the left hemisphere is responsible for processing featural information (Bourne, 2005; Damasio, Damasio & Van Hoesen, 1982). One interpretation of this is that female bilateralisation in face processing means that women possess greater access to mechanisms of face perception that are present in both hemispheres. Thus, women may capitalise on processing input from both configural and featural processing regions of the brain; allowing them to reap the benefits from each hemisphere's processing input (Bourne, 2005). Such a combined input from both hemispheres may account for the female advantage in face perception. Conversely, men's right hemispheric dominance is paralleled to configural processing, and may underpin the male advantage for gestalt processing.

Apparent sex differences in processing strategies suggest that men and women rely to different degrees on different neural networks for processing visual information. These sex-specific preferences for different processing streams may lay the foundation from which male and female differences in perception operate. Specifically, such differences may account for a general female capacity for a more integrated (across both hemispheres) and rich integration of visual information. This unique female preference for such processes allows stronger communication between identification regions of the brain that together enable a rich representation of a visual stimulus. These uniquely female cognitive functions may be the precursory stages of processing that underpins an advantage for perceiving faces.

Influence of reproductive hormones

Many of the attempts to establish the biological mechanisms that underpin these sex differences refer to the role of hormonal influences. Many studies have demonstrated that sex-specific steroids may be important factors guiding sex differences in certain cognitive abilities, and also variation in such abilities that occur within a sex. Reproductive hormones such as oestrogen have been shown to have a significant impact on spatial cognition. While oestrogen is present in both sexes, its concentration is far greater in the female organism, and is one of the predominant reproductive hormones modulating the process of ovulation (Thornhill & Gangestad, 2008). A cardinal feature of oestrogen is its sudden peak during mid-cycle, marking the point at which ovulation has commenced. During other phases of the menstrual cycle it remains lower, and during menstruation oestrogen levels are at their lowest (Wilcox et al., 2001), see section 3 for elaboration. Interestingly, an inhibitory effect of oestrogen has been found for spatial perception in females where high oestrogen levels are associated with poorer spatial performance. For example, female performance on spatial tests such as mental rotation tasks are best during menstruation, such that when oestrogen levels are at their lowest, women's spatial perception is improved (Sherry & Hampson, 1997; Silverman & Philips, 1993; Hampson & Kimura, 1988; Postma et al., 1999). In contrast, the ovulatory peak in oestrogen is accompanied by the poorest performance, with lowest scores occurring during ovulation and the mid-luteal phase (Hausmann et al., 2000; Phillips & Silverman, 1997; Silverman & Phillips, 1993; Moody, 1997; Hampson, 1990). Importantly, these cyclical shifts in spatial ability are not found in oral contraceptive-users whose ovulation is inhibited by synthetic hormones; evidence that further implicates oestrogen as a hormonal mechanism for influencing females' capacity for spatial perception (Moody, 1997). During periods of low oestrogen levels, females' spatial performance becomes similar to that of males, where the general male advantage for spatial tasks outlined earlier subsequently diminishes. For example, during menstruation (characterised by low oestrogen levels), previously found sex differences in male and female performance on spatial tests lessens and in some cases vanishes (McCormick & Teillon, 2001; Moody, 1997). It should be noted and acknowledged, however, that some findings do not identify such a relationship between low oestrogen levels and better spatial performance (Epting & Overman, 1998; Rosenberg & Park, 2002), where it has also been suggested that this relationship is found only for 3 dimensional tasks of mental rotation (Hausmann et al., 2000). Moreover, similar investigations of hormonal influences upon spatial perception have shown a similar, but positive relationship between testosterone and spatial ability. One consistently found effect is the curvilinear relationship between testosterone and spatial ability. Here, an optimal level of testosterone is associated with the best male performance on spatial tasks. Testosterone levels above or below this optimal amount of the hormone are associated with poorer spatial performance (Gouchie & Kimura, 1991; Moffat & Hampson, 1996). This facilitatory effect of testosterone is not restricted to males, but is positively associated with better spatial cognition in both sexes. Male participants receiving an exogenous administration of testosterone (raising their baseline levels of the hormone up to 150%) demonstrated that the artificial increase in testosterone was accompanied by enhanced spatial cognition (Janowsky, Oviatt & Orwoll, 1994). In a similar study, female rats received administration of testosterone to hippocampal regions during prenatal development. The result from postnatal tests revealed that spatial performance in matured female rats was synonymous to that of their male counterparts (Roof & Havens, 1992).

In studies of face perception, a positive association is demonstrated between oestrogen levels and female participants' ability to recognise faces. When oestrogen levels are higher, women are more likely to be better at recognising faces. Interestingly, this correlation is not true for male participants, or for predicting women's performance on other tests of episodic memory, suggesting that face recognition in women may be uniquely sensitive to levels of oestrogen (Yonker et al., 2003). While the effect oestrogen cannot entirely account for the female advantage in face recognition, similar studies concerned with hormonal influences in face perception yield similar evidence of a sometimes indirect effect of oestrogen. For example, studies of the relationship between oestrogen and the female hippocampus have revealed an oestrogen effect upon the structure and function of this brain region that is valuable in facial processing (McEwen et al., 1997; Woolley et al., 1997). Here, oestrogen has been shown to facilitate hippocampal synaptic connections in female rats, where this effect is enhanced when oestrogen levels are higher (McEwen et al., 1997; Desmond & Levy, 1998). An example of this effect occurs during ovulation, where the mid-cycle peak in oestrogen is accompanied by greater synaptic numbers in this region of the brain (Desmond & Levy, 1998). As the hippocampus is implicated in both episodic memory and spatial perception (Nyberg et al., 1996; Burgess, Maguire & O'Keefe, 2002), and as face perception is considered an extension of episodic memory, it seems a logical inference that effects of sex hormones in hippocampal regions may subsequently also produce measurable effects in face perception. Supporting evidence of this notion comes from The Baltimore Longitudinal Study of Aging. This study in particular has provided a wealth of evidence regarding the effects that natural changes in oestrogen have upon cognitive functioning across the female life span. These findings demonstrate the role that oestrogen plays in the healthy maintenance of the brain regions that are implicated in unique female processing strategies and cognitive abilities. For example, oestrogen replacement therapy is associated with a reduction in age-related shrinkage of regions that are paramount to face perception, such as the hippocampus and fusiform gyrus (Brizendine, 2006). This finding is also supported by behavioural data whereby oestrogen replacement therapy is also associated with greater visual memory, particularly for facial cues (Resnick & Maki, 2001; Robinson et al., 1994). Together, these findings suggest that while oestrogen may underpin female advantages in face perception, it may also be a primary tool for maintaining these female abilities. Findings such as these suggest that oestrogen in the female brain is important in maintaining healthy structure and functioning of the regions of the brain that govern facial processing. Variations of oestrogen concentration may be the proximal mechanism responsible for the unique cognitive processes and abilities that are observed in female cognition. This notion allows for the adoption of evolutionary approaches, where many of these posit that such hormonal mechanisms within cognition operate specifically to serve an evolutionarily valuable function. This notion shall be further discussed in later sections.

A further indirect effect of oestrogen and face perception comes from findings that show a small but significant interaction between oestrogen and oxytocin. Many areas of research implicate oxytocin's role in encouraging prosocial behaviours among both human and non-human primates (see MacDonald & MacDonald, 2010 for review). Although oxytocin is a neuropeptide, aspects of visual perception in women may receive indirect benefits of oestrogen via its agonistic effect on oxytocin. Research has established a relationship between the two hormones, where an artificial increase in oestrogen has resulted in a significant increase of oxytocin in the hypothalamic regions of the brain (Quiñones-Jenab et al., 1997). This is a consistent finding, and has been considered as an influential factor allowing female engagement in both bonding and sexual behaviours (McCarthy, 1994). This indirect effect of oxytocin is further supported by behavioural data, where a rise in both hormones is accompanied by increased prosocial behaviour. If higher levels of oestrogen are associated with higher levels of oxytocin, then we may also expect this effect to be true during ovulation. Around this time, when conception likelihood is highest, an indirect effect of oestrogen (upon oxytocin) to encourage engagement in prosocial behaviour should be expected to facilitate mating efforts in females. Evidence of this is demonstrated by higher levels of oxytocin that facilitate face to face non-verbal communication (Guastella, Mitchell & Dadds, 2008), an enhancement for discrimination of facial emotions (Schulze et al., 2011; Domes et al., 2007), particularly positive facial expressions (Marsh et al., 2010) and general facial processing (Domes et al., 2013). Together these findings suggest a further way that oestrogen may have an enhancing effect facial processing. If this is the case, as findings suggest, this evidence is supportive of the notion that female sensitivity to facial stimuli may be underpinned by oestrogen. And importantly, that this female advantage may be underpinned by oestrogen in such a way as to facilitate and encourage perceptual processing to maximise changes of successful reproduction.

Together, these findings demonstrate that cognitive abilities in men and women are undoubtedly sensitive to variation in reproductive hormones. The emergence of these sex differences is guided by waxing and waning of testosterone and oestrogen during the earliest stages of development. These hormonal effects persist into adulthood, where for women, they significantly influence variation in certain perceptual domains. It is likely that not only are these hormonal and proximal mechanisms determining differences in male and female functionality, but also for nuance variation in the perceptual functionality of women. This conclusion allows for evolutionary based explanations to consider the possibility that these hormonally modulated sex differences are adaptive mechanisms within perception that have been purposefully selected by nature (Gaulin & Fitzgerald, 1986).

Functionality of sex differences in perception

Evolutionary explanations of sex differences in perception posit that distinct sets of cognitive abilities have been selected by nature to maximise male’s and female's chances of reproduction and survival (Silverman & Eals, 1992; 1994). The Hunter-Gatherer Hypothesis offers one of the primary explanations for such male and female superiority on certain cognitive tasks. This hypothesis claims that sex differences (such as those outlined in previous sections) are vestigial traits left from the gender-specific roles of our Pleistocene ancestors (Silverman & Eals, 1992; 1994). According to this hypothesis, an early division of labour during this time period meant that females, as gatherers and child rearers, were equipped with cognitive skills facilitating these roles. In contrast, hunters without the physical burdens of child bearing and reading meant that males were equipped with cognitive abilities that would satisfy maximum reproductive output and hunting success. These divisions of labour are considered to account for the male superiority in spatial cognition, and the female superiority in visual memory and identification. Respectively, these sex-typical cognitive abilities allowed males the spatial skills required for the successful pursuit of prey, and females the cognitive abilities required for remembering rich gathering locations and strategies (Eals & Silverman, 1994; Silverman & Eals, 1992; Gaulin & Fitzgerald, 1986).

One of primary concepts inherent to the Hunter Gatherer Hypothesis is the notion that Pleistocene women were less likely to experience vast home ranges. Instead, they would spend more time in closer proximity to a primary social unit, in rearing infants and gathering food supplies (Tooby & DeVore, 1987; Eals & Silverman, 1994; Silverman & Eals, 1992). Inherently related to this concept is the idea that women are universal caregivers. Examples of similar female-based social constructs are witnessed today in modern tribes such as the Yanomami and Hadza tribes of South America and Tanzania. Within these tribes, male hunters advance across vast landscapes in search of food while females rely on close social units to provide for and raise generations of children (sometimes recognised as the Grandmother Effect)(Hawkes, 2004; Roberts, 2010). Many evolutionary theorists believe that these examples of modern day hunter-gatherers demonstrate accurately similar social conditions of a Pleistocene past. It has been proposed that as a result of hundreds of thousands of years of child rearing, it is no surprise that face perception in women is such a valuable ability. This notion is further supported by findings of a female advantage in verbal communication and articulation; important tools for engaging in social behaviours (Weiss et al., 2002). Nurturing, and both the social and maternal bonding that is implied by this, inherently require a propensity for facial processing. It is therefore a natural consequence that women may engage well in such intimate social functioning (Hawkes, 2004; Fisher, 2010). In a similar conclusion, Golstein and Chance (1970) attributed women’s higher performance for recognising faces to occur as a result of this disparity between male and female interests. They concluded that, unlike men, women have a natural tendency and therefore greater interest in looking at faces. This explanation accounts for general findings of female advantage in facial processing, including both the recognition bias for same sex faces, and the perception of infant faces, outlined above. Female advantages in visual memory, visual identification and face perception are considered to be underpinned by the greater reliance of ventral stream processing in women. Perceptual skills that allow a rich analysis of fine visual properties are the kinds of visual mechanisms necessary for successful object and facial processing. The female propensity for recognising faces has also been related to the way in which the female brain is optimised for successful reproduction. This interpretation relies on the notion that there is a deliberate and functional relationship between female reproductive hormones and face perception, such that when conception is most likely, higher levels of oestrogen influence optimality in female cognitive performance. This interpretation accounts for oestrogen's facilitatory effect upon facial recognition, and the strengthening of synaptic neural connections in regions associated with ventral processing that may underpin this face perception (Desmond & Levy, 1988; Derntl, 2008). Enhanced facial processing during this period of high fertility enables a female to be more responsive to facial information. This basic function is important, as it lays the foundation for an array of cognitive functioning, including non-verbal facial communication, processing of facial cues, and identification of conspecifics, offspring, and potential mates.

1.2 Sexual selection as a motive for advantages in females' face perception

The functional accounts briefly discussed in section 1 offer palatable explanations of specific female advantages in perception. An overarching notion across these accounts is that these perceptual advantages have been selected by nature to facilitate ancestral female behaviours such as optimal mate selection and social bonding. However, to fully understand the root of these perceptual advantages in women, it is important to consider their evolutionary origin. Understanding the relationship between perceptual behaviours in modern females and their evolutionary origin is crucial for also understanding *why* and *how* females have become equipped with advantages in face perception. This section provides a brief overview of the way in which sexual selection has provided a unique female capacity for processing facial information and cues that may facilitate successful reproduction.

Gamete disparity

An important factor that has been posited as a significant determinant in the evolution of advantages in females' face perception is the notion of female investment. This refers to the degree to which a female organism invests in her offspring from the earliest stages of its development (Dawkins, 2006). This notion necessitates an understanding of the vast differences in the quality and quantity of male and female sex cells. Human male gametes (sperm cells) are small and numerous, and with only a short lifespan their sole purpose is to achieve fusion with a female gamete. Comparably, the human female gamete (egg cell) is large in size and provides a rich basis from which a new organism will grow. This nature of mammalian reproduction is such that from the very moment of conception, by the time a male's biological investment is complete; a female's investment has only just begun with a large contribution of energy and resource in the developing offspring (Dawkins, 2006). Once the transient function of the sperm cell is complete, the female continues her investment as she harbours and nourishes the developing zygote for the next 40 weeks of gestation. Her investment does not end here, but is guaranteed to continue for an indefinite period of time after birth. This early disparity between gametes theoretically allows for a male organism to benefit from greater reproductive output that requires only transitory investment (Dawkins, 2006). Female organisms on the other hand are endowed with a physical investment that extends into the postnatal development of her offspring. The commitment of offspring bearing and rearing means that a female's potential for reproductive output is therefore far less than that of a male. By the time gestation is complete, a female will have successfully endowed her genes in only one offspring whose father may potentially (and theoretically) have profited from endowing his genes in a number offspring far greater than only 1. These sex differences in biological investment are considered to lay the foundation for parental investment; where even before successful fertilisation a female organism is inherently bound to a high degree of pre and postnatal investment (Dawkins, 2006).

Choosy females

The degree to which humans invest in their offspring's pre and post-natal development is an important determinant of their mate choices. Because a female's biological investment in her offspring is intrinsically greater than that of her mate, and because her mate is more likely to (in reproductive terms) benefit from only a transitory investment per female, a female organism will benefit from being "choosy" when selecting a mate. Females' preferences for qualities in prospective mates are therefore optimal. Ensuring that the offspring whom her investment is bound to (who is also responsible for the continuation of her own genes) is equipped with successful and appealing genes is crucial (Trivers, 1972; Dawkins, 2006; Puts, 2010). While her mate's investment is potentially only fleeting at the point of conception, his genetic contribution to her offspring is absolute. The offspring will be the vessel in which both their genetic legacy survives, regardless of the degree to which a male will invests after conception. Selecting who will provide the other half of her offspring's genes is therefore a formidable task for a female. While there is no guarantee of her mate's presence during any postnatal rearing, it is his genes that she will inadvertently strive to nurture in her offspring. There is therefore an evolutionary pressure for a female to select a mate who will endow her offspring with good genes. The notion of inclusive fitness posits that in this evolutionary situation, the best way for a female to ensure the survival of their own genes is to produce genetically healthy offspring in whom these genes are likely to survive (Hamilton, 1964). Because of these evolutionary pressures for optimal mate selection, female mate preferences are considered to have been largely shaped by sexual selection. These selective mechanisms ensure that a female is more likely to favour desirable characteristics of genetic fitness that will be inherited by her future generations (Darwin, 1859). Females whose mate selection is guided by preferences for characteristics that advertise genetic fitness or sometimes a capacity for parental investment, will benefit from copulating with a mate who will best equip her well-provided-for offspring with genes that will not only survive, but will also be equally as successful in reproducing (Thornhill & Thornhill, 1983; Macrae et al., 2002; Buss, 1989). In this manner, both the characteristic displays of genetic quality, and subsequent sexual preferences for these characteristics, will be inherited by her successive future generations (Darwin, 1859; Trivers, 1972; Thornhill & Thornhill, 1983; Buss, 1969).

Mechanisms of sexual selection

Understanding the perceptual mechanisms that guide female mate preferences is fundamental to understanding in this field of research. In order to ensure successful reproduction with an appropriate mate, the perceptual capacity for both the identification of an attractive mate and engaging in non-verbal commutation is essential. Both of these precursors for successful copulation with an ideal mate require a propensity for face perception by allowing for successful detection, identification and attention to reproductively relevant physical cues. These abilities naturally require a female to be able to process evolutionarily relevant cues within her environment. Perceptual mechanisms readily available for identifying and responding to these visual cues underpin and necessitate advantages in females' perception of faces. This sensitivity to evolutionarily significant stimuli has been proposed as one of the visual mechanisms facilitating a female's ability to detect and seek out reliable cues of genetic quality amidst an array of potential mating partners (Tooby & Cosmides, 1990; Kopell et al., 1969). One primary source of cues such as these comes from the faces of others. Already from the earliest stages of its development, the human visual system is well attuned to viewing faces (Heron-Delaney, Wirth & Pascalis, 2011; Johnson et al., 1991; Chien, 2011), where this specialised process allows the encoding of a spectrum of information that is central to non-verbal communication and individual recognition (Kanwisher & Yovel, 2006). It is therefore not surprising that the same source of cues central to social-cognitive functioning is also a valuable source for displaying the visual indices of heritability implicated in female mate preferences. Certain aspects of females' face perception may therefore exist as adaptive mechanisms in perception that facilitate processes important for identifying physical cues of fitness in mates. This notion suggests that females may also benefit from perceptual behaviours that facilitate reading social cues that harness social bonds and strengthening non-verbal bonding strategies with infants (relating to the Grandmother Effect). This capacity for processing facial stimuli is therefore, from an evolutionary perspective, considered to be a core component of female perception. The visual processes that underpin these perceptual behaviours are central to understanding the mechanisms that maximise reproductive success and harness a females' inclusive fitness.

1.3 Attraction as a mechanism of sexual selection

The universally experienced appeal of an attractive face is a core component of mate selection (Gangestad & Thornhill, 2008). Although many concepts of beauty exist on a spectrum of cultural and social diversities, evolutionary theory posits that there remain undertones of a universal, biologically based concept of beauty (Dutton, 2009). Attraction to a fixed set of physical characteristics has been proposed as a primary perceptual mechanism enabling identification of an optimal mate (Gangestad & Thornhill, 2008). This includes the notion that both men and women universally experience a preference for facial characteristics such as symmetry and averageness. Equally, but also very differently, both sexes also display preferences for sex-typical facial features in the opposite sex. These sex-specific preferences are thought to originate from selective pressures differently faced by males and females in their pursuit of identifying the ideal mate. This physically ideal mate is different for males and females, and so both sexes subsequently display preferences for exaggerated features typical of the opposite sex (Gangestad & Thornhill, 2008). Interestingly, while men's preferences for an ideal mate appear to be consistent over time, research in female attraction reveals both nuanced and striking variation in her sexual preferences that appear to occur relative to her hormonal state (Gildersleeve et al., 2013). This section provides an overview of consistencies in facial attractiveness and attraction across both men and women. The way in which reproductive hormones guide both the development of these attractive qualities and their development will also be discussed. Importantly, this section addresses a concept that is central to this thesis; that for women, sexual preferences do not remain static, but are instead sensitive to hormonal shifts across the menstrual cycle.

Consistencies in facial attractiveness

Facial symmetry

A consistently preferred physical characteristic displayed by both men and women is facial symmetry (Little, Apicella, Marlowe, 2007). Preferences for physical displays of symmetry are thought to reflect an attraction to cues of developmental health. This is based on the notion that consistent weaknesses in resisting environmental pathogens and mutations during an organism's development will leave behind asymmetrical scars of these developmental shortcomings (Scheib, Gangestad & Thornhill, 1999; Møller & Swaddle, 1997). A facially symmetrical individual may therefore be more likely to have successfully defended itself against environmental toxins which could otherwise hinder healthy development. Preferences for symmetrical cues of developmental health may have been selected by nature to aid the mate selection process, enabling detection of genetically fit mates (Little, Apicella & Marlowe, 2007). Support of this notion that symmetrical features are reliable cues of heritable and therefore desirable immunoresistence comes from research that demonstrates a positive association between an individual's features of symmetry and reproductive output. For example, more symmetrical individuals are more likely to reproduce; leaving behind a greater number of descendants who are less likely to experience vulnerability to disease (Møller & Thornhill, 1997; Møller & Thornhill, 1998; Thornhill & Gangestad, 1994; Waynforth, 1998). The logical conclusion that males and females should therefore reap biological benefits from selecting symmetrical mates is also supported by behavioural data. For example, both men and women display a general preference for more symmetrical faces (Koehler et al., 2002; Perrett et al., 1999), where the owners of such faces not only report experiencing greater amounts of short-term sexual partners (Rhodes, Simmons & Peters, 2005) but whose faces are also judged as appearing subjectively healthier than their more asymmetrical counterparts (Grammer & Thornhill, 1995). Selecting a mate based on symmetrical characteristics may therefore be biologically rewarding for the offspring that an individual leaves behind; endowing offspring with healthy and equally attractive features is an ideal way to ensure that an organism's own genes will propagate in the generations he or she leaves behind.

Facial averageness

A second marker of universal preference is the averageness of a face. Facial averageness is regarded to be a prototypical example that is representative of all faces in the population, and may have an important although perhaps subtle effect on the extent to which it is perceived as attractive (Alley & Cunningham, 1991). Preferences for facial averageness are thought to be an additional mechanism that harnesses inclusive fitness. As with physical symmetry, those with more average faces also experience a greater number of short-term sexual partners (Rhodes, Simmons & Peters, 2005) and are also rated as being attractive (Langlois, Roggman & Musselman; Langlois & Rogmann, 1990; Alley & Cunningham, 1991; Valentine, Darling & Donnelley, 2004). In a study measuring this average effect on attractiveness, a sample of "average" faces were created as a composition of 32 individual faces put together in order to create the prototypical representation of their aggregate. These composite average faces scored higher ratings of attractiveness than the individual faces from which they were composed (Langlois, Roggman & Musselman, 1994; Langlois & Rogmann, 1990). It has been proposed that these preferences for average faces may be a product of the visual system's fluency in detecting stimuli with average properties, such that they are quicker and simpler to process. Average faces may thus be preferred because they require less visual effort and attention, enabling more rapid recognition (Perrett, 2010).

While characteristics of symmetry and averageness may be consistently attractive, research has shown that these are not necessarily the sole determinants governing how an individual judges the attractiveness of another's face. It has been suggested that, while such universally preferred traits are generally found to be fairly attractive, other facial features may be equally important, if not more reliable cues to ideal and optimal qualities in a mate (Alley & Cunningham, 1991; Langlois & Rogmann, 1990). These include physical features and characteristics of sex-typical faces.

Preferences for sexually dimorphic faces

Ontogeny of the male and female face

Males and females experience different developmental trajectories, whereby natural fluctuations and exertion of sex hormones during growth guide the development of sex-typical facial features. Sex differences in exposure to hormones such as oestrogen and testosterone determine the development of robustly different facial bone structure and features that together constitute a typical "female" or "male" face, respectively. Although oestrogen is present throughout a young female's pre and postnatal development, the oestrogen surge experienced during adolescence marks a significant milestone during female development. This stage of development is associated with the maturation of female secondary sexual characteristics such as breast development and an increase in waist-hip ratio (Melmed et al., 2011). The same growth promoting effects of oestrogen also inhibit development of the rapid bone growth responsible for bold facial features in men, creating a female-typical neotenous facial appearance. As a result, female faces are typically composed of petite features such as a smaller nose, narrower jaw line, subtler brow ridges, and "feminine" characteristics such as thicker lips and larger eyes (Enlow, 1982; Thornhill & Gangestad, 1996; Perrett, 2010). On the other hand, the development of a male's face is largely shaped by levels of androgens that he experiences throughout puberty. Testosterone is the primary male sex hormone, and promotes the development of masculine features that emerge during adolescence such as darker skin tone, prominent brow ridges, accentuated jaw line, presence of facial hair and greater facial width. Together these facial features compose the appearance of a typically “masculine” male face (Thornhill & Gangestad, 1996; Enlow & Hans, 1996; Scheib, Gangestad & Thornhill, 1999; Frost, 2011; Penton-Voak & Chen, 2004). This is supported by findings that show an association between testosterone and physical displays of male-typical qualities; men with higher testosterone levels are also likely to have faces that appear more masculine (Penton-Voak & Chen, 2004; Roney et al., 2006).

These sexually dimorphic facial features are the cues that we rely on to distinguish between male and female faces, and lay the foundation of male and female preferences for sexually dimorphic faces. Sex-typical features of male and female faces are considered to be hormonal markers of favourable qualities advertising their possessor’s suitability as a mate; youthful and fertile females, and genetically fit males (Perrett, 2010; Feinberg, 2008). Selective preferences deemed as the mechanisms of sexual selection rely upon these sexually dimorphic features, such that men tend to prefer characteristics of a typically "female" face, while women tend to prefer those of a typically "male" face. Attraction to exaggerated sex-typical features has been proposed to occur as a response to enhanced cues of sex-typicality (Rhodes et al., 2003; Perrett et al., 1998). Research from ethology demonstrates that this phenomenon is clearly observed among other animals, such as intense colouration of ornate male birds (Siefferman & Hill, 2005; Hill, 1990; Andersson, 1982) and large horns in male ruminant mammals (Harvey & Bradbury, 1991; Andersson, 1994). It has been proposed that for the same function, sexual preferences for such accentuated features also operate within humans (Wickler, 1973).

Consistencies in male preferences for female faces

As previously mentioned, physical makers of oestrogen in a female face may serve as the physical signals of female fertility. Oestrogen levels are intimately related to feminine facial features (Smith et al., 2006) and are reliable predictors of a female's successful fertilisation and conception risk (Baird et al., 1999; Lipson & Ellison, 1996). Male preferences for these feminine female cues relate to the disparity in male-female reproductive capacity. As discussed in section 1.2, male reproductive interest is such that his capacity for reproductive success relies primarily on the opportunity to conceive more offspring in numerous females (Dawkins, 1976; Thornhill & Thornhill, 1983). Because oestrogen correlates with feminine facial features and fertility, males who prefer these female-typical cues stand a greater chance of successfully investing their mating efforts in the pursuit of fertile females. Males who benefit from succeeding a larger reproductive output from the pursuit of fertile females will therefore allow for preferences for female-typical features to survive in the offspring he is thus more likely to leave behind (Fraccaro, 2010; Perrett et al., 1998; Law Smith et al., 2006; Little, 2013; Thornhill & Gangestad, 2006; Buss, 1989; Jones, 1995). Male preferences are therefore consistent and uniform in their function; males need only prefer fertile females at all times in order to establish their genes in a greater number of offspring. Their preferences for oestrogen-dependent female features are therefore consistent. Indeed, behavioural data supports this notion: photographs of female faces taken during the most fertile phase of their menstrual cycle receive higher scores on ratings of femininity, attractiveness and apparent health (Smith et al., 2006; Roberts et al., 2004; Puts, 2013; Bobst & Lobmaier, 2012). Additionally, males display greater sexual preferences for women of an age that corresponds to the mid-twenties peak in female fertility (Buss, 1989; Dunson, Colombo & Baird, 2002). These male preferences for female-typical features therefore function to attract a male organism to a female who displays signals of youth and fertility (Perrett et al., 1998; Law Smith et al., 2006; Little, 2013; Thornhill & Gangestad, 2006; Buss, 1989). Male preferences are therefore uniform in nature in that they are concerned only with the identification and attention to fertile females; a state of functionality that for male organisms does not change.

Unique female preferences for male faces

Research concerned with sex differences in facial attraction reveal that females' preferences, unlike those of their male counterparts, are not static but vary relative to fluctuations in female reproductive hormones. In the first instance, findings show that females display preferences for male-typical, "masculine faces". For example, "masculine" male faces score more highly on ratings of attractiveness, perceived dominance and apparent health (Keating, 1985; Johnston et al., 2001; Scheib, Gangestad & Thornhill, 1999; Johnston et al., 2001). For example, when presented with images of composite male faces with enhanced sex-typical characteristics (such as larger eyes, eyebrows, and jaw), those with the most enhanced male characteristics such as accentuated cheekbones and larger chin were subjectively rated as appearing both more dominant and more attractive by females (Keating, 1985; Cunningham, Barbee & Pike, 1999). The Immunocompetence-handicap hypothesis explains that despite the inhibitory effects of testosterone upon the immune system, successful development of exaggerated male features are markers of disease resistance and immunocompetence; qualities that are costly for a male to bear (Grossman, 1985; Folstad & Karter, 1992; Boothroyd, Lawson & Burt, 2009; Smith et al., 2006; Puts, 2010; Gangestad & Thornhill, 2003; Penton-Voak & Perrett, 2000; Grafen, 1990). Such qualities typical of a male face are not only related to attractiveness, but are also found in men whose sperm is ideal in shape and size (Soler et al., 2003). The female preference for accentuated male-typical features therefore reflects a sexual interest in male-typical cues of health and genetic fitness (Buss, 1987; Alley & Cunningham, 1991). Females who are attracted to, and therefore select a masculine mate stand a greater chance of not only producing a son that is equally as attractive to other females, but also offspring who are equipped with stronger immune defence. In both of these instances, the survival of female's genes is indirectly facilitated via the survival and health of the bodies she instils them in.

Yet, these preferences for male-typical faces are not found to be consistent over time. Rather, female sexual preferences in different contexts (such as preferences for either short or long term mating partners) has revealed a trade-off between degree of attraction to extreme male-typical traits and an aversion to learned associations between physical masculinity and negative behaviours (Keating, 1985; Roney et al., 2006). These findings of optimal female preferences often rest on the notion that enhanced female preferences for indices of masculinity occur only relative to her interest and consideration of a short-term sexual partner. Female preferences for more femininised male faces, on the other hand, appear to occur within context of her search specifically for long-term mating partners who are likely to provide an equal interest in parental investment. This disparity in female preferences for varying degrees of physical male masculinity is perhaps an adaptive compromise between the reproductive benefits and undesirable behavioural qualities such as dishonesty, dominance and polygamous behaviour that are associated with masculine males (Perrett et al., 1998; Johnston et al., 2001; Mazur & Booth, 1998; Rhodes, Simmons & Peters, 2005). Importantly, such shifts in female preferences do not occur only in relation to context of short and long-term sexual partners, but are influenced by the additional dimension of fertility fluctuation that occurs across the menstrual cycle. A unique characteristic of female sexual preferences is that sensitivity and attraction to male-typical facial qualities fluctuates relative to fertility shifts associated with the menstrual cycle. This is recognised as The Cycle Shift Hypothesis, and demonstrates that cyclical variation in female preferences may function as the perceptual mechanisms of sexual selection in women.

1.4 The Cycle Shift Hypothesis

Previous sections have highlighted the influential effect of reproductive hormones upon visual perception in women. An important component of this relationship is the way in which female sexual preferences display systematic patterns of variation across the menstrual cycle. These cyclic shifts in female face perception provide insight into way in which reproductive hormones exert both nuanced and striking effects on female cognition. This section addresses the theoretical and empirical literature assessing fluctuations in females' face perception across the menstrual cycle. It shall explore these with reference to adaptive accounts provided by evolutionary theory who posit that shifts in female perception have been deliberately shaped by sexual selection in females in order to harness their inclusive fitness (Gildersleeve et al., 2013).

Hormonal shifts across the human female reproductive cycle

The menstrual cycle typically lasts around twenty-eight days. During this time, a woman will experience a diversity of hormonal, physical and mental alterations. This ebb and flow of female reproductive hormones modulates fertility shifts, and is wholly responsible for the occurrence of ovulation. Across the twenty-eight days, a female will pass through three distinct phases of her cycle: the follicular (days 1-10), ovulatory (days 11-14) and luteal phase (days 15-28) (Mikolajczyk & Stanford, 2005), see Figure 2.

The follicular phase begins on day 1 and marks the beginning of a new cycle. Here, follicle stimulating hormone (FSH) and luteinising hormone (LH) increase via activity in the hypothalamus. Together these hormones promote the maturation of follicles in the ovary, where one of these will eventually form a fully matured ovum (female gamete). Once fully matured, the female gamete begins preparation for fertilisation. Throughout the remainder of the follicular phase, the ovum begins to steadily increase what were previously low levels of oestrogen. These relatively low levels of oestrogen and progesterone inhibit the hypothalamus from preparing any more follicles for maturation. This means that from here, a female's chances for conception fall entirely on this particular ovum. Approaching the ovulatory phase, the ovum continues to secrete oestrogen. These levels increase to a threshold whereby a surge in luteinising hormone is elicited. This surge in luteinising hormone continues to encourage the production of oestrogen, and together high levels of the two hormones mark the onset of ovulation. This unique state of hormones occurs around day fourteen of the cycle, and marks a narrow window during which conception can occur. In the six days prior to day fourteen, fertility levels gradually climb to a peak. It is across these six consecutive days that a single case of unprotected sex is most likely to result in successful conception (Wilcox, Weinberg & Baird, 1995; Wilcox et al., 2001). This mid-cycle peak in oestrogen is also accompanied by an increase in testosterone (Guerrero et al., 1976), which has been considered to facilitate a female's sexual interest while fertility levels are high. Immediately after this period, a sharp decline in oestrogen signifies that the fertile window has closed. At this stage, the female has entered the luteal phase of the cycle. This is characterised by oestrogen levels that continue to fall, while progesterone levels climb gradually in anticipation of the implantation of a fertlisied ovum. This is considered as the potentially pregnant phase of the cycle, where upon realisation that an egg has not been fertilised, progesterone and oestroen levels continue to fall. This decline in the two hormones concludes at the end of the luteal phase (often characterised as premenstruation), marking the end of the cycle around day twenty-eight (Guttridge, 1994; Beaudoin & Marrocco, 2005).

In contrast, women using hormonal contraceptives have a very different experience of the hormonal fluctuation across their menstrual cycles. Although there are an array of different hormonal contraceptives available to women, this thesis is concerned specifically with the effects of combined oral contraception. The primary reason for this is that the locus for action in these contraceptives is the prevention of natural ovulation, and consequentially the prevention of pregnancy (Speroff, Darne, 2010; Brunton, Chabner, Knollmann, 2012). This allows a direct comparison between freely cycling women who experience naturally occurring ovulation, and women whose ovulation has been artificially inhibited by synthetic hormones. Combined oral contraceptives comprise both oestrogen and progesterone. These synthetic hormones mimic and enhance the effects of their natural analogues. Together, these artificial levels of progesterone and oestrogen inhibit the release of luteinising hormone and follicle stimulating hormone from the hypothalamus. This antagonistic effect prevents the maturation of follicules within the ovaries, meaning that a mature ovum cannot develop to ovulation. Additionally, inhibition of luteinising hormone also prevents oestrogen levels from peaking at any point during the cycle (Speroff, Darne, 2010; Brunton, Chabner, Knollmann, 2012).

Understanding the rhythmicity in female reproductive hormones is central to understanding the biological mechanisms that underpin behaviour. It is posited that evolutionary pressures faced by early female humans were eased by the beneficial effects of female sex hormones (Puts, 2006). For example, changes in female behaviour associated with natural variations in these hormones are proposed to have been selected by nature to facilitate optimal reproduction in women. While it is clear how these hormones modulate female fertility and certain aspects of sexual behaviour, their effects upon the female visual system remain unclear (Young, 1978).

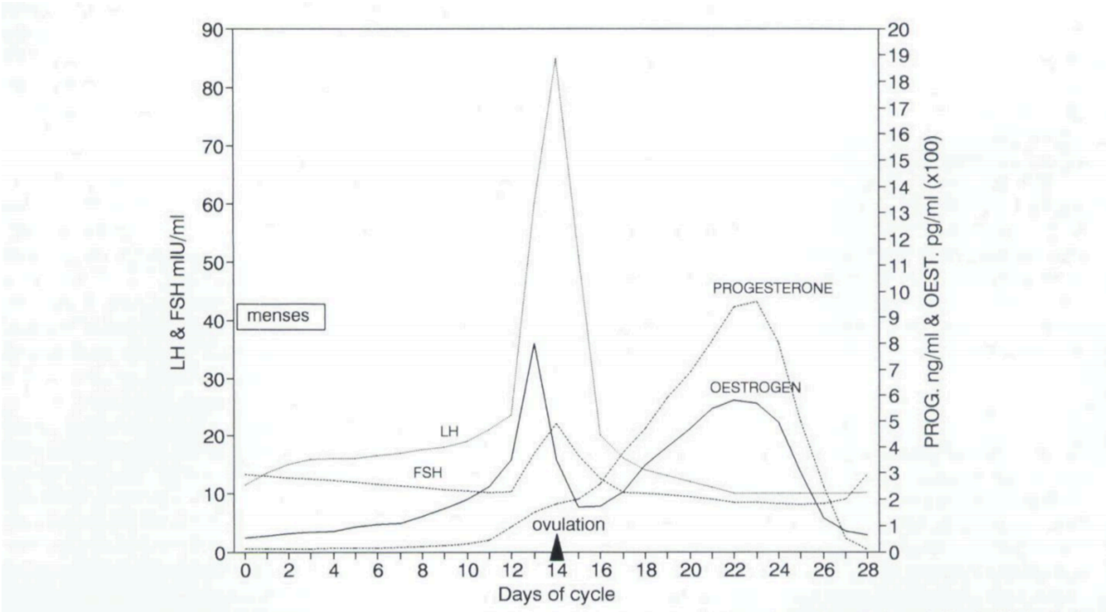

Figure 2 Fluctuations in female reproductive hormones across a normal 28-day cycle (taken from Guttridge, N. M. (1994) Changes in ocular and visual variables during the menstrual cycle. *Ophthalmic and Physiological Optics*, *14*(1), 38-48.)

Cyclical shifts in female sexual behaviour

Findings from behavioural studies demonstrate that aspects of female sexual behaviour change across the menstrual cycle. The majority of these findings provide evidence for an elevation in sexually orientated behaviour and motivation during ovulation, discussed later. During mid-cycle, where conception likelihood reaches its highest level throughout the entire menstrual cycle, female behaviour is reoriented towards opportunities that are likely to maximise a female's chances of sexual encounters. These effects tend to only be witnessed in freely cycling women, who experience naturally occurring ovulation in the absence of hormonal contraceptives. For these women, the mid-cycle peak in oestrogen and testosterone is accompanied by an increase in sexual arousal and physical sensation, where this immediately dissipates after the ovulatory peak (Udry & Morris, 1970). This rise in sexual interest may be responsible for the additional increase in flirtatious behaviour that women experience during high fertility. Engaging more in flirtatious behaviours does occur in isolation, but is considered facilitatory to additional findings that women are generally more likely to initiate and engage in sexual intercourse (Hill, 1988; Harvey, 1987; Matteo & Rissman, 1984). However, this enhanced sexual interest is not always necessarily directed towards one sexual partner. Instead, female attention may be directed at more than one male at any given time, with women reporting greater sexual fantasies about, and attraction to, individuals other than their primary partner during this period of the cycle (Gangestad, Thornhill & Garver, 2002). Similar findings show that in the days preceding ovulation, there is a significant increase in the probability that a woman will engage in extra-pair relationships, regardless of her current relationship status (Gangestad, Thornhill & Graver, 2002). As previously mentioned, humans appear to be a moderately polygamous species, and together these findings further demonstrate then when most fertile, the female organism becomes more aware of and responsive to a greater number of sexual cues. This means that during ovulation, female preferences are not wholly invested in one mate but replaced by an open interest in array of prospective mates. This enhanced interest for extra-pair sex when conception risk is high facilitates identification and selection of the best quality genes (Roberts, 2004). Increasing both interest in candidate mates and desire for sexual instigation allows a fertile female to maximise her reproductive potential (Harvey, 1987).

Using objective measures, research concerned with female sexual interest has also demonstrated cyclical shifts in implicit behaviours. In particular, studies of pupillometry have shown that when fertility is high, the female autonomic nervous system displays a shift in interest toward sexually significant stimuli. Pupil dilation, or pupil diameter, is a reliable index of sexual interest, operating independently and outside of conscious awareness (Aboyoun & Dabbs, 1998; Zuckerman, 1971; Bervick, Kling & Borowitz, 1971). In a study measuring women's pupillary responses to an array of male faces with pupil diameters of varying degrees, women were more attracted to male faces with larger pupils around day nine of the cycle. While day nine marks a relatively early stage of the menstrual cycle, and is not necessarily associated with peak fertility, it does denote the onset of the gradual climb towards maximum fertility (Wilcox et al., 2001). Therefore, while female interest in larger male pupils does not reflect greater attraction to cues of genetic quality, it does signify a significant increase in sexual interest that begins in the prelude to ovulation. A peak in interest from fertile females in response to potential signals of sexual interest from other males may facilitate a sexual interest. These findings are proposed as evidence of the stage of the menstrual cycle where a female begins to identify potential mates displaying a mutual sexual interest. These may perhaps be the precursory stages to eventual mate selection (Caryl et al., 2009). A similar study compared pupil dilation across the menstrual cycle, specifically in response to sexually significant stimuli. During the menstrual, ovulatory and luteal phases of the cycle, women were presented with images of either partners and celebrities whom they considered attractive (sexually significant) or images of non-sexually relevant faces. Results showed that during the ovulatory phase of the cycle, women's pupillary responses were greatest in response to their partner and attractive celebrities. These findings demonstrate that when fertility is high, the female visual system is readily attuned to viewing sexually significant stimuli. This attention is not only tuned to primary partners but also toward other men, indicating an increase in female interest for extra-pair encounters. Importantly, this effect was confined only to naturally ovulating women, where it was not found in users of oral hormonal contraceptives (Laeng & Falkenberg, 2007). Together these findings demonstrate that during periods of high fertility, the female autonomic nervous system orientates visual attention towards stimuli of reproductive significance. These cyclical shifts in implicit interest demonstrate naturally occurring behaviours that facilitate mate selection and copulation.

The Cycle Shift Hypothesis

As this section has discussed so far, there is a rich understanding of the way in which female reproductive hormones fluctuate across the menstrual cycle. Both their mode of action and their effects upon fertility and sexual behaviour in women are well understood. However, their secondary influence upon perceptual behaviours in women is a relatively new area of research. One area of research in particular offers an adaptive account of the way in which natural shifts in female sex hormones translate to meaningful changes in female perception. The Cycle Shift Hypothesis is grounded in evolutionary theory of sexual selection. It posits that a female's capacity to identify a range of suitable mates is enhanced during high fertility. It relies partly on research demonstrating the use of facial information as a perceptual tool for assessing the genetic quality in prospective mates, claiming that the female visual system becomes especially attentive to these cues when conception likelihood is high. As a result, females experience adaptive shifts in their sexual preferences across the menstrual cycle. Therefore, central to the Cycle Shift Hypothesis is the notion that female mate preferences are not fixed. Instead, they are dynamic aspects of perception that operate relative to fluctuations in fertility associated with the menstrual cycle. Heightened attention to the physical indicators of phenotypic condition enables the female organism to identify and invest mating efforts in males that are most likely to provide her offspring with good genes. This heightened preference for cues of heritability around ovulation is posited to exist as an evolved strategy to optimise a female's reproductive output (Macrae et al., 2002; Perrett & Penton-Voak, 2000). Importantly, these cyclic shifts in female perception appear to operate within fine constrains of fertility windows occurring across the menstrual cycle. The average female menstrual cycle contains 9 days of maximum fertile phase, where day 12 marks the highest risk for conception, compared to day 14 where this probability dramatically falls (Wilcox et al., 2001).

Evidence for the Cycle Shift Hypothesis

Research demonstrates that cyclical preferences appear to operate across a range of sensory modalities, not only in vision. During the fertile phase of their cycle, naturally cycling women show a greater preference for scents belonging to men with symmetrical features (Grammer, 1993; Thornhill & Gangestad, 1999; Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999). Preferences for male voices also shift across the menstrual cycle. Lower progesterone levels are associated with an increase in preference for artificially masculinised vocal traits in male voices, suggesting that masculine voices may be more attractive to women when fertility is high (Puts, 2006; Feinberg et al., 2006). These findings demonstrate that mechanisms for detecting honest signals of phenotypic and genetic quality operate across a range of sensory modalities in women. For mechanisms of selection in visual perception, there is an array of research demonstrating a consistent co-occurrence of preferences for certain male characteristics and the fertile phase of the menstrual cycle.

Cyclical shifts in preferences for healthy faces

According to the Cycle Shift Hypothesis, systematic variation in preferences for symmetry may have important reproductive benefits for female observers. Enhanced sensitivity to cues of developmental health when fertility is high allow a female to select a mate who is likely to instil these ideal qualities in her offspring. Enhanced preferences for symmetrical faces during fertility are therefore a useful tool for mate selection (Scheib, Gangestad & Thornhill, 1999). Studies measuring preferences for symmetrical cues across the menstrual cycle have found this to be the case, where peak fertility is associated with an increase in preferences for more symmetrical faces. When rating attractiveness for short- term relationships, women demonstrate greater preferences for symmetrical male faces during the phase where probability of conception is high, rather than at times of the cycle when she is less likely to become pregnant (Little et al., 2007). These findings suggest a positive effect of oestrogen in modulating female preferences for symmetrical cues, where this influence is especially apparent during mid-cycle. Similar research suggests that preferences for facial cues of current health may not only be modulated by oestrogen, but rather elevated levels of progesterone are also responsible for influencing female attraction to physical signals of healthy individuals. For example, women tend to prefer faces appearing subjectively healthier during the luteal phase of their menstrual cycles. This phase is characterised by lower oestrogen levels and a mild peak in progesterone. Preferences for apparent health that occur during this phase therefore seem to operate within the context of pregnancy, as they are magnified in pregnant women and in those taking oral contraceptives (whose progesterone levels are artificially increased). These findings are considered to demonstrate the importance of progesterone concentration in the modulation of disease and infection avoidance in women, particularly when the female immune system is vulnerable during pregnancy. Preferences for healthy individuals when progesterone levels are high allow women to reap direct benefits by avoiding individual's who may carry infections potentially harmful to her developing offspring (Jones et al., 2005). The relationship between female reproductive hormones and preferences for cues of health appear to be context dependent; preferences for physical health may occur as a function of mate choice or of infection resistance during pregnancy, and relies upon different hormonal mechanisms respectively.

Cyclical shifts in preferences for masculinity

A growing body of evidence suggests that female preferences for exaggerated male features are enhanced during the ovulatory phase of the menstrual cycle. These findings are generally considered as evidence of an association between fertility and preferences for physical indicators of immunocompetence (Grammer & Thornhill, 1994; Thornhill & Gangestad, 1976). One such example of this relationship comes from studies of female preferences for variations in male facial skin tone. Skin tone is typically darker for male faces, and is recognised as an androgen-dependent male trait (Frost, 2011). Preferences for lighter male faces are greater during the luteal phase of the menstrual cycle, suggesting that when fertility levels are low, women are less interested in traits of masculinity when making judgements of attraction (Frost, 1994). Similar results were found in a study where participants were asked to rate their attraction to an array of faces across several stages of their menstrual cycle. Facial stimuli were male and female faces that had been modified to create an average of each sex's face, and their "exaggerated" versions. These "exaggerated" faces were each composed of varying degrees of masculinity and femininity, in such a way as to synthesise the naturally occurring sex-typical traits that develop during puberty. Results found cyclical shifts in female participants' preferences, where high oestrogen levels during ovulation were associated with greater female preferences for slightly more masculinised male faces (Johnston et al., 2001). This positive relationship between oestrogen and masculinity preferences has been consistently found across other studies. Penton-Voak et al. (1999) measured female preference for male faces across three phases of the menstrual cycle. In the nine days preceding ovulation onset female participants displayed preferences for more masculine male faces. This effect was found to occur only during high fertility, where masculine preferences were not found outside of the late follicular phase of the cycle (Penton-Voak & Perrett, 1999).

Similar findings further support the notion that this effect is confined to the fertile window; naturally cycling female observers are more likely to rate masculine-enhanced average male faces more favourably when observation takes place during the late follicular phase of their menstrual cycle (Penton-Voak & Perrett, 2000). These findings are often interpreted as evidence of an oestrogen modulated preference for honest testosterone-dependent signals of immunocomptence. Thus, high levels of oestrogen during mid-cycle have been implicated as the biological mechanisms underpinning enhanced attraction to physical markers of good genes (Gangestad et al., 2005). Adaptive shifts in sexual preferences for these markers are posited to have been equipped by sexual selection to ensure the conception of healthy offspring. This interpretation gains support from studies adopting direct measures of the relationship between oestrogen and preferences for physical cues of testosterone-dependent traits. For example, women with higher oestrogen concentrations display stronger preferences for faces of males with higher concentrations of testosterone (Roney & Simmons, 2008). Similarly, oestrogen concentration in female observers has been found to be a reliable predictor of the extent to which she perceives androgynous faces to be attractive. When experiencing higher levels of oestrogen, women were more likely to prefer facial cues that were indicative of high levels of testosterone. As a result, highest oestrogen levels during the fertile phase of the cycle resulted in the strongest preferences for facial cues of high testosterone. These effects were found to be modulated only by oestrogen levels, reinforcing the concept that the same hormone responsible for ovulation also determines attraction cues that are relevant to reproductive benefits (Roney, Simmons & Gray, 2011). These cyclical shifts in sexual preferences appear to occur regardless of a females' current relationship status. Women with current partners display a stronger preference for more masculine faces than those without a partner (Little et al., 2002). These findings highlight that polygamous behaviours are inherent in both sexes, by which optimal mate choice in women is not hindered or constrained by her current relationship status.

Interestingly, research has shown that enhanced preferences for masculinity during periods of high fertility are accompanied by preferences for femininity when fertility levels are low. Interpretations of these findings have proposed that females have adopted dual preferences as result of conditional mate choice strategies (Perrett, 2000). Dual preferences may allow a female to select an ideal mate conditional, or relative to, her current hormonal status. For example, as previously discussed males inherently have a greater capacity for reproductive output. An evolutionarily stable strategy for males is therefore to adopt short-term mating behaviours that will result in the greatest number of offspring (Scheib, 2001). During ovulation, such male behaviour may be irrelevant providing he displays physical indicators of good genetic quality. However, when her fertility levels drop, suitable mate criteria of less fertile females shifts rapidly. Here, it may pay a female to be more attracted not to males with the best genes (as she is unlikely to conceive), but to males who display behavioural traits that are compatible with parental investment. While interest in good genes is useful for deciding who will biologically father our offspring, deciding who may be best to raise these offspring during the “potentially pregnant” phase of the cycle is a different decision entirely. Unreliable, philanderer males are unlikely to provide an ideal level of investment in any of their offspring (Boothroyd, Lawson & Burt, 2009; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1976). Female preferences therefore function relative to her mating priorities that are governed by her hormonal state. This creates separate and contrasting female preferences for short and long term partners. When fertile, the female visual system becomes attentive to cues of genetic and phenotypic qualities. When comparably less fertile, there is a greater interest for physical characteristics that are indicative of trustworthiness and reliability. For example, behavioural data demonstrates a preference for femininity during low probability of conception. Here, in the same study demonstrating a preference for masculine faces during mid-cycle, women were also more likely to prefer more feminine faces when observation took place outside of their fertile window (Johnston et al., 2001). Similarly, when rating attraction to male faces within context to preferences for short or long term relationships, women preferred to receive direct gaze from feminine male faces. These findings suggest that when in search of a long term partner, women are motivated to socially engage more with men displaying feminine characteristics (Conway, Jones, DeBruine, & Little, 2010). Feminine faces such as these are perceived positively by women as appearing subjectively more trustworthy (Smith et al., 2009). Almost like a hormonal tipping scale, these findings demonstrate that enhanced preference for signals of genetic quality during high fertility are reduced in favour of traits of parental investment when fertility is low (Puts, 2006). These interpretations may also account for findings where preferences for masculine faces during high fertility appear to have a maximum effect. Overly masculine faces have often been met with a decline in ratings of attractiveness, suggesting an optimal level for masculinity. This is perhaps an adaptive compromise between the reproductive benefits and undesirable behavioural attributes associated with masculine traits (Johnston et al., 2001; Mazur & Booth, 1998). While mid-cycle preference for a masculine male would have provided a direct, short term advantage for Pleistocene females in the form of good genes for her offspring, these were not accompanied by a guarantee of help with shared parental investment (Puts, 2010; Puts, 2006; Gangestad, 1973; Gangestad, Thornhill & Graver, 2002).

Together these findings demonstrate that the female organism is equipped with an array of perceptual tools required for optimal mate selection. These processes are governed by natural variation in reproductive hormones, allowing for adaptive shifts in female visual perception that guide her sexual preferences. These shifts operate within the biological constraints of fertility that shift across the menstrual cycle. As a result, aspects of female face perception are not static, but inherently dynamic in nature.

1.5 Limitations facing current research

There are several criticisms facing current research and accounts of cyclical shifts in female preferences. These constraints can be placed into three categories, referring to the empirical, methodological and theoretical limitations that together question the reliability of present results supporting the Cycle Shift Hypothesis. This section reviews these limitations and uses them as a framework for understanding the importance of adopting a novel scope through which to investigate adaptive shifts in female preferences.

Empirical limitations

The primary limitation facing the Cycle Shift Hypothesis is the degree of inconsistency in findings that assess cyclical variation in female sexual preferences. As this section will discuss, the lack of a general consensus for a mid-cycle peak in female preferences for physical indicators of genetic quality raises the question of whether the Cycle Shift Hypothesis provides an accurate model of mate selection in women. Together, inconsistencies across findings are building two bodies of evidence, which either uphold or propose the rejection of the theory. This lack of consistency has very recently been discussed across several meta-analyses, and attributed to a range of different factors, addressed in the following section.

First of all, it has been argued that there is a general lack of evidence supporting the notion that fertile women display enhanced preferences for physical cues of genetic quality in mates. Boothroyd, Lawson and Burt (2009) measured the association between female preferences for indices of phenotypic quality in faces. According to the Cycle Shift Hypothesis, an association should exist between women's preferences for physical cues to fitness, such as facial symmetry and masculinity. However, no such association was found between preferences for facial symmetry, averageness, or masculinity. Interestingly, women's preferences for masculinity negatively correlated with preferences for symmetrical faces. These findings have been interpreted as evidence suggesting a weakness in the Cycle Shift Hypothesis, as they do not provide evidence of a collective attraction to and preference for physical markers of fitness (Boothryod, Lawson & Burt, 2009; Wood et al., 2012). It could however be that Boothroyd, Lawson & Burt (2009) did not measure such an association because the study itself did not measure these preferences in any relation to the menstrual cycle. Although we should expect an association between preferences for all such markers of fitness, perhaps this association becomes more pronounced when conception likelihood is highest. Koehler et al. (2006) measured this influence of conception likelihood in relation to female preferences for physical cues of fitness. During high and low periods of fertility, female participants rated attraction to faces belonging to males with a good health history, and to symmetrical and average faces. No evidence of enhanced attraction to faces belonging to these healthy individuals during fertility was observed. These results cast doubt on the extent to which fertile females experience enhanced attraction to physical cues indicating long-term health. An additional study did find supporting evidence of a general preference for symmetrical faces among female observers, but found that these preferences were not enhanced when women were most fertile, or when attractiveness ratings were based on males' suitability as a short term partner (Koehler, Rhodes & Simmons, 2002). In a similar study, Peters, Simmons and Rhodes (2009) used hormonal assays to measure preferences for masculine and symmetrical male faces during either high or low fertile periods of the menstrual cycle. Attractiveness ratings were provided for these two faces during the ovulatory and luteal phases of the cycle. These results showed no significant differences in preferences for either masculine or symmetrical cues. Wood et al. (2012) assert that amidst these mixed findings, there is a considerable lack of robust evidence of a menstrual cycle effect upon female mate preferences. When viewed across both published and unpublished findings, the body of evidence demonstrating this significant effect becomes smaller. In their overview of the findings illustrating cyclic female preferences, Wood et al's (2012) meta-analysis found that one third of findings actually reveal *reverse* effects, whereby the mid-cycle peak in fertility appears to be associated with preferences for characteristics indicative of poorer genetic quality. For example, a replication of Penton-Voak and Perrett's (1999) finding of an increased female preference for masculine characteristics found that the direction of these preferential shifts might not be as robust as the initial 1999 study concluded. Using the same stimuli of Caucasian and Asian male faces ranging in degrees of masculinity and femininity, Harris (2011) found the opposite effect. Harris (2011) reported that during the fertile phase of their cycle, females rated feminine faces as appearing more attractive. These results are in direct contradiction to Penton-Voak and Perrett's (1999) and (2000) findings of increased attraction to masculine rather than feminine male faces in the days preceding ovulation. In 2012, Harris re-analysed the initial 2011 data in order to further demonstrate that systematic shifts in female preferences remained absent, regardless of whether these effects were measured in women during the most fertile phase of their life. Harris (2012) re-analysed the data set to include younger female observers, and used the same counting forward method (to estimate ovulation) as Penton-Voak and Perrett (2000) to test women from the first day of menstruation to day 5, days 6-14 after menstrual onset, and again on days 15-28 of their cycle. Again, Harris (2012) found the opposite effect, whereby females displayed enhanced preferences for feminine and not masculine male faces during their fertile phase of their menstrual cycle. In their meta-analysis, Wood and Carden (2014) argue that a general bias in publication of statistically significant research findings makes it difficult to portray a true representation of the number of studies finding no evidence in support of the cycle shift hypothesis. According to Wood and Carden (2014) and Harris (2012), this publication bias suggests that there may exist a body of unpublished findings demonstrating no effects of menstrual cycle phase upon female mate preferences. To rely on published findings revealing statistically significant cyclic shifts in female preferences is therefore to rely on a biased representation of findings. Wood et al (2012)'s meta-analysis has been criticised for arbitrarily reporting unpublished findings resulting in an unclear representation of mixed findings in support of the Cycle Shift Hypothesis. According to Gildersleeve, Hasleton and Fales (2014) a re-analysis of such data reveals a robust body of findings demonstrating clear shifts in female preferences. Additionally, Gildersleeve, Hasleton & Fales (2014) argue that regardless of both published and unpublished findings demonstrating no cycle effect on female sexual motivations, these do not negate the existence of findings that *do* provide robust evidence for the hypothesis (Gilversleeve et al, 2013). It is also important to note that significant effects of subtle and nuanced changes in perception are sensitive phenomena to measure. The venture to identify the presence of such effects should therefore be considered in relation to a wider body of research in cognitive psychology that *does* provide supporting evidence for systematic shifts in female preferences. Gildersleeve et al. (2013) highlight that while shifts in female mate preferences may be difficult to distinguish in visual perception, there exists a body of robust evidence demonstrating that these effects extend to other cognitive domains and also in other mammalian species (see Gildersleeve et al., 2013 for a review). However, consistent reports of subjectively constructed meta-analyses provide an unclear representation of findings in support of the cycle shift hypothesis. This discrepancy across findings has often been attributed to inconsistencies in the methods employed across these different studies.

Methodological limitations

A primary concern raised in the debates of the equivocal findings outlined above often refer to way in which the fertile phase is calculated and used to categorise female participants. The way in which ovulation is calculated and predicted to occur may have a significant influence on the outcome and direction of results (Gilversleeve et al, 2013). Often, studies have relied upon subjective self reports of menstrual cycle patterns in order to calculate when a female is most likely to ovulate. However, an inherent issue with this method is that it allows for errors in the precision of reported dates. Wood et al (2012) claim that Gildersleeve et al's (2013) conclusion of robust evidence for the cycle shift hypothesis was derived from studies using subject self-reports to predict ovulation. According to Wood et al (2014) relying on such self-reports of menstrual cycle details includes individual errors for tracking hormonal patterns. This claim is supported by findings where, upon retrospection, one third of women miscalculated day of cycle by up to 3 days (Wegienka & Baird, 2005). While this is a small number of days to miscalculate, it could result in significant errors when estimating the fertile phase for each menstrual cycle. Gildersleeve et al. (2013) also acknowledge that subject self-reports are not sufficient to confirm ovulation. Such subjective self-reports of cycle patterns are used in addition to either the counting forwards or backwards method for predicting a female's fertile window (Penton-Voak & Perrett, 1999; Penton-Voak & Perrett, 2000). However, use of either of these methods is unlikely to be a sole determinant of the size and direction of findings, as Wood et al (2012) argue. This is demonstrated in Penton-Voak & Perrett's (1999; 2000) significant findings of systematic shifts in female preferences, where one study adopted the use of the counting backwards method, while the other adopted the use of the counting forwards method, respectively. Harris (2012) refers to the alternating use of either the counting forwards or backwards method when predicting ovulation, noting that often, these two separate methods are arbitrarily adopted and used interchangeably without explanation. If findings of cyclic female preferences are robust, we should perhaps expect to observe them through consistent use of the same methodology.

An alternative measurement of ovulation is the use of hormonal assays to track hormonal fluctuation across the menstrual cycle. Wood and Carden (2014) argue that when these hormonal tests are used to validate ovulation, effects of shifts in female preferences diminish. From this, they conclude that in light of using more precise measurements of fertility, effect sizes in support of the Cycle Shift Hypothesis will decrease. Wood and Carden (2014) argue that these findings demonstrate the importance of adopting empirical measurements of a female's hormonal status, as they provide reliable findings that demonstrate no systematic shifts in female sexual interests when fertility is accurate measured. However, the use of hormonal assays to confirm ovulation does not assure reliability when identifying the fertile phase of the cycle. The way in which these hormonal assays are delivered has an equally important influence on detecting ovulation. For example, Peters, Simmons and Rhodes (2009) found no enhanced interest in masculine or symmetrical faces during the ovulatory phase compared to the luteal phase of the cycle. Ovulating women were tested and classified as such via the use of luteinising hormone tests to confirm ovulation. Once this surge was confirmed participants were tested within 48 hours. However, while luteinising hormone is a reliable marker of the ovulatory peak, once this peak has occurred, ovulation and therefore conception likelihood levels very quickly collapse. A useful example of this fast decline in fertility levels is provided by Wilcox et al. (2001), who demonstrate that for women trying to conceive it may *not* be useful to wait until the day of ovulation to engage in intercourse. This is because as the days preceding the ovulatory peak also encapsulate the fertile window; once the ovulatory peak has occurred, this window very quickly closes. The same reasoning can be applied to the present research, and may account for findings such as Peters, Simmons & Rhodes (2009) who find no evidence of a mid-cycle peak in preferences for masculinity or symmetry. Waiting to confirm that ovulation has occurred before testing (within 48 hours) may result in missed opportunities to test in the fertile days prior to this peak, therefore also resulting in missed opportunities to accurately measure an effect of fertility. Peters, Simmons and Rhodes' (2009) comparison of female preferences between their classification of the ovulatory and luteal phases of the cycle may therefore have been hormonally too similar to identify an effect. If the participants were inadvertently tested after the ovulatory window had closed, levels of oestrogen (and therefore fertility) may have been of a similar level to when tested during the luteal phase of the cycle. Wilcox et al (2001) demonstrate in their findings that there are approximately 9 days where female fertility is highest, where levels peak on day 12, very quickly dissipating after day 14. Related to the issue of confirming ovulation is the number of days constituting the "fertile window". In their meta-analysis, Wood et al (2012) claim that broader fertile windows are associated with producing greater evidence of shifts in female preferences. The researchers interpret this as evidence of research artefacts; that specific designs such as larger fertile windows have been deliberately adopted in order to assure significant findings. However, Gildersleeve et al. (2013) strongly argue against this claim, stating that while the individual's fertile window may be small (approximately 48 hours), distributed across the cycles of many women causes individual variation in such windows to widen the overall fertile window of a participant group. Therefore, when measuring a collection of women who are predicted to be ovulating, it is important to account for a wide distribution of the average 9 day fertile window per female (Wilcox et al., 2001). By limiting this window, in such a way that Wood et al (2014) propose is necessary to identify an individual female's ovulatory window, the likelihood of detecting an effect of ovulation lessens (Gildersleeve et al., 2014).

In conclusion, outcomes of repeated meta-analyses demonstrate subjectivity and the over-looking of a holistic representation of mixed findings. This consistent use of meta-analytic techniques (Gildersleeve, Haselton & Fales, 2014; Gildersleeve et al., 2013; Wood & Carden, 2014; Wood et al., 2012; Harris, 2011; Harris, 2012) supporting each polarity in the debate appears only to serve as a means of extending this debate further without any significant consolidation across findings. Additionally, inconsistencies across the methods responsible for such mixed results demonstrate the importance of adopting research techniques that are sensitive and empirically sound. Arbitrary and inconsistently generated experimental designs and techniques previously adopted demonstrate that such methods are unable to produce consistent and reliable findings.

Theoretical limitations

In addition to empirical and methodological limitations, the Cycle Shift Hypothesis also faces criticism of the theoretical framework upon which it is based. Such criticisms range from notions of female infidelity to the reliability of physical indicators of genetic quality. These theoretical limitations are born from the inconsistencies emerging across findings (such as those outlined above) and raise uncertainty regarding the theoretical validity of the Cycle Shift Hypothesis. These shall be discussed only briefly, as the primary concern of this thesis is not with the theoretical underpinning of the Cycle Shift Hypothesis, but with establishing a useful and novel method to measure cyclical variation in female visual perception. Discussing these theoretical limitations is therefore useful in demonstrating the importance of adopting a new approach to investigating sexual selection in females. Several of these key theoretical limitations are outlined and summarised by Harris (2011; 2012). A core theoretical structure inherent to the Cycle Shift Hypothesis is the notion that adaptive shifts in sexual motivation occur in order to maximise females' reproductive output. This involves behavioural shifts that enable her to identify and access a range of ideal mating partners that will ensure her offspring are equipped with genes that will prosper. Inherent to this notion are therefore characteristics of infidelity and polygamy in female behaviour. However, Harris (2012) criticises this proposition of female infidelity on the basis that findings do not provide evidence of any significant shift of female interest to males other than her primary partner. According to Harris (2012), evidence that fertile females retain a sexual interest in their primary partner casts doubt on the key notion that females look to engage in extra-pair mating when conception is most likely. By this logic, we may expect to observe an apparent shift in female sexual interest from her primary partner towards other males during peak fertility. However, the Cycle Shift Hypothesis does not necessarily predict such absolute shifts in sexual interest. An important consideration here is that while the Cycle Shift Hypothesis posits that female sexual preferences and behaviour will change according to fertility, it does not assert that such fertility shifts wholly govern changes in female sexual interest. An overarching concept of the hypothesis is that cyclical variation in female preferences exist as vestigial remnants of ancestral conditions. In early modern humans these preferential shifts may have served as useful tools predominantly guiding female mate selection. However, within perception of modern women today these may be preserved as nuance effects, as opposed to being the single determinants responsible for female preferences. The hypothesis itself does not deny the value of experiential and societal influences upon the process of mate selection. It would therefore be a misconception of the Cycle Shift Hypothesis to interpret the lack of an absolute shift (or displacement) of sexual interest as a weakening of its theoretical construct. Instead, findings *do* demonstrate a subtle but present extension of female sexual interest towards males other than her primary partner. These include findings such as those outlined previously, whereby fertile women report greater sexual fantasies and interest towards men other than their primary partner (Gangestad, Thornhill & Graver, 2002), may dress more provocatively (Haselton, 2007) and engage in more flirtatious behaviour with men other than their primary partner (Durante & Li, 2009). Just as ovulation may subtly encourage behaviours related to infidelity in women, societal and cultural values of monogamy may preserve an interest in a female's current partner. These effects of reproductive hormones and external factors upon female preferences are not mutually exclusive, as Harris' criticism may suggest. Evidence of this claim comes from Harris' (2012) comment that single women reporting increased sexual interest in other men is not evidence of extra-pair mating, as the study excluded those who were in current relationships (Gueguen, 2009). However, this finding may be useful in demonstrating the subtle increase in motivation for extra-pair mating in women, because it controls for the social construct that places value upon monogamy (by testing only women whose responses were not influenced by current relationship). Additionally, Gildersleeve et al. (2013) provide findings that they claim to be clear evidence of an increase in female interest towards other males. Regardless of their relationship status, women whose current partners display less characteristics of genetic quality report greater attraction to other men when fertile. In conclusion, to reject the Cycle Shift Hypothesis in theory and research due to lack of findings demonstrating a pertinent shift in female preferences is to misinterpret a core concept of the hypothesis itself. Instead, as opposed to relying on evidence of dominant changes in female sexual interests, it may be useful to investigate the way in which these subtle effects are manifested in finer attributes of female perception. Implicit measures of such behaviours shall be discussed later. An additional theoretical criticism facing the Cycle Shift Hypothesis is the extent to which females rely on male-typical facial cues as reliable indicators of their genetic quality. If it is the case that such physical markers do not exist, the Cycle Shift Hypothesis is inherently weakened by a lack of evidence of the physical indicators responsible for eliciting such shifts in perception. Folstad and Karter (1992) propose the notion that male-typical traits such as masculinity exist as honest indicators of their possessors' suitability as a mate. These cues are considered as putative markers of males' genetic quality, where the cycle shift hypothesis relies upon this notion in explaining adaptive shifts in female preferences for these cues when they are most fertile. However, Boothroyd et al. (2009) found no association or additive effect of preferences for masculinity in female observers when these were combined with other reliable features of genetic quality (such as symmetry and averageness). These results raise doubt in the extent to which masculine features may be considered reliable cues of interest for fertile women. Harris (2011) claims that biologically driven reorientation of female interest towards such cues is not sufficiently supported by behavioural data. If this is the case, findings demonstrating cyclical preferences for masculine male faces lack theoretical support. However, it may be the case that male-typical masculine features are not such strong physical cues influencing the mate selection process in women. Gildersleeve et al. (2013) argue that this is not sufficient evidence to suggest that masculinity preferences do not exist, but that there is perhaps something else significant within a typically male face that makes it increasingly appealing to fertile female observers. In this instance, it is therefore necessary to consider and investigate the stimulus properties present in attractive male faces that may be better able to account for enhanced female preferences during ovulation (Gilversleeve et al., 2013; Boothyroyd, Lawson & Burt, 2009). Together, such criticisms of the theoretical framework of the cycle shift hypothesis illustrate that by its very nature, the hypothesis requires sensitive and cautious investigation. It is important to remember that experiments of this kind are concerned with very subtle and nuance aspects of perception. Measurements and designs used to investigate these should therefore be adopted in the same way. The theoretical claims outlined above highlight the importance of a more intricate investigation of stimulus properties in faces, and the associated visual mechanisms for processing these. In doing so, it may become possible to isolate the basic properties of faces that receive greater attention relative to subtle variations in female fertility.

A further and important theoretical consideration to make is the extent to which these evolutionary accounts of female perception provide an accurate understanding of sexual selection in human females. Such adaptive accounts posit that fertility-dependent shifts in female preferences have been selected by nature as mechanisms for ensuring females' may identify genetically suitable mates when most fertile. However, Gould and Lewontin (1979) assert that there is a value in the awareness of several limitations facing such evolutionary paradigms. It is important to note that while it is possible to measure any given behaviour in the present time, and to speculate from such observations its evolutionary function and history, these secondary analyses are vulnerable to subjective interpretation. Here, it is important to remember that it is not possible to directly observe the evolutionary changes that such behaviours have been subjected to and have consequently shaped by. Instead, our observations are limited to only their *current* utility, function, and mechanisms of control. From this, we may construct proximate predictions for how and why these behaviours evolved to their present day form. Gould & Lewontin (1979) refer to an architectural analogy that serves as a useful tool for constructing such predictions. When considering any given observable behaviour, it is important to discern the differences that may exist between the behaviour's current and original function. For example, upon initial observation the spandrels of San Marco appear to provide a structural value that is intrinsic to the rest of the basilica's architecture. Despite this appearance, the spandrels were constructed as a secondary addition purely for their aesthetic contribution. This contrast between the spandrels' seemingly structural function and actual aesthetic function demonstrates the limitations to understanding behaviour that evolutionary theories may inadvertently impose. This analogy demonstrates the importance of considering the difference between a behaviour's current qualities and the qualities for which it was initially selected. To assume a direct relationship between current and originally selected function is to include subjectivity and potential misinterpretation in accounts of behaviour. This analogy is directly applicable to research concerned with sexual selection in women. While many findings demonstrate systematic and seemingly functional shifts in female sexual preferences, it is important to maintain that although these accounts neatly define the evolutionary function of such behaviours, such accounts may not provide an absolute explanation for their existence. To accept an adaptive account on the basis of its palatability, or to replace one "inaccurate" account with another more plausible version, is to prevent a dynamic formulation of new perspectives. Here, the acceptance of any single account of behaviour as definitive creates rigidity and inhibits further investigation and consequently our understanding of behaviour. This is demonstrated across the collectively inconclusive meta-analyses outlined above, whose intentions appear at face value to either support or reject the cycle shift hypothesis as a robust account of female sexual preferences. In light of these current debates, the value of adopting a pluralistic approach when investigating cyclical variation in female perception becomes apparent. An initial step towards this pluralistic approach is to reconsider the ways in the Cycle Shift Hypothesis is investigated, the primary objective with which this thesis is concerned.

1.6 Constructing a mechanistic explanation of the Cycle Shift Hypothesis

In light of the empirical, methodological and theoretical limitations outlined above, it becomes apparent that a new approach to investigating the Cycle Shift Hypothesis is necessary. While it is possible to adopt sensitive and optimally accurate methods when estimating female hormonal status, the relationship between empirical findings and theoretical framework needs to be discussed. Overall, this section aims to provide an outline for why providing a mechanistic account of the cycle shift hypothesis may be a useful approach. With reference to Tinbergen (1963), this section discusses the rationale and objective for providing such a mechanistic explanation for cyclic shifts in female perception.

Not knowing

Gould & Lewontin's (1979) architectural analogy highlights the natural limits of our perspective when investigating the evolution of behaviour. The inability to view the evolutionary development of any given behaviour means that we can only speculate as to the reasons for which it was selected by nature in the first place. These boundaries in our capacity for observation often delimit accounts of behaviour proposed by evolutionary psychology. However, this reason alone, although discouraging, does not justify the rejection of such theoretical accounts of behaviour. Although we cannot directly observe the ancestral conditions responsible for shaping female sexual preferences, it can be argued that current perceptual behaviours already exist as the direct observers of our evolutionary history, and that our measurements of these is sufficient enough observation (Tooby, 1990). Evolutionary accounts of such behavioural phenomena must therefore be reminded of these limitations, conducting their analyses with caution and optimal objectivity. This requires, as Gould and Lewontin (1979) note, openness to different approaches and methods of investigation when measuring behaviour. This concept relies on the notion that there are natural limits to our understanding and access to truth, despite the extent to which we adopt the scientific approach (Feynmann & Leighton, 1988; Dawkins, 2013). Uncertainties in the outcome of our investigations are inherently important in the pursuit of knowledge and understanding. While they demonstrate limits in our capacity to provide an absolute and accurate account of sexual selection in females, they allow for an openness in our scientific investigation (Krauss, 2012). There is therefore a natural conjecture in evolutionary psychology, but the very uncertainty that makes is so also motivates the necessity for a pluralistic approach in such research. It is therefore necessary to avoid succumbing to ridged theories simply because they are palatable, as these only inhibit the growth of our understanding (Gould & Lewontin, 1979). Instead, other avenues of investigation must be considered, one of which this thesis proposes. As opposed to extending the search for overt systematic shifts in female preferences, or the discussions regarding the extent to which these findings are reliable, this thesis proposes a mechanistic investigation of such phenomena. Although providing a mechanistic explanation of female sexual preferences is a relatively novel and understudied approach in this field of study, measuring their proximal mechanisms optimises objective and scientific investigation. In searching for visual mechanisms in early perceptual processes, we may continue to refine and improve current evolutionary accounts of sexual selection in females to the best of our ability. Natural advancements in the methods for measuring these phenomena will undoubtedly occur, enabling the continued use of novel and increasingly accurate tools for investigation. In turn, these advancements will extend and refine our current models and understanding of the way in which sexually selective processes operate in modern women today (Gildersleeve et al., 2013; Wood & Carden, 2014).

Identifying the proximate mechanisms of behaviour

According to Tinbergen (1963), when questioning the nature of any given behaviour, there are four perspectives from which to consider it. The two perspectives employed by this thesis are the biological function and mechanisms of control of a given behaviour. These two perspectives require the consideration of a behaviour's *functional value* and *mechanisms of control,* representing the rationale and objective of this thesis, respectively. Considering the functionality of behaviour relates to the rationale of this thesis. This perspective is reminiscent of Gould & Lewontin (1979) in that Tinbergen also warns of the limits to our understanding and attribution of a behaviour's functional value. While we may speculate of the seemingly adaptive function of cyclic shifts in female perception, we must also recognise that simply because they appear to currently serve a particular function, this may not be a true representation of their adaptive origin. It is important then to be wary of formulating erroneous interpretations and inferences regarding the original function of these perceptual shifts. The second perspective refers to a behaviour's mechanisms of control, and demonstrates the objective of this thesis. Investigating the proximate mechanisms underpinning these perceptual shifts in females may provide insight that allows for greater accuracy in interpretations of their original functions. According to Tinbergen (1963), a behaviour's mechanisms of control operate at both high and lower levels of cognition. This includes influences from neurochemical, neuroanatomical, and hormonal factors. These mechanisms are not dissociable but instead part of a complex interplay responsible for underpinning the operation of a behaviour. This mechanistic perspective entertains the notion that sexual selective processes in females may be operating at both higher (as findings suggest) but also at lower levels of perception. If it is the case that such preferential shifts occur in higher levels of female cognition, it may also be the case that these exist and originate within earlier visual processes. Investigating the proximal mechanisms responsible for cyclical shifts in female preferences may therefore provide a deeper understanding of the way in which hormonal factors govern early visual processing in the female visual system.

Intentions of the present research

So far this thesis has presented an array of findings that demonstrate unique facets of female perception. A general consensus is that these female advantages for certain perceptual processes may facilitate adaptive shifts in female sexual preferences. Cycle Shift Hypothesis posits that these perceptual shifts may have been selected by nature to facilitate attention to reproductively relevant stimuli. However, also presented in this section is the array of mixed findings and limitations facing the Cycle Shift Hypothesis. Together, these findings and their associated criticisms demonstrate a current situation in the field whereby inconsistent meta-analyses are unable to reach a general conclusion regarding the validity of the Cycle Shift Hypothesis. This chapter thus far has addressed the necessity for a new approach to investigating sexual selection in females. Here, the natural limitations in the scientific approach have been discussed. However, these have been discussed in such a way as to highlight the importance of adopting novel techniques for measuring and observing cyclical shifts in female perception. The objective here is to accept and approximate the limitations of our observations of such evolutionary behaviours. A tool for achieving this has been proposed in reference to Tinbergen (1963) in the adoption of a mechanistic account of cyclical shifts in female preferences. Many accounts of cyclic variation in female perception formulate explanations beyond empirical findings. Instead, it may be useful to investigate the potential visual mechanisms that may underpin such variation; a perspective which is rarely discussed within the literature. For example, identifying both the stimulus properties eliciting female visual attention, and the way in which this attention varies across the menstrual cycle, will enable a novel observation of the way in which early visual mechanisms may be influenced by variation in female reproductive hormones. These investigations will allow us to take further steps in addressing the question of whether these hormonal effects provide any vestigial functions in women today, or if they occur simply as inadvertent side effects of natural hormonal variation across the menstrual cycle. The strength of this relationship between current utility and original function will remain open to a degree of uncertainty and interpretation. However, adopting a mechanistic perspective may provide a valuable insight into the way in which early perceptual processes could be influenced by changes in female fertility.

The following section will address current findings within psychophysical literature indicating a potential relationship between female reproductive hormones and low-level visual processes. If it is the case that such a relationship exists, these findings may open new avenues for theoretical discussion regarding the mechanisms of female sexual selection.

1.7 Cyclical variation in low-level visual perception

Previous sections have provided evidence demonstrating that cyclical variation in certain aspects of female perception. Here, natural fluctuation in oestrogen and progesterone are considered to exert a functional influence upon perception, in facilitating sensitivity and responsiveness to evolutionarily relevant stimuli such as faces. However, a relatively unaddressed question within this literature is the existence of potential mechanisms within perception that may underpin these cyclic shifts in perception. It may be that these effects upon higher-level perceptual processes are rooted in, and begin during lower, more basic visual processing. In adopting a mechanistic approach for investigating this question, it is important to consider a potential effect of hormonal fluctuation at in lower-level visual processes. Here, this section discusses the existing body of evidence suggesting that such a relationship between female reproductive hormones and low-level visual processing may exist.

Visual sensitivity across the menstrual cycle

There is a range of evidence from psychophysical studies demonstrating that across the menstrual cycle, women experience changes in visual sensitivity. Studies demonstrating these effects often refer to visual thresholds, whereby lower thresholds translate to greater visual sensitivity. For example, DeMarchi and Tong (1972) measured two flash fusion thresholds during the luteal and menstrual phases of the menstrual cycle. Two flash fusion tasks require participants to identify the point at which two separate flashes become perceived as one. These 2 flashes are presented closely in time, such that the time interval between each presentation decreases until the initial 2 flashes are no longer discernable. Two flash fusion thresholds are therefore a measure of the point at which two flashes are perceived as one, where lower thresholds reflect greater accuracy for discerning between the two flashes. These thresholds were measured across 3 days of women's menstrual cycles, taking place from the late luteal into the early menstrual phase. Results showed that thresholds were highest pre-menstrually, suggesting that during this time temporal visual sensitivity was worse compared to during the beginning of the menstrual cycle (DeMarchi & Tong, 1972). A similar study adopting the same experimental methods compared 2 flash fusion thresholds across 5 stages of the menstrual cycle (Wong & Tong, 1974). Here, naturally cycling women and those using combined oral contraceptives performed 2 flash fusion tasks on days 1, 5, 10, 15 and 26 of their menstrual cycles. Findings demonstrated an increase in visual thresholds during the pre-menstrual phase of the cycle. Additional fluctuations in these thresholds were also found in naturally cycling women. Here, lower thresholds during mid-cycle suggest that naturally cycling women are more sensitive to temporal discrimination when fertile (Wong & Tong, 1974). Replications of these findings provide further evidence that such a mid-cycle peak in temporal visual sensitivity that may be specific to women who experience naturally occurring ovulation. Friedman and Meares (1978) also found evidence of enhanced performance on 2 flash fusion tasks occurring in ovulatory phase of 2 consecutive menstrual cycles. Here, greater visual sensitivity was identified only during the days preceding ovulation in naturally cycling women. Outside of this window, sensitivity was comparable to that of women using oral contraceptives. These results suggest that for the days of the menstrual cycle where fertility is highest for naturally cycling women (Wilcox et al., 2001), visual temporal sensitivity is significantly enhanced (Friedman & Meares, 1978). Similarly designed studies using visual detection procedures have found similar trends. Barris, Dawson and Theiss (1980) used visual detection procedures requiring participants to detect the presence of a target letter stimulus. Performance for these tasks was used as a measure of scotopic visual thresholds across the menstrual cycle. These findings support evidence of a mid-cycle peak in visual sensitivity in tasks relying on visual detection abilities. Enhanced visual detection therefore also appears to co-occur with ovulation in naturally cycling women. Female participants were tested across 7 consecutive days during the middle of their cycle, where an increase in performance on visual detection tasks were highest on the day corresponding to highest basal body temperature (a measure used to predict high fertility). This trend was also consistent when measured across 3 consecutive cycles of one participant, although this trend was not statistically significant. However, in a similar study, visual detection across 4 stages of the menstrual cycle showed significant variation only in the form of decreased visual detection performance during the premenstrual phase of the cycle (Ward, Stone & Sandman, 1978).

This enhancing effect of fertility for visual sensitivity in women has also been considered in relation to the attentional validity effect. The attentional validity effect occurs during visual detection tasks, whereby a target stimulus appears at a previously cued location, causing an increase in reaction times to identify a target stimulus. It therefore refers to the extent that visual attention to a target stimulus is facilitated by a previous stimulus cue. It has been proposed that greater visual sensitivity may be underpinned by an attentional validity effect that is enhanced during mid-cycle (Beaudoin & Marrocco, 2005). Women's performance on tasks of cued target detection was measured for 3 phases across the menstrual cycle. Findings revealed that ovulation was associated with a decrease in reaction times for cued validity effects, compared to an increase in these reaction times on the days before and after the ovulatory peak. Female participants displaying a peak in basal body temperature also displayed quicker reaction times for detecting cued targets, indicating an increase in visual attention during this time of high fertility. Additionally, quicker reaction times were not found in women who failed to show a peak in basal body temperature, strongly suggestive of a relationship between enhanced cued validity effect and the occurrence of ovulation in women. These findings have been interpreted as evidence of an attentional facilitation and enhancing effect for visual attention, which may aid attention to particular stimuli (Beaudoin & Marrocco, 2005).

Functionality of increased visual sensitivity during high fertility

Although the above evidence suggests a degree of discrepancy with regards to *where* in the menstrual cycle changes in visual thresholds occur, greater visual sensitivity is generally found to occur when fertility is highest for naturally cycling women. These findings have been interpreted in several ways. The pre-menstrual rise in visual thresholds indicative of poorer visual sensitivity are often attributed to changes in criteria for women in the latter half of their menstrual cycles. Such other accounts implicate a possible effect of progesterone during the premenstrual phase of the menstrual cycle. Here, changes in criterion levels in women may have a significant effect on task performance, such that women's responses are delivered with greater caution and apprehension (DeMarchi & Tong, 1972). A further interpretation of enhanced visual sensitivity during mid-cycle is provided by Kopell et al. (1969), who propose a potential direct and functional neuro-endocrine relationship between visual sensitivity and female reproductive hormones. Here, Kopell et al's (1969) theory of general arousal interprets these findings as evidence of a general and deliberate peak in visual sensitivity when female fertility levels are high. According to Kopell et al. (1969), greater visual sensitivity during this time may facilitate enhanced attention to, and detection of evolutionarily relevant stimuli. However, further evidence of cyclical shifts in visual sensitivity demonstrates limitations facing this account. Consistent with Barriss, Dawson and Theiss' (1980), Scher, Pionk and Purcell (1981) found evidence of lower visual thresholds for dark-adapted conditions. Across 5 phases of the menstrual cycle, naturally cycling women displayed a mid-cycle peak for dark-adapted visual sensitivity. However, this pattern is not the same for light-adaptation tasks, such that for these tasks, visual thresholds remain consistent across the menstrual cycle. These results are not consistent with Kopell's (1969) notion of a global peak in visual arousal, suggesting instead that such cyclic variation may be specific to a particular region of visual processing (Scher, Pionk & Purcell, 1981). Similarly, it has also been proposed that enhanced visual sensitivity during mid-cycle may be task-specific. Scher, Purcell and Caputo (1985) compared visual acuity during a target identification task between menstruating and ovulating women. Their findings revealed that performance for tasks of visual acuity was *poorer* during the ovulatory phase of the menstrual cycle. Although these findings do not appear to provide supporting evidence of a mid-cycle peak in visual sensitivity, they do highlight the importance of considering the way in which an increase in arousal may have implications for perception. Here, the authors propose that it is the increase in visual sensitivity during peak fertility that is responsible for inhibiting target identification under dark-adapted conditions. Under such conditions, they propose that a fertile female's visual system may become oversaturated, thus reducing the contrast of any given stimulus. Therefore, although these findings do not direct contradict Koepll et al's (1969) theory of general arousal, they do demonstrate that such an increase in visual sensitivity may not always provide advantages for perception, but may in fact hinder performance in certain perceptual processes (Scher, Purcell & Caputo, 1985). Kopell's proposed account of general arousal, although referred to within the literature is therefore often considered with caution in addition to other accounts of increased visual sensitivity, including cognitive changes in criterion experienced by women premenstrually, or simply as inadvertent side effects of fluctuation in female reproductive hormones.

Methodological inconsistencies

A primary issue within the literature outlined above is the degree of methodological inconsistencies that together create a difficulty when considering the relationship between female reproductive hormones and low-level visual processes. The first and most relevant is the phase of menstrual cycle during which female participants are tested. When observing effects of visual perception in relation to fluctuation in female reproductive hormones, it is important to consider the very nature of the menstrual cycle. The nature of the menstrual cycle is such that a female's hormonal status is not by any means stable, but is instead in a continuous state of change. Therefore, in order to establish whether there is an effect of fertility, it is important to consider the role of oestrogen in such investigations. The mid-cycle peak in oestrogen is indicative of ovulation, and so to formulate conclusions of cyclic shifts in perception without testing having occurred during this phase of the cycle provides an unclear representation. Often, measuring across the menstrual cycle helps to provide baseline measurements for high versus low levels of fertility in female participants. For example, oestrogen levels are drastically different during ovulation compared to during menstruation, however this difference is far smaller when viewed at the luteal and menstrual phase of the cycle (Scher, Purcell & Caputo, 1985; Parlee, 1983). For example, DeMarchi and Tong (1972) concluded form their findings that visual sensitivity does vary across the menstrual cycle. Here, they found that thresholds for visual sensitivity were highest during the premenstrual phase of the menstrual cycle. However, during this study, visual thresholds were only measured across 3 days spanning the end of the luteal phase and into the early menstrual phase. Measurements did not, therefore, take place during or across the middle of the menstrual cycle, and are therefore not representative of changes in visual sensitivity occurring as a result of fertility. When visual thresholds are measured consistently across the cycle (Wong & Tong, 1974), cyclic changes in visual sensitivity are more pronounced, where findings consistently demonstrate a peak in visual sensitivity during and around the time of ovulation for naturally cycling women (Wong & Tong, 1974; Barris, Dawson & Theiss (1980). While this issue is concerned with cyclical variation *within* female participants, a similar issue is the lack of investigation *between* female participants. For example, when observing such influences of ovulation, a useful comparison is to investigate such variation not only across the menstrual cycles of women, but also in relation to women who do not experience naturally occurring ovulation. A useful measure here is therefore to include a control participant group as a baseline measurement for performance when naturally occurring ovulation is artificially inhibited. Without such a comparison, limitations arise when interpreting findings as occurring as a primary result of ovulation. For example, Scher, Purcell and Caputo (1985) compared visual sensitivity between menstruating and ovulating women and reported finding that performance was poorer during the ovulatory phase. However, their study did not include a representation of female participants who did not experience naturally occurring ovulation. Without such a participant comparison group, it is difficult to discuss these effects of visual sensitivity in relation to shifts in female fertility.

1.8 Summary

Sections within this chapter have discussed evolutionary accounts of cyclic shifts in female perception. However, such accounts do not always address the potential visual mechanisms responsible for this variation. In a similar way, psychophysical accounts of hormonal influences upon low-level vision, although limited, do not tend to discuss these findings in relation to their possible functional value. Additionally, mixed and inconsistent methodology across these findings creates difficulty in establishing the nature of cyclic shifts in visual sensitivity. Further investigation is necessary to establish the nature and potential functionality of such cyclic shifts in visual sensitivity, and to address this variation as a potential mechanism related to the Cycle Shift Hypothesis. The potentially relative importance of hormonal influence upon such processes may be a useful contribution to both fields of literature, as this is a highly understudied topic.

In this thesis, I present 2 studies that assess potential sex differences in visual perception, and in particular the extent to which these differences are influenced by female reproductive hormones. In chapter 2, I present a study of contrast sensitivity as measured across the menstrual cycle. In chapter 3, I present a study of continuous flash suppression as a measure of facial emotion detection. Chapter 4 discusses findings from these 2 experiments within context of sex differences in visual perception and the Cycle Shift Hypothesis.

Chapter 2: Contrast sensitivity across the menstrual cycle

2.1 Introduction

Findings from psychophysical studies outlined in the previous chapter demonstrate an array of evidence suggesting that during the most fertile phase of the menstrual cycle, women experience enhanced visual sensitivity. However, as previously discussed, inconsistencies in the methodology across these findings creates uncertainty with regards to *where* in visual processing this enhancement is occurring. Additionally, methods employed to measure these effects across the menstrual cycle are also not consistent in the research, such that these changes in visual sensitivity are not always measured in direct relation to fertility shifts in women. This chapter therefore addresses findings of enhanced visual sensitivity derived from studies of contrast sensitivity. Here, such studies provide a measure of visual sensitivity with a greater degree of methodological consistency, and with more direct reference to hormonal shifts across the menstrual cycle.

Contrast sensitivity refers to the way in which the visual system detects the salience of a stimulus' contrast, relying on the magnitude of difference between varying light and dark components of which it is composed. Visual thresholds for contrast sensitivity therefore represent the very minimum level of intensity difference between these light and dark components required to evoke an observer's recognition of a barely visible stimulus (Mather, 2006; Milner & Goodale, 1995). Lower thresholds of contrast sensitivity can therefore be interpreted as increased sensitivity for detecting a stimulus. Consistent findings from psychophysical experiments demonstrate that contrast thresholds are different for different spatial frequencies, and also that the visual system appears to have an optimal level of sensitivity for identifying intensity differences (and therefore sensitivity to) stimuli whose spatial content is composed of mid-range spatial frequencies (around 4 cycles/degree) (Klein et al., 1997). These findings demonstrate that the human visual system is therefore most attuned to viewing contrast differences in stimuli whose spectral composition consists of such mid-range spatial frequency content (Leguire et al., 2011). As spatial frequency content increases or decreases, the visual system becomes less able to detect changes in contrast (Campbell & Robson, 1968). Surprisingly, the investigation of sex differences in such low-levels of visual perception is a relatively understudies topic (Guttridge, 1994). Brabyn & McGuinness (1979) measured differences between male and female contrast thresholds for different spatial frequencies ranging from .4 to 10 cycles/degree (cpd). Here, participants were required to adjust the contrast level for gratings with different spatial frequency content. Contrast levels for each grating were increased until participants' indicated the point at which they became visible. Results demonstrated that women's thresholds for lower spatial frequencies were smaller than those belonging to men, suggesting a subtle advantage in contrast sensitivity in women (in relation to smaller spatial frequencies). However, similar psychophysical studies have demonstrated no such sex differences in visual processing of different spatial frequencies. Solberg and Brown (2002) measured sex differences in contrast sensitivity and response times for different spatial frequencies (.05, 1.5, 3, 6 and 12 cpd gratings). However, results revealed no significant sex differences in response times for detecting any spatial frequencies, suggesting that perhaps women do not possess an advantage for detecting low spatial frequency information (Solberg & Brown, 2002). Interestingly, however, some (although little) research has investigated changes in contrast sensitivity across the menstrual cycle.

Johnson and Petersik (1987) provide preliminary findings of cyclical variation in contrast sensitivity occurring across the menstrual cycles of 2 naturally ovulating women. Participants were measured every day across a single menstrual cycle, based on the notion that arbitrarily segmenting the menstrual cycle based on hormonal status is futile. Instead, daily measurements allow for inclusion of individual variation in reproductive hormones that dynamically change throughout the cycle's duration (Parlee, 1983; Johnson & Petersik, 1987). Contrast thresholds were measured for 2, 4 and 16 cpd gratings on a daily basis. Here, participants were required to "rank up" the contrast level of each grating until the point at which they became barely visible, thus providing an absolute threshold for detecting a grating. Results revealed cyclical changes in visual contrast thresholds in the 2 naturally cycling women, where these cyclic shifts in contrast sensitivity were not observed in the 2 control subjects (1 male and 1 non-menstruating female). This cyclic variation in contrast sensitivity was such that women displayed greater sensitivity for detecting 4cpd gratings during the postovulatory phase of their cycles. These findings were interpreted as evidence of a hormonally-mediated enhancement in an already sensitive visual channel. Similarly, Dun and Ross (1985) also measured contrast sensitivity for 8, 18, and 26 cpd. Their findings demonstrated that contrast sensitivity was highest in the postovulatory phase of 10 naturally cycling women, revealing that variation in contrast thresholds vary between days 5 and 32 of the menstrual cycle.

However, although these two studies provide evidence of cyclic fluctuation in contrast sensitivity, several methodological inconsistencies remain. While Johnson and Petersik (1987) attribute their results to a hormonal influence existing in naturally cycling women, these findings were not compared to women not experiencing a natural menstrual cycle. Their comparison (control) group consisted of only 1 female, who reported both breastfeeding and having no experience of menstruation in the months surrounding time of testing. This lack of comparison of cyclic variation in female participants *not* experiencing "normal" menstrual cycles also creates uncertainty with regards to whether or not these cyclic shifts in contrast sensitivity were wholly responsible for naturally occurring shifts in female reproductive hormones. Additionally, the 2 naturally cycling women could not be tested for 4 days during their cycle, where average contrast thresholds were generated for these missing data (Johnson & Petersik, 1987). Although the study provided an intricate measurement across the menstrual cycle, the way in which these missing days may have influenced findings was not addressed in the analysis. The extent to which changes in contrast sensitivity reliably occur across the menstrual cycle, and the way in which this variation is related to natural fluctuations in female fertility, remains open for further investigation.

The findings outlined here provide evidence to suggest that cyclic changes in contrast sensitivity may reliably occur both between and within sexes. However, here it is important to return to this thesis' rationale for adopting a mechanistic approach for investigating the cycle shift hypothesis. While there is no certainty in the implication of contrast sensitivity as a mechanism for underpinning cyclic shifts in female perception, findings do suggest an interesting and potentially significant influence between this visual channel and changes in female reproductive hormones. Existing literature addressing this relationship does not provide evidence enough to formulate a clearer answer to this question. Therefore, this thesis proposes an extended investigation of this relationship in order to gain further insight into the way in which contrast sensitivity may be influenced by naturally occurring changes in female fertility. While contrast sensitivity may not be wholly, or at all responsible for such cyclical variation demonstrated by the cycle shift hypothesis, investigation here seems to be a logical step for investigating such potential low-level mechanisms.

In this experiment, we measure contrast sensitivity for 1, 4 and 16 cpd across a single menstrual cycle in both naturally cycling women and women using combined oral-contraception. Because we investigate these effects in relation to the cycle shift hypothesis, which implicates the occurrence of ovulation as an important factor governing shifts in female perception, users of combined pills were used as only this form of oral contraception inhibits natural ovulation. Measurements were taken across three cardinal phases of the menstrual cycle, the ovulatory, luteal and menstrual phases. The latter two provide useful baseline measurements for comparing performance against high-fertility phases of the cycle (ovulation). Additionally, contrast sensitivity in males was also measured across 3 test sessions in order to further investigate sex differences in such visual processes. The anticipated outcome here was, by nature, unprecedented. Based on limited and equivocal findings in the current literature the direction of expected effects was unclear. Based on findings from Brabyn and McGuinness (1979), women's visual thresholds may have been expected to decrease for lower spatial frequencies, where an enhanced effect of this may have been expected mid-cycle. In comparison, findings from Johnson and Petersik (1987) suggested an expected finding of a fluctuation in contrast thresholds for mid-range frequencies, where these effects could be confined to only naturally ovulating women. However, based on Solberg and Brown's (2002) findings, we may perhaps have expected to identify no difference either between or within men and women at all. Again, this very point refers to the exploratory nature of this thesis, and highlights the potential contribution of the present experiment to both fields of psychophysics and evolutionary psychology.

2.2 Methods

Participants

A total of 49 participants were recruited overall, and were categorised into three groups. The naturally cycling female group comprised 21 female participants (mean age: 21.6 years), who were *not* using hormonal oral contraceptives of any kind. Female oral contraceptive users were one of the two control groups, and consisted of 14 female participants (mean age: 20 years) who were currently *using* hormonal oral contraceptives at the time of testing. All 14 of these female contraceptive users were consistently using the "combined pill" at the time of testing, such that artificial levels of *both* oestrogen and progesterone inhibited naturally occurring ovulation. The combined oral contraceptive pills included brands such as: Yasmin, Rigevidon, Loette 28, Marvelon, Yaz and Microgynon. The third group consisted of 14 male participants (mean age: 21.5 years). All participants were recruited on a voluntary basis, taking part in exchange for either monetary reward or to achieve credits required for a compulsory undergraduate research module. Although this experiment was concerned with measuring the effect of variation in female reproductive

hormones, males were also recruited as control participants. This secondary control group served as a reliable comparison group for investigating variation in contrast sensitivity both between sexes and within female groups. Previous studies have demonstrated the importance of adopting this relative view, as opposed to investigating the effects in isolation of one participant group (Guapo, 2009).
All female participants who took part in the experiment first completed an online pre-screening questionnaire to ensure eligibility to take part in the study (see appendix). Across all 49 participants, 1 male reported using Isotretinoin, 2 females using Sertraline, 1 female using Fluoxetine, and 1 female using Levaxin. None of these medications were considered to influence visual sensitivity. Participants requiring corrective lenses adopted the use of these for the duration of all experimental sessions.

Design

A 3(group)x3(spatial frequency)x3(cycle phase) mixed-design was used across repeated measures testing sessions. Contraceptive use and sex determined participants' allocation to the naturally cycling, oral contraceptive users, or male group. This categorisation process was the between-subjects factor. Stimuli were sinusoidal gratings of three different spatial frequencies: 1, 4, and 16 cycles/degree (cpd). Overall, three experimental test sessions were calculated to take place across three of the critical phases of female participants' menstrual cycle. This included the early follicular phase (or menses) occurring between days 1-7 of the menstrual cycle; the ovulatory phase, occurring between days 11-14 of the cycle; and the luteal phase, occurring between days 17-28 of the cycle. Male participants were also tested across three experimental sessions, these were distributed across the same time lapses as for female participants. Spatial frequency and phase of the menstrual cycle were therefore the within-subjects factors. Contrast thresholds (the contrast required to accurately report the orientation of gratings on 75% of trials) were measured for each spatial frequency. This response therefore represented the dependent variable.

Apparatus

Stimuli were presented using a VIEWPIXX 3D monitor, viewed from a distance of 65 cm. The monitor screen was 52 centimeters wide and 29 centimeters tall. The screen resolution was 1920x1080 pixels, with a refresh rate of 120Hz and an average luminance of 50 cdm-2l. Each pixel subtended 1.43 arc min. Stimuli were presented at 10 bit resolution. Observers' responses (deciding the orientation of each sinusoid) were recorded using the RESPONSEPixx response box. Stimuli were generated and presented using MATLAB and the Psychophysics Tool box extensions (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007).

Stimuli

Stimuli for the experiment were Gabor patches with a spatial frequency of 1,4 or 16 cpd. The standard deviation of the Gabors was two hundred times the wavelength of the sinusoid. This resulted in stimulus gratings of high spatial frequencies being presented in smaller windows, and larger windows for lower spatial frequencies. This ensured the same number of cycles for all spatial frequencies. The orientation of the sinusoid on each trial was ±45 degrees away from vertical, either clockwise or anticlockwise. Six contrast levels were used, each presented forty times in a randomised order. For 1cpd gratings, the Michelson contrast levels used were 0.001, 0.002, 0.003, 0.004, 0.005 and 0.0075. For the 4cpd gratings, the contrast levels used were 0.001, 0.015, 0.002, 0.003, 0.004 and 0.005. For the 16cpd gratings, the contrast levels used were 0.02, 0.03, 0.04, 0.05, 0.05, 0.06 and 0.07. These contrasts were selected after extensive pilot measures, run in order to establish the appropriate contrast variations for each spatial frequency. Examples of these stimulus gratings are presented below in Figure 3.

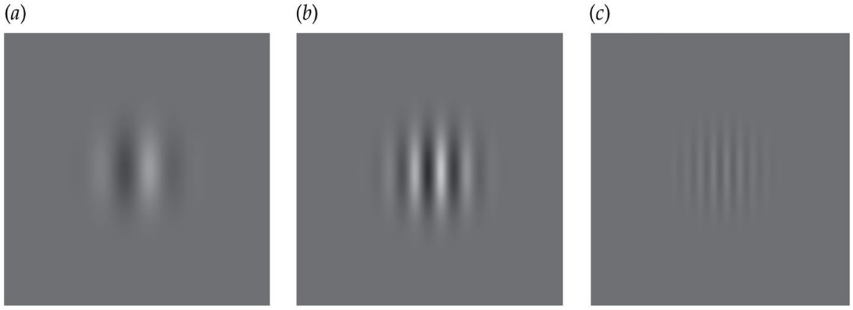

Figure 3. Examples of Gabor gratings with increasing frequency (left to right). Each representing low, mid-range and high spatial frequencies.

Procedure

Before taking part in the experiment, female participants completed an online prescreening questionnaire to ensure that they met the set of criteria required to take part (see Apprendix). This included: reporting a cycle length of no more than 35 days, experiencing regular and consistently occurring menstruation, and in the three months prior to the experiment having no experience of: pregnancy, breastfeeding, or emergency contraception.

Participants were tested individually in a quiet room and informed that the nature of the study was concerned with visual perception. Before the onset of the first trial participants performed a short demonstration trial of high contrast gratings to familiarise them with the task. All female (naturally cycling women and users of combined oral contraceptives) participants were tested within the time frames of 3 phases of their menstrual cycle, such that each participant was tested during their early follicular phase (days 1-7 of cycle), ovulatory phase (days 11-14 of cycle) and luteal phase (days 17-28 of cycle). Male participants were tested across 3 experimental sessions, spaced 1 week apart to reflect similar time intervals. Using a repeated measures design, each female participant began testing during the ovulatory phase of her cycle, followed by the luteal and early follicular test sessions.

Female participants' cycle position was estimated using information submitted via the online questionnaire. From this, using the counting backwards method a "fertile window" was calculated for each observer. This methodological procedure was adopted for its reliability in determining the high fertility days of the cycle (Gildersleeve et al., 2014). This method is based on the consensus that the day of ovulation occurs fourteen days prior to next menstruation onset (beginning of next cycle) (Macrae, 2002). Each female participant therefore began the first test session during the calculated fertile phase, followed by testing during the luteal phase, where the final test session confirmed that next menstrual onset had occurred.

For each of the three test sessions, three blocks of 240 trials were presented to participants. For each trial, a fixation cross was presented for 250 milliseconds, followed by the stimulus for 500 milliseconds. Using a two-alternative forced choice procedure, participants used a left or right button on the response box to indicate whether the Gabor was tilted leftwards or rightwards from vertical. After responding, a fixation cross would appear before onset of the next trial. The trials for each spatial frequency were presented in three separate blocks; the order of these blocks within a testing session was randomized. Within a block, each contrast level was presented 40 times, in a randomized order. Experiments were performed in a dimly lit laboratory.

2.3 Results and conclusion

Within each testing session, gratings of a single spatial frequency were presented at 6 contrast levels. Each contrast level was presented 40 times. We recorded the proportion of times that the participant correctly reported the orientation of the grating for each level. This was then used to create a contrast sensitivity function. We fit a cumulative Gaussian function to these data, and used this to determine a contrast detection threshold. This was defined as the contrast required for the participant to correctly identify the orientation of the grating on 75% of trials.

Means and standard deviations of contrast detection thresholds were calculated for each group and for each spatial frequency, measured across all 3 phases of the menstrual cycle (3 equivalent test sessions for male participants). Mean contrast detection thresholds are visible in figures 4, 5 and 6 below. A 3(group)x3(frequency)x3(phase) mixed ANOVA was used to analyse the data. This included participant group as the between-subjects factor (14 males, 14 oral contraceptive users, 21 naturally cycling women). The two within-subjects factors were frequency (1, 4, 16 cpd) and phase (ovulation, luteal, menstrual).

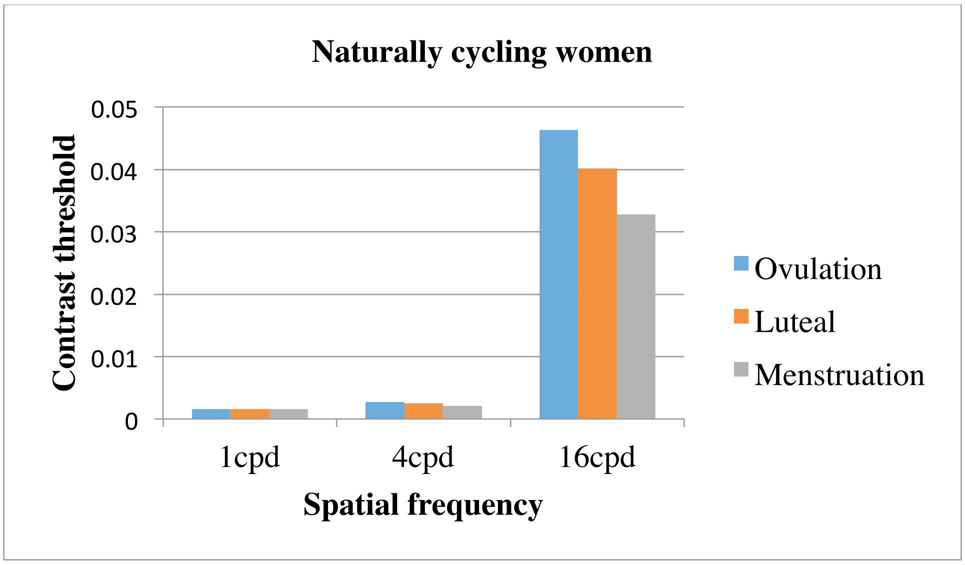

Figure 4: Mean contrast thresholds for 1,4 and 16 cpd gratings, across the 3 experimental sessions in naturally cycling women.

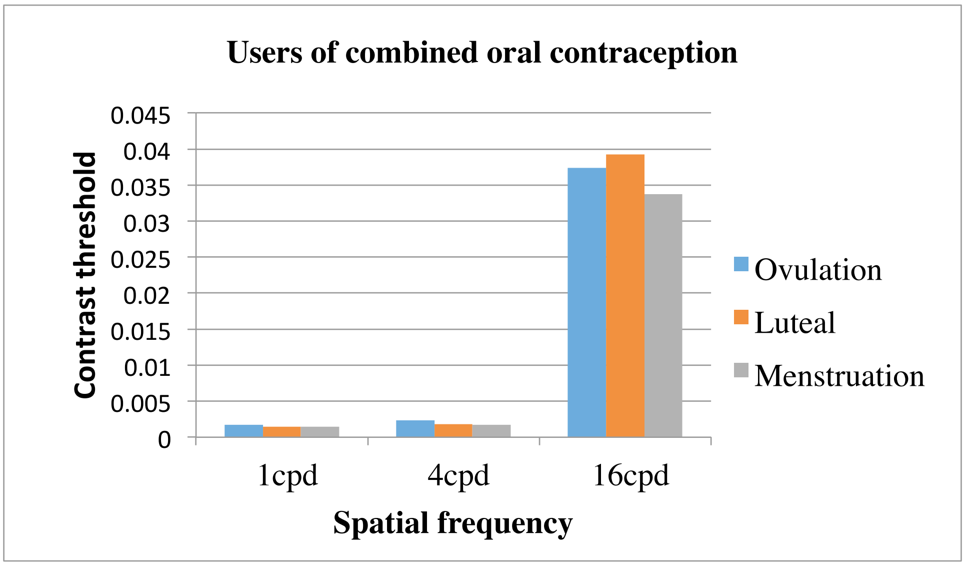

Figure 5: Mean contrast thresholds for 1,4 and 16 cpd gratings, across the 3 experimental sessions in female participants using combined oral contraceptives.

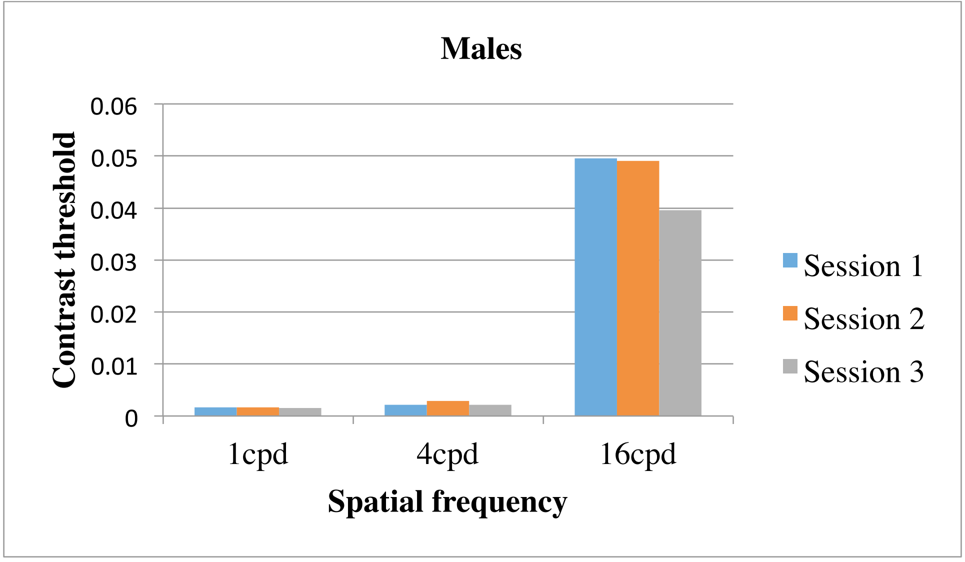

Figure 6: Mean contrast thresholds for 1, 4 and 16 cpd gratings, across the 3 experimental sessions in male participants.

A significant main effect of spatial frequency (*F*(2, 92) = 58.28; p = <0.001), showed that when pooled across participant group and phase, there was a significant difference in contrast thresholds across the 3 spatial frequencies. Paired samples t-tests were used to compare thresholds across the 3 frequencies. These revealed significant differences between thresholds for all pairs of frequencies. A significant difference was found between gratings of 1 (mean: .0016, SD: <.001) and 4 (mean: .0023 SD:.001) cpd gratings (t(146)=-6.38, p =<.001) where contrast thresholds were lower for 1 cpd gratings than for 4 cpd gratings. Contrast thresholds for both 1 and 4 cpd gratings were significantly different from those for 16 (mean:.407 SD: 0.38) cpd gratings. A significant difference between 1 and 16 (mean:.407 SD:.038) cpd gratings revealed that contrast thresholds were significantly greater for 16 cpd gratings (t(146)=-12.78, p =<.001). This was followed by a significant difference in thresholds for 4 and 16 cpd gratings (t(146)=-12.809, p =<.001). Overall, significantly different contrast thresholds for each of the 3 spatial frequencies demonstrated that sensitivity was greater for lower spatial frequency gratings (1 cpd) than for mid-range (4 cpd) gratings. The additional finding that sensitivity was lowest for gratings composed of higher spatial frequencies (16 cpd) is consistent with findings from previous studies. This finding further demonstrates that under normal photopic conditions, less contrast is required for (and therefore lower thresholds) identifying lower frequency gratings composed of 1 and 4 cpd. Higher spatial frequencies such as the 16 cpd gratings presented in the present experiment become increasingly difficult to discriminate as spatial frequency increases (Campbell & Robson, 1968). This significant main effect therefore confirms that for higher spatial frequency gratings (16 cycles/deg), contrast thresholds are higher across all participants and regardless of sex, contraceptive use or menstrual cycle phase. This effect is demonstrated in the figures below.

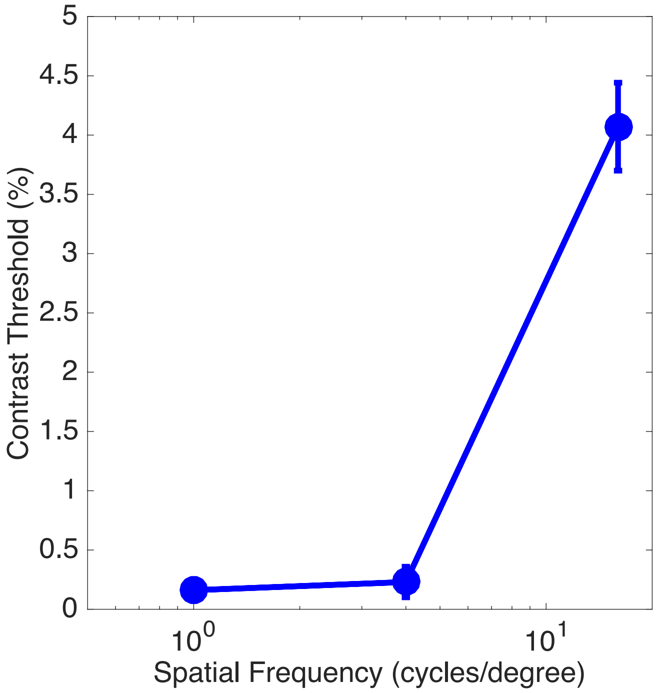

Figure 7: Contrast thresholds for 1,4 and 16 cpd gratings, pooled across all participants and experimental sessions.

Additionally, a significant main effect of cycle phase was also found (*F*(2, 92) = 4.94, p = 0.009), revealing a significant difference in contrast thresholds occurring across each of the 3 test sessions. However, as illustrated in Figures 4, 5 and 6 this effect translates to a gradual practice effect across the three experimental sessions where performance is highest on the final session.

In order to observe differences between participants' thresholds independently of this practice effect, 3 two-way ANOVAs were performed to compare thresholds across participant groups separately for each experimental session. These included the between-subjects factor of group (naturally cycling women, combined-pill users, males), and the within-subject factor of frequency (1, 4, 16 cpd). The first two-way ANOVA measured differences in contrast thresholds for each of the 3 spatial frequencies during the *ovulatory* session (session 1). Here, the significant effect of frequency was maintained (*F* (2, 4) = 55.61, *p*= <.00) but there was no significant effect of group (*F* (2, 46) = 68.17), *p*= .713). Together with the fact that there was no significant interaction between frequency and group (*F* (4, 92) = .37, *p*= .84), these results show that contrast thresholds did not differ between participants for any of the frequencies during the ovulation test session. These findings are shown in Figures 6.

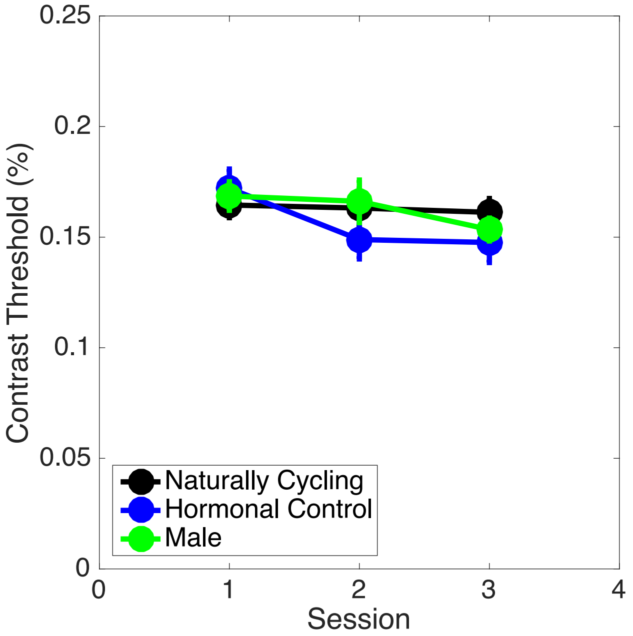

Figure 8: Contrast thresholds for 1 cpd gratings, across the 3 experimental sessions.

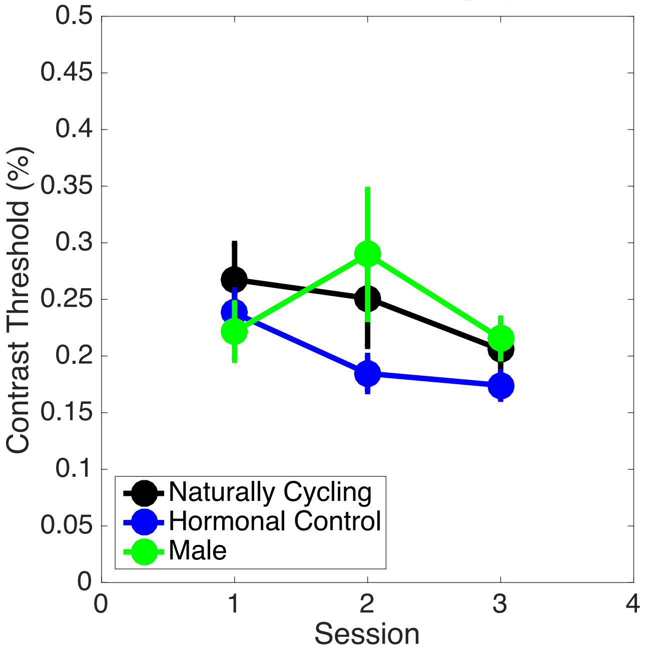

Figure 9: Contrast thresholds for 4 cpd gratings, across the 3 experimental sessions.

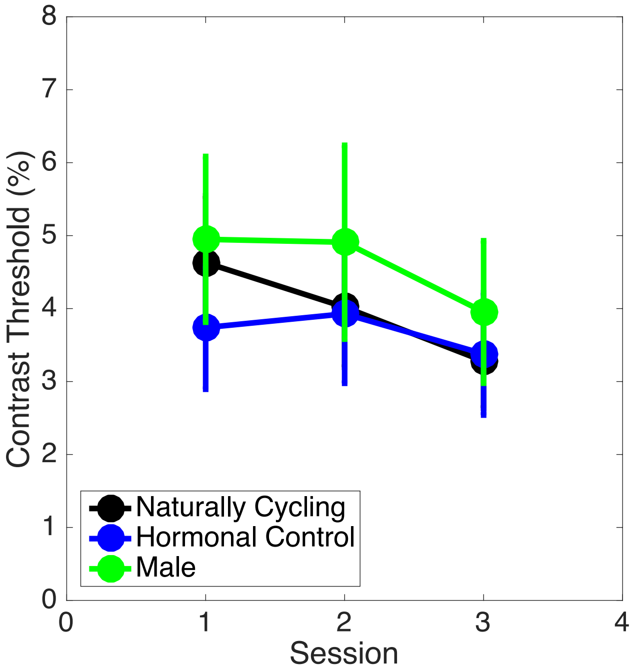

Figure 10: Contrast thresholds for 16 cpd gratings, across the 3 experimental sessions.

The second two-way ANOVA measured for the same difference in contrast thresholds for the 3 spatial frequencies during the *luteal* session (session 2). A significant effect of frequency was maintained (*F* (2, 4) = 47.9, *p*= <.001), and there was no significant effect of group (*F* (2, 46) = .29, *p*= .75). Together with a non-significant interaction between frequency and group (*F* (4, 92) = .24, *p*= .91), this demonstrated that during the luteal (second) test session, contrast thresholds for none of the 3 frequencies differed between participants. These findings are shown in the figures above.

Finally, a third two-way ANOVA measured for differences in contrast thresholds for the 3 spatial frequencies during the *menstrual* session (session 3). The significant effect of frequency was consistent (*F* (2, 4) = 52.54, *p*= <.001) and there was no significant effect of group (*F* (2, 46) = .20, *p*= .81). A third non-significant interaction between frequency and group (*F* (4, 92) = .20, *p*= .82) further showed that for the final test session, contrast thresholds were not different for any of the spatial frequencies between participants. These findings are shown in Figure 8.

Together, the 3 two-way ANOVAs demonstrate that regardless of practice effects developing across experimental sessions, each session when viewed in isolation revealed no significant differences between or within male and female contrast thresholds for all spatial frequencies. A non-significant interaction between phase and group, *F* (4, 92) = .51, *p* =.732, demonstrated that across all 3 groups contrast thresholds did not differ as a function of menstrual cycle phase (for female participants) or test session interval (for male participants). A non-significant interaction between frequency and group, *F* (4, 92) = .245, *p*=.912, further confirms that contrast thresholds for different frequencies also did not differ as a function of group. Overall, no significant differences in contrast thresholds were found across any of the 3 participant groups, *F* (2, 46) = .261, *p* = 0.771.

Together, these results demonstrate that contrast sensitivity does not differ either between or within sexes. Contrast sensitivity in women was not significantly different to that measured in men, nor were there significant differences in contrast sensitivity within women. These findings suggest that within women, the use of hormonal contraceptives does not have a significant effect upon visual sensitivity. The initial notion that we may have expected to find a mid-cycle peak in visual sensitivity (lower contrast thresholds) in naturally ovulating women was not supported by data from the present experiment. While a significant effect of experimental phase was identified for all 3 groups, these findings can be attributed not to fluctuation in hormone levels, but to practice effects occurring across all participants. In conclusion, naturally cycling women did not display a mid-cycle peak in visual sensitivity when fertility was predicted to be highest. This emphasises the importance of measuring contrast sensitivity not only in naturally ovulating women, but also in women whose natural ovulation has been inhibited by contraceptive use and in men. For this analysis, these controls allowed a direct measure of contrast sensitivity in relation to different levels of fertility. It is therefore unlikely that contrast sensitivity function can be implicated as one of the underlying mechanisms of cyclical shifts in female perceptual behaviours.

Chapter 3: Emotion detection under continuous flash suppression across the menstrual cycle

3.1 Introduction

Recent research concerned with the way in which facial emotional expressions undergo processing has revealed that facial displays for certain emotions appear to undergo processing quicker than others. For example, faces portraying fearful expressions are detected more often than both happy and neutral faces (Milders et al., 2006), where these findings have often been attributed to a threat-bias during processing (Ohman & Mineka, 2001). This advantage for processing threat-related stimuli is posited to occur as an adaptive mechanism within the visual system, where visual attention and processing is preferentially dedicated to evolutionarily relevant stimuli (LeDoux, 1998; Ohman & Mineka, 2001). According to this notion, the human visual system is therefore equipped with dedicated neural processing streams enabling quick detection of stimuli that may be crucial for survival. In early modern humans, non-verbal communication would have relied upon such visual cues for evaluation of contextual information. The threat-bias resulting in quicker detection of fearful faces is therefore considered to provide a vestige of an early mechanism for processing non-verbal cues of evolutionary significance (LeDoux, 1998). However, recent accounts of this processing bias suggest that visual mechanisms responsible for dedicating priority for processing such faces may rely on the specific low-level properties of which these faces are composed (Gray et al., 2013). In particular, Gray et al., (2013) posit that this processing bias for threat related stimuli is not governed by the evaluation of an expression's emotional value or significance. Instead, it is its composite spectral properties (such as spatial frequency and contrast) responsible for eliciting activation of quick and specialised processing streams (LeDoux, 1998; Gray et al., 2013). This notion has been upheld by recent findings that the spatial frequency content within a face determines the way in which the face will be processed in the brain. Faces composed of low and high spatial frequency information are subjected to very different processing streams. Fearful faces composed of low spatial frequent content, for example, undergo quick and holistic processing via the dorsal processing stream (Vuilleumier et al., 2003). These fearful faces composed of low spatial frequency content also attract faster attention from the visual system (Bannerman et al., 2012). Together these findings demonstrate that isolating the visual properties of a

stimulus is a novel tool for observing the way in which these properties are valuable content used when the visual system evaluates the significance of a stimulus.
In further examination of the extent to which such low-level information is responsible for processing emotional faces, Grey et al. (2013) adopted the use of continuous flash suppression methods. Here, two separate images are presented to each eye, where the nature of binocular rivalry is such that each will compete for visual processing. Gray et al. (2013) paired a highly salient noise pattern with a fearful face, and measured the point at which the face arose from suppression (against the noise) in becoming visible to the observer. The less time taken to perceive a face in the presence of a salient noise stimulus suggests that despite the noise-suppression, the visual system maintains an ability to detect and process information that the face is composed of. Here, Gray et al. (2013) provided evidence that fearful faces emergence from suppression faster than happy or angry faces. Importantly, this advantage in processing was preserved for artificially manipulated faces (where higher-level configural information is removed). These results suggest that processing biases for facial emotional expressions may rely primarily on low-level stimulus properties (such as spatial frequency and contrast) that are persevered under conditions of artificial manipulation (Gray et al., 2013).

Together these findings suggest that low-level processes in visual perception underpin higher-level perceptual functioning such as face perception. However, as outlined in Chapter 1, certain aspects of facial perception are vulnerable to hormonal fluctuations across the menstrual cycle. Given the research that demonstrates hormonal shifts in higher-level perceptual behaviour, it may also be expected that such shifts may occur at lower-levels of visual processing. Evidence suggests that this may be the case. For example, cycle effects in emotion processing found by Derntl et al. (2008a) who measured amygdala activation during an emotion recognition task between women in the ovulatory or luteal phase of their menstrual cycles. They found that activation during emotion recognition was stronger during the phase of the menstrual cycle where fertility (and oestrogen levels) is highest. In a similar experiment, Derntl et al. (2008b) found that women during the same high fertility phase of the menstrual cycle displayed better performance on tasks of emotion recognition in faces. Here, they found that these effects were correlated with the oestrogen peak during the follicular phase of the cycle, paired with a negative correlation with progesterone levels (Derntl et al., 2008 b). These findings implicate the role of oestrogen as a potential hormonal mechanism of facial emotional processing in women. This notion is supported by studies measuring the relationship between oestrogen and emotion processing regions of the brain. As outlined in Chapter 1, research has shown a positive association between oestrogen and aspects of face perception in women. Higher oestrogen levels have been shown to produce a facilitatory effect for facial processing in the female visual system, such that higher levels of the hormone are associated with improvement in women's recognition of faces (Yonker et al., 2003). Empirical evidence shows that sites of action for oestrogen are distributed within regions of the brain implicated in emotion and facial processing such as the limbic system. A neural structure within this system is the hippocampus, a region of the brain implicated in episodic memory. Episodic memory comprises the processing and retention of auto-biographical experiences, and the associated emotions and contextual information that they evoke, thus playing a significant role in face perception (Baddeley, Eysenck & Anderson, 2009). Research has demonstrated that oestrogen appears to play an important role in both the functioning and maintenance of this limbic structure. Higher levels of the hormone are associated with greater density of hippocampal synaptic connections where the hippocampus itself comprises a number of oestrogen receptors (Schughrue, Merchenthaler, 2000; McEwen et al., 1997; Desmond & Levy, 1998). This effect of oestrogen is extended to adjacent temporal regions also implicated in face perception such as the fusiform gyrus (Brizendine, 2006; Resnick & Maki, 2001; Robinson et al, 1994). An additional limbic structure includes the amygdala, responsible for emotional processing both as an internalised process and for perceiving emotional displays in the facial expressions of others (Baddeley, Eysenck & Anderson, 2009). Research has revealed that within this limbic structure there is an abundance of oestrogen receptors, suggesting that the amygdala may be an important locus for oestrogen influence (Österlund & Hurd, 2001). Together these findings suggest a potentially important relationship between cyclical fluctuations in oestrogen and facial emotion processing in women. It may be the case, as these findings suggest, that oestrogen may exert an activating effect in the female visual system, operating specifically to facilitate advantages in female perception, such as facial processing (Broverman et al., 1968). Such cyclic effects are considered to harbour a functional value. Enhanced facial processing is considered to occur during high fertility in order to facilitate social interaction and nuanced non-verbal communication. This enhanced sensitivity to facial emotional displays may therefore be a prerequisite behaviour for mate selection and sexual initiation, as it provides a basis for social-emotional bonding between conspecifics (Macrae et al., 2002; Derntl, 2008b).

If aspects of facial perception are driven by low level visual processing (Gray et al., 2013), and these same processes are vulnerable to fluctuation in female reproductive hormones (Macrae et al., 2002), then to what extent should we expect to observe these cyclic effects within low-level visual processes? The present experiment is an integration of these two fields of study. In the first instance, we adopt empirical and theoretical framework provided by Gray et al. (2013), who demonstrate that facial emotion processing is likely underpinned not by high-level evaluative mechanisms, but simply by spatial frequency sensitive channels responsible for processing basic stimulus properties. In the second instance, evidence and interpretations outlined by evolutionary accounts of emotion processing in female raises the question of whether such cyclic effects occur for the processing of such basic stimulus properties (namely spatial frequency) in facial emotional expressions.

Here, we produce a replication and extension of Gray et al. (2013). Response times for detecting the presence of faces portraying 4 different emotions (anger, fearful, happy, disgust) were compared to those portraying only neutral expressions. This part of the experiment measured the extent to which other emotional expressions may benefit from advantages in processing, alike that implicated in the threat-bias. Like Gray et al. (2013) these effects were then measured under a different condition, whereby faces were manipulated. Here, faces were inverted and contrast reversed, such that their basic properties were retained and higher-level properties erased. This provided a measure of the extent to which basic stimulus properties within other emotional expressions influenced response times under continuous flash suppression conditions. As a further extension, and one which address the question above, these effects for response times between emotional expressions under both normal and manipulated conditions were compared between groups of men and women. Additionally, to investigate the extent to which facilitatory effects of oestrogen may operate at such low-level of visual perception, we compared these response times to normal and manipulated faces between naturally cycling women who were ovulating during testing, and naturally cycling women who were menstruating at testing.

3. 2 Methods

Participants

A total of 62 (mean age 24.8 years) participants were recruited on a voluntary basis, taking part on either non-compulsory basis or in exchange for a monetary reward. Of these 62 participants, 14 were male (mean age 28.1 years) and 48 were female (mean age 24.2 years). Several participants reported using medications including combined-oral contraceptives, Paroxetine, Sertraline and Thyroxin. All 62 participants took part in a facial detection task, for faces displaying a range of emotions, measured using continuous flash suppression methods. Together, data from these 62 participants were collectively used during the first analysis of the experiment. This first analysis of *all* participants allowed for a replication and extension of Gray et al's (2013) study of facial detection. However, the second analysis was concerned with the effects that individual differences (such as sex and menstrual cycle phase) may have upon this process of face detection for emotional faces. The initial participant group of 62 was therefore categorised accordingly.

Twenty-six participants were excluded from the second analysis; reasons for this selection process are discussed in the next section. The remaining 36 participants were categorised for analysis as follows: 15 naturally cycling and menstruating females (mean age 26.2 years), 7 naturally cycling and ovulating females (26.1 years), and 14 males (mean age 28.1 years). One male reported using Escitalopram, one female using Thyroxin, and one female using Sertraline.

Design

Analysis 1: Emotion recognition in 62 participants

A two-way within subjects design was used across repeated measures. All 62 participants took part in one experimental session lasting approximately 30 minutes. The 2 factors were the emotional expression of the face and facial manipulation. Emotional expression included five levels: faces displaying either angry, fearful, happy, disgusted or neutral expressions. Manipulation of these faces included 2 levels; facial expressions presented in their natural form (upright, without negation), or emotional expressions that had been artificially manipulated (negated and inverted). Response time to identify the location of an emotional expression, composed of either manipulated or normal characteristics, was measured as the dependent variable.

Analysis 2: Individual differences in emotion recognition

A 3(group)x5(emotional expression)x3(facial manipulation) mixed-design was used across repeated measures. Here, the addition of the between-subjects factor allowed for emotion recognition to be observed in relation to hormone-related individual differences. Here, response times from 36 of the 62 participants were categorised into 3 groups: naturally cycling and ovulating females (n=7), naturally cycling and menstruating females (n=15), and males (n=14). This allowed emotion recognition to be compared between fertile and non-fertile women, and also in comparison to that of men. As for analysis 1, two factors included emotional expression and facial manipulation. Emotional expression and facial manipulation. Emotional expression included five levels: faces displaying either angry, fearful, happy, disgusted or neutral expressions. Manipulation of these faces included 2 levels; emotional expressions presented in their natural form (upright, without negation), or emotional expressions that had been artificially manipulated (negated and inverted). Response time to identify the location of an emotional expression, composed of either manipulated or normal characteristics, was measured as the dependent variable.

Apparatus

Stimuli was presented using MATLAB with Psychophysics Toolbox extensions (Brainard 1997; Pelli, 1997; Kleiner et al, 2007) on a Dell Precision T3600 computer. This also employed the use of a NVIDEA Quadro K5000 graphics card and DATAPixx visual stimulator. Stimuli were presented on a 19 inch Sony Trinitron CRT monitor, at a viewing distance of 90 centimeters, where 1 pixel subtended 1.6 arcmin. Luminance calibration was achieved using a Minolta LS-100 photometer, where maximum luminance of the monitor was 139.7 cdm^{-2}. The Sony Trinitron CRT monitor had a spatial resolution of 1280x1024 pixels, with a refresh rate of 100 Hz. Observers' responses (deciding the location of each face) were recorded using the RESPONSEPixx response box. The method of continuous flash suppression (presentation of two images separately to each eye) was achieved using NVIDIA 3D vision liquid-crystal shutter goggles. These were used for the duration of the study, in addition to participants' own corrective lenses where necessary.

Stimuli

Facial stimuli were taken from the Karolinska Directed Emotional Faces set (KDEF: Lundqvist, Flykt, & Öhman, 1998). These consisted of facial pictures of 20 individuals (10 male and 10 female actors). These faces displayed 5 emotional expressions: anger, fear, happiness and disgust, with the inclusion of neutral as a comparison expression. These expressions were presented under 2 manipulation conditions. Each emotion was presented in its natural form (upright with retained luminance polarity), and also in an artificially manipulated form (rotated by 180 degrees with retained luminance polarity). This gave the appearance of 5 emotional expressions that were either "natural" looking, or inverted with a negated appearance (illustrated in Figure 2). Gray et al. (2013) stated that the use of such artificially manipulated faces was necessary for isolating low-level stimulus properties implicated in facial emotion processing. When manipulated, higher-level (emotionally evaluated) information is removed and thus such facial emotion processing relies upon the low-level stimulus properties that remain in tact despite such manipulation. For all faces, external features such as hairline were excluded. Each of these faces was presented at 100% Michelson contrast. Facial stimuli were presented one at a time, against a background of noise-pattern composed of 500 individual rectangles in varying between 0 and 1 Weber contrasts. The width and height of the rectangles varied randomly between 37.6 arc min and 108 arc min (20 and 60 pixels). The size of facial stimuli was fixed for all faces, at 16 degrees wide and 20 degrees tall (512x640 pixels). Faces were presented immediately after each response, reaching full contrast in one second.

NVIDIA 3D vision liquid-crystal shutter goggles were used to deliver two different images to each eye, simultaneously. This pairing included the presentation of one facial stimulus to one eye, while the other received a salient noise-pattern similar to that presented on the monitor screen. This method was also employed by Gray et al. (2013) in order to measure the point at which each emotional expression emerges from suppression and into observers' conscious awareness.

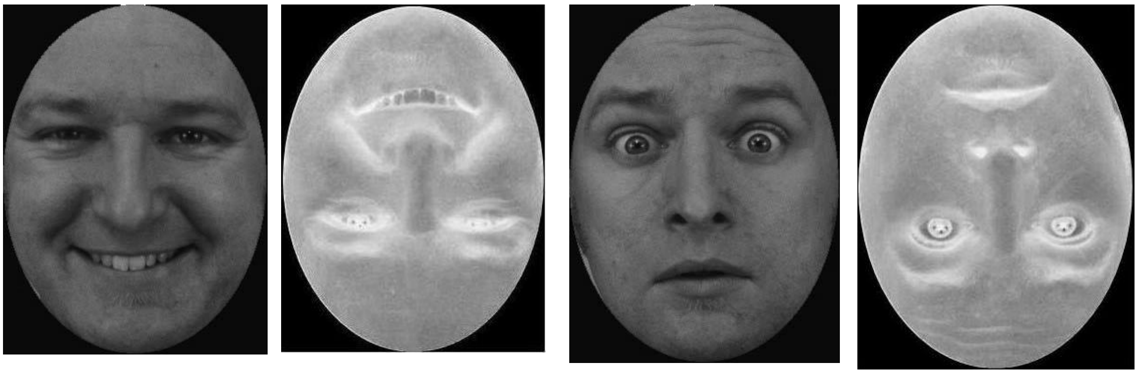

Figure 11 (left) & 12 (right): Figure 11 portrays a happy emotional expression presented in both natural and manipulated form. Figure 12 portrays a fearful emotional expression, presented in both natural and manipulated form.

Procedure

Participants were tested individually in a quiet room and informed prior to the experiment that the nature of the study was concerned with face perception. Each participant took part in one experimental session, lasting approximately 30 minutes. Experimental sessions were divided into two blocks of 160 trials (5(expressions)x2(facial manipulation)x4(faces)x4(repetitions of each stimulus). Overall, there were 320 trials for each participant in a single experimental session. Within each block, a single face portraying one of the 5 emotional expressions appeared, reaching full contrast at one second. This was presented to participants via the monitor screen in addition to the stimuli presented via the NVIDIA 3D shutter goggles. The presentation of the next trial was determined by participants' use of the response box. Using a two-alternative forced choice procedure, participants used a left or right button on the response box to indicate the instant at which they were able to perceive a face on either the left or right side of the screen. After completing the first block of 160 trials, a short break was followed by the second block of 160 trials. The end of this second block marked the end of the experiment.

For the 22 female participants included in the second analysis, dates for testing were arranged based on their current menstrual cycle phase. These female participants were tested at one of two phases of their menstrual cycle: menstruation or ovulation. Menstruation was confirmed by each participant, during the first week of the cycle that comprises the early follicular phase (days 1-7). Ovulation was confirmed using the counting backwards method such that participants provided the dates of their most recent and next expected menstrual onset. From the latter date, 14 days were subtracted which provided an optimal estimation of when ovulation was most likely to occur. Female participants tested during this window (days 11-14) were categorised as being in the fertile group.

3.3 Results

Two separate analyses were conduced for this experiment.

Analysis 1 included data from all 62 participants as a replication of Gray et al. (2013).

Analysis 2 was performed as an extension of Gray et al. (2013) in observing hormone-related individual differences in facial detection for different emotional expressions. For this second analysis, data was analysed from 36 of the initial 62 participants used in Analysis 1. The selection process determining the 36 participants for the second analysis was based on participants’ categorisation into 1 of 3 groups.

The first group were male participants (n=14) where no criteria were necessary in order to take part in the experiment. The second group were naturally cycling, ovulating females (n=7). The third group were naturally cycling, menstruating females (n=15). The criteria required for allocation to either of the female groups were determined via a pre-screening questionnaire. This included: reporting a cycle length of no more than 35 days, experiencing regular and predictable menstruation, and in the 3 months prior to the experiment having no experience of: pregnancy, breastfeeding, or emergency contraception. Together these carefully selected 36 participants were included in the second analysis. Here, the remaining 18 from the initial 62 participants were excluded from the second analysis as they did not meet the criteria required to take part. Additionally, a further 8 female participants were also excluded from the second analysis (5 menstruating and 3 ovulating users of combined oral contraception) as these were not sufficient numbers of participants to include as an additional control group during the second analysis.

Analysis 1: Emotion recognition in 62 participants

For the overall 320 trials, means and standard deviations were calculated for all 62 participants. Mean response times were calculated for each of the 5 naturally presented (non-manipulated) emotional expressions and also for these 5 emotions when manipulated. These are presented in Figure 13.

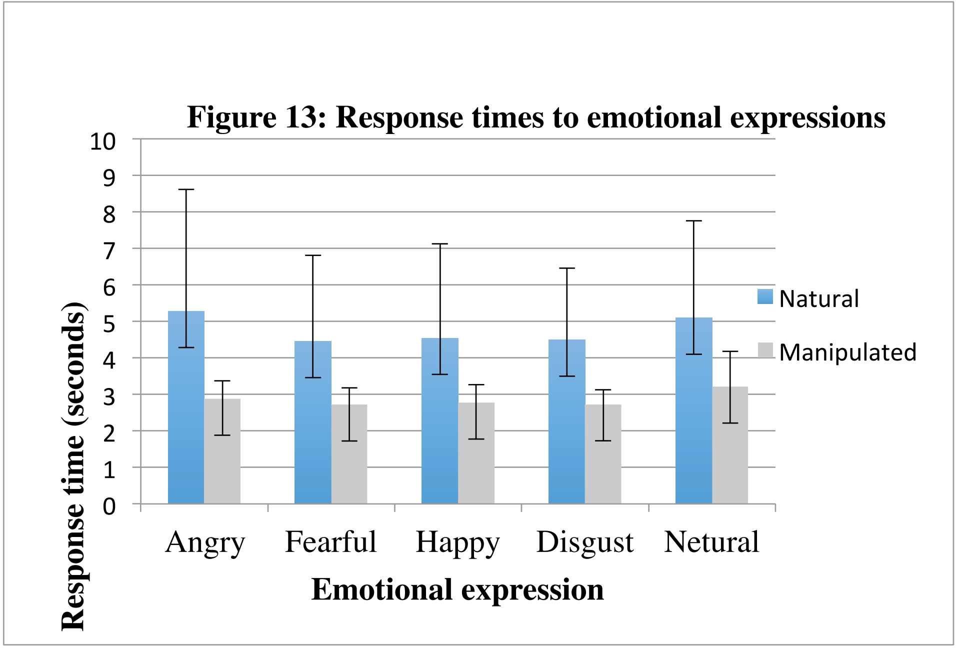

Figure 13: Mean (standard deviation) response times for 5 emotional expressions and two manipulation levels, pooled across 62 participants.

A 5(expression)x2(manipulation) within-subjects ANOVA was used, where the within-subjects factors included the emotional expression and the manipulation. Emotional expression contained 5 levels, corresponding to 5 different facial emotional displays: angry, fearful, happy, disgust and neutral. Manipulation contained 2 levels and corresponded to faces that were either presented naturally or in a manipulated form (negated and inverted). A significant main effect of manipulation (*F* (1, 61)= 47.41, *p*= <.001), revealed a difference in response times to detect the presence of natural faces compared to manipulated faces, where manipulated faces were quicker to identify than natural faces. Secondly, a significant main effect of emotion expression (*F* (4, 244)= 15.55 *p*= <.001) revealed differences in response times to detect the presence of different emotional expressions. Together, these significant effects were accompanied by a significant interaction between emotional expression and manipulation (*F* (4, 244) = 5.44, *p* =<.001), suggesting a dual effect of emotional expression and manipulation upon response time when perceiving a face. These findings suggest that emotional expression does influence response times when perceiving faces, but also that the level of manipulation within each face may also influence their salience.

In order to determine the effect of each emotional expression on response times, differences in response times between the 4 emotion expressions and neutral were measured using paired samples t-tests. A further 4 paired samples t-tests measured the same difference in response times between the 4 manipulated expressions and manipulated neutral faces. These are displayed in Table 1 and reflect the extent to which mean response time for natural and manipulated emotional expressions differed from their neutral comparatives. These calculated values were then subjected to paired samples t-tests, displayed in Table 2. These comparisons demonstrate that in almost all cases, every emotion, regardless of whether it is presented as its natural form or manipulated, was perceived more quickly than neutral faces. The exception to this was found for naturally presented angry faces, where no significant difference was found in response times for natural angry faces compared to natural neutral faces. In order to identify whether these advantages (quicker response times) for processing emotional expressions was significantly different depending upon the manipulation of the face, further paired samples t-tests were conduced. These comparisons, presented in Table 3, demonstrate that when manipulated, all 4 emotional expressions receive quicker response times compared to manipulated neutral faces. In contrast, when presented in their natural form, fearful, happy and disgusted faces receive quicker response times compared to natural neutral faces. However, naturally presented angry faces are not responded to quicker than natural neutral faces. These quicker response times may reflect a processing bias for the 3 emotional expressions when they are presented in their natural form. Also, importantly, this processing advantage is preserved even despite manipulation of the facial expressions. Interestingly, results show that the manipulation of angry faces appears to facilitate response times, where the same effect is not found for natural angry faces.

Emotional expression (manipulated)	**t-value**	**df**	**Sig. (2-tailed)**
Angry	-4.04	61	<.001
Fearful	-5.12	61	<.001
Happy	-5.96	61	<.001
Disgust	-4.62	61	<.001

Emotional expression (natural)	**t-value**	**df**	**Sig. (2-tailed)**
Anger	1.06	61	0.294
Fearful	-5.25	61	<.001
Happy	-5.90	61	<.001
Disgust	-3.62	61	0.001

Table 1: Paired comparisons of response times between 4 emotional expressions and neutral faces, for naturally presented and manipulated facial stimuli.

Bias comparisons	**t**	**df**	**Sig (2-tailed)**
Natural Angry vs Manipulated Angry	2.41	61	0.019
Normal Fear vs Manipulated Fear	-1.41	61	0.164
Normal Happy vs Manipulated Happy	-1.01	61	0.315
Normal Disgust vs Manipulated Disgust	-0.93	61	0.357

Table 2: Paired comparisons of response biases for natural versus manipulated faces.

Overall, these results demonstrate that for all participants there is a significant effect of expressions on the time taken to respond to facial stimuli. The threat bias identified in previous findings (Gray et al., 2013) was also found in the present analysis, where response times were quicker for fearful faces. Additionally, like Gray et al's (2012) findings, this effect was also preserved when faces were manipulated. Interestingly, results from the present study also demonstrate what appears to be a similar processing advantage for other emotional expressions, such as happiness and disgust. Both happiness and disgust receive quicker response times than neutral faces, and these effects are preserved even when the emotional expressions are manipulated. An additional interesting finding is that the lack of a similar effect was found for angry faces, whose response times were not quicker compared to neutral faces. Furthermore, the finding that happy faces were also quicker to detect than neutral faces, and that this effect too was preserved when happy faces were manipulated is an interesting finding. The significant effect of manipulation showed that inverted and negated stimuli received quicker response times. These perhaps unexpected findings shall be discussed further within the discussion of this thesis. Overall, results from analysis 1 replicate previous findings of threat-related facial expressions harbouring an advantage during processing, but also provide additional evidence that this advantage may not only be confined to threat-related stimuli.

Analysis 2: Hormone-related individual differences in emotion detection

For the overall 320 trials, means and standard deviations were calculated for the 32 selected participants. Mean response times were calculated for each of the 5 naturally presented (non-manipulated) emotional expressions and also for these 5 emotions when manipulated. These are presented in Figure 14. This analysis included a between-subjects variable of participant group to measure emotion detection in relation to hormone-related individual differences.

A 3(group)x2(manipulation)x5(expression) mixed ANOVA was used, where the within-subjects factors were emotional expression and manipulation. Emotional expression contained 5 levels, corresponding to 5 different facial emotional displays: angry, fearful, happy, disgust and neutral. Manipulation contained 2 levels and corresponded to faces that were either presented naturally or in a manipulated form (negated and inverted).

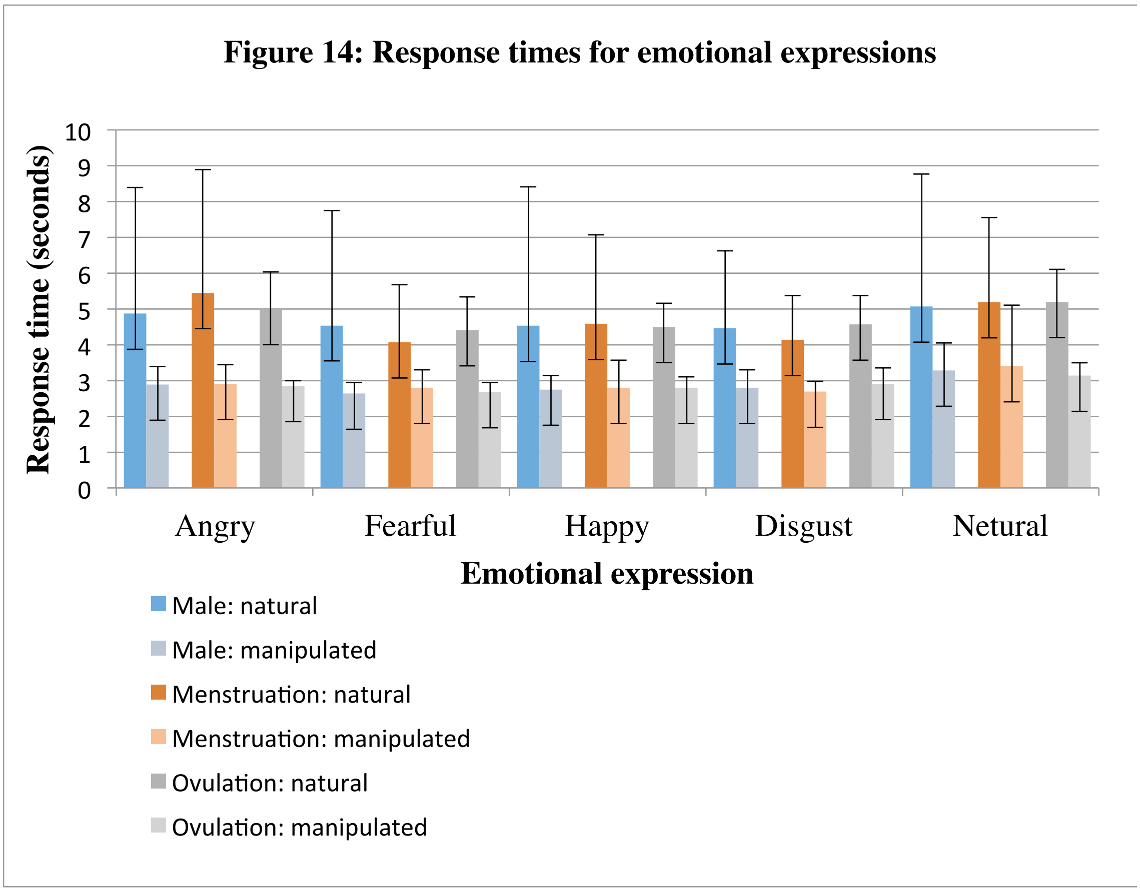

Figure 14: Mean response times (standard deviations) for emotional expressions for 3 participant groups: males, naturally cycling and ovulating females, and naturally cycling and menstruating females.

A significant main effect of manipulation (*F* (1, 33)= 22.86, *p*= <.001) revealed a difference in response times to recognise the presence of natural faces compared to manipulated faces, where participants were quicker to detect manipulated faces. Secondly, as found in analysis 1, a significant main effect of emotional expression (*F* (4, 132)= 8.40, *p*= <.001) revealed differences in response times to detect different emotions. These disparities in response times for the different emotional expressions and their manipulation levels are illustrated in Figure 14. These significant effects were accompanied by a non-significant interaction between manipulation and emotion expression (*F* (4, 132)= 2.15, *p*= .08), demonstrating that response times did not vary for different expressions as a function of whether or not they were presented in their natural or manipulated form. A non-significant interaction between manipulation and group (*F* (2, 33)= .006, *p*= .99) and also for expression and group (*F* (8, 132)= .60 *p*=.77) demonstrated that response times for emotional expressions or their manipulation levels did not vary as a function of their observer's group. Response times for faces portraying different expressions, or presented in either natural or manipulated form, did not vary relative to sex or fertility levels in female observers. Finally, a non-significant 3 way interaction between group, manipulation and expression (F (8, 132)= .78, *p*= .62) further shows that variation in response times for different emotional expressions and manipulation levels do not occur across different groups of participants. Overall, the non-significant effect of the between subjects factor (F (1, 33)= 22.96, *p*=.87) shows that regardless of emotional and expression and manipulation level, there were no differences in response times for faces between males, naturally cycling ovulating women, and naturally cycling menstruating women. Together these results extend and replicate findings from analysis 1, in that emotional expression and manipulation content of faces encourage differences in response times to facial stimuli. However, when these effects are measured in relation to sex differences, and variation in female fertility levels, results form the present study show that no such hormonal differences have an effect upon readiness to detect facial emotion expression.

In order to establish further whether response times for faces vary *within only female participants,* a second 2(group)x2(manipulation)x5(expression) mixed ANOVA was used. Here, the within-subjects factors remained the same as the previous 2 analyses, with the new between-subjects factor as participant group (naturally cycling ovulating females versus naturally cycling menstruating females). No significant main effect of manipulation (F (1, 20)= 37.76, p= <.001) and expression (F (4, 80)= 4.70, p= <.001) demonstrate that response times do vary relative to emotional expression and manipulation of faces. No significant interaction between expression and manipulation (F (4, 80)= 2.00, p=.10) showed that response times across all females for emotional expressions did not vary as a function of their manipulation level. No significant interaction was found between manipulation and group (F (1, 20)= .03, p=.87) or expression and group (F (1, 80)= .56, p=.69). Women's response times for detecting facial emotional expressions and manipulated faces did not differ as a function of whether observers were ovulating or menstruating. These estimated hormonal differences did not significantly influence their response times to any of the 5 emotional expressions, or 2 levels of manipulated faces. No significant 3 way interaction (group, manipulation, expression) (F (4, 80)= .47, p=.75) further shows that regardless of emotional expression and manipulation level, response times were not different for ovulating women compared to menstruating women. A non-significant between-subjects effect (F (1, 20)= 199.66, p=.99) further supports the finding that fertility differences in women does not exert a significant effect upon emotion detection in facial stimuli. These findings are illustrated in Figure 13. These findings shall be further discussed in Chapter 4.

Chapter 4: Discussion

4.1 Interpretation of present findings

Experiment 1 measured contrast sensitivity for 1, 4 and 16 cpd gratings across the menstrual cycles of naturally cycling women and users of combined-oral contraception. We also performed the same measurements for men across 3 similar time intervals to assure that if there *was* variation in female performance that it was due to fertility shifts related to the menstrual cycle. Results from this experiment revealed that contrast sensitivity was not different between men and women, regardless of spatial frequency content. Additionally, analysis measured for differences in contrast sensitivity both between and within women. In the first instance, no evidence was found to suggest that there are sex differences in contrast sensitivity. Secondly, findings not provide evidence to support the notion that contrast sensitivity may be positively influenced by naturally occurring ovulation compared to the inhibition of this natural process by synthetic hormones. In addition, no changes in contrast sensitivity across the 3 experimental sessions were found for naturally cycling or contraceptive-using females, showing that across the menstrual cycle contrast sensitivity in naturally cycling women did not change relative to shifts in females' hormonal status. Here, no peak in sensitivity was observed for spatial frequencies of 1, 4 or 16 cpd. There are 2 primary interpretations of these findings. Firstly, that methodological limitations encountered in the experiment may be responsible for the lack of effects found. It may be the case that the sensitivity of the psychophysical procedures used was weakened by the use of a within-subjects design. Repeated measures, although benefitting from a measurement of individual variation in hormones, were likely responsible for the presence of practice effects seen across all participants (see Figures 8, 9 and 10). Lack of direct hormone measurements confirming ovulation in female participants may have weakened the probability of testing taking place during peak fertility. The extent to which these two methodological variables may have produced a combined effect responsible for the lack of effect measured remains open for discussion. The second interpretation for the present findings is simply that it is unlikely that contrast sensitivity can be implicated as one of the potential low-level visual mechanisms underpinning cyclic shifts in female perception. However, it is important to consider here the popular aphorism that lack of evidence from the present findings does not necessarily equate to evidence that such low-level mechanisms in female perception are absent. This interpretation simply suggests that visual processes or aspects of visual sensitivity other than contrast sensitivity may be more likely candidate mechanisms. Inherent to the process of attempting to identify potential mechanisms within visual perception is the probably occurrence of experiments where no effects are found.

Experiment 2 was performed as a replication and extension of Gray et al. (2013). Here, we conducted a replication of the initial (2013) experiment in measuring response times to detect fearful compared to neutral faces. We also measured response times to detect angry, happy, disgusted and neutral faces in order to measure advantages for processing in other emotional expressions. The threat-bias was supported by quicker response times for fearful as opposed to neutral faces, and quicker response times were also found for facial displays of happy and disgusted emotions. The faster detection of fear, disgust and happy expressions (compared to neutral) were preserved despite the manipulation (negation and inversion) of the faces displaying the expression. These findings support and extend those of Gray et al. (2013) in providing further evidence of advantages for processing emotional expressions when only basic stimulus properties are preserved. However, findings also revealed some unexpected effects. First, the finding that manipulated facial stimuli received faster detection times suggests that manipulated faces are more salient and thus detected quicker by the visual system; not a finding that would be expected given the "face inversion effect" (Kanwisher, Tong & Nakayama, 1998). However, manipulated facial stimuli in the experiment were not only subjected to inversion but were also reversed for luminance polarity. This combined technique for creating manipulated stimuli meant that not only was configural information disrupted but also that stimuli also appeared noticeably more negated. This is apparent in Figures 11 and 12 above. It may perhaps be that manipulation of this kind causes stimuli to appear higher in perceived contrast, accounting for greater salience and therefore quicker response times. Secondly, angry expressions did not receive quicker detection times compared to neutral faces; an effect that did not change under manipulated conditions. This finding may be surprising given the theoretical underpinning of the threat-bias in perception. If it is the case that threatening stimuli are more salient and therefore “break suppression” faster than neutral stimuli, then this effect may be expected for both fearful and angry faces, assuming that both would be useful in threat-avoidance. The strangeness of this result is further enhanced when considered in relation to the fact that the present findings showed quicker response times for happy compared to neutral faces. There are two avenues for interpreting this finding. Firstly, it may be the case that the spectral properties of angry faces simply (and inadvertently) do not meet the criteria required for undergoing specialised processing. Therefore regardless of a potential higher-level functional value of such faces, the low-level properties of which they are composed are simply not those required for preferential processing. A second avenue for interpretation may speculate that differences in such low-level properties across expressions may influence differences in their saliency. Findings from experiment 2 do demonstrate that some emotional expressions appear more salient than others. It may therefore be useful to investigate the potential low-level properties that are driving this expression effect. A body of recent research concerned with this suggests that basic properties such as spatial frequency may determine the way in which different emotional expressions undergo preferential, subcortical processing (Vuilleumier et al, 2003; Holmes, Winston & Eimer, 2005; Vlamings, Goffaux & Kemner, 2009; Stein et al, 2014).

The second analysis for experiment 2 analysed data in such a way as to measure differences in facial emotion detection between men and women, and within women (relative to differences in fertility levels). Here, we posited that based on recent evidence of cyclic effect for emotion perception in women, we may expect to also observe these cyclic effects occurring within lower-levels of visual processing for basic stimulus properties; proposed by Gray et al. (2013) as the mechanism responsible for facial emotion processing. However, consistent with experiment 1, these findings revealed no significant sex differences for detecting emotion expressions. Additionally, no significant differences in emotion detection were found to occur relative to differences in oestrogen levels in ovulating or menstruating female participants. These results suggest that female reproductive hormones do not appear to enhance facial emotion processing for females in general, nor when they are tested during the time of the cycle that fertility is estimated to be highest.

4.2 Avenues for further research

Avenues for further research shall be discussed briefly, and in particular, shall address some of the methodological limitations highlighted in the previous section of this chapter. In relation to experiment 1, the trade-off effect encountered through the use of a within-subjects experimental design is such that, despite accounting for individual variation in hormones for each participant, repeated test sessions did seem to facilitate the presence of practice effects occurring. Koehler et al. (2006) refined this design to ensure that female participants were tested during both the menstrual and ovulatory phase, but randomised these test sessions so that half of participants were tested during the menstrual phase first, and half during the ovulatory phase first. Additionally, it has been argued that the arbitrary segmentation of the menstrual cycle into distinct hormonal phases is futile when measuring the effects of fluctuation in hormonal levels. According to this criticism, this very categorisation process renders observations from proving an accurate representation of the dynamic and consistent variation in female reproductive hormones (Parlee, 1983; Johnson & Petersik, 1974). An alternative to this method may be measuring female participants across several consecutive days mid-cycle. This method may be particularly useful when interested in effects of ovulation, as it is precisely within this mid-cycle time frame that the most distinct changes in fertility levels occur. There are many mixed conclusions regarding the number of days during the menstrual cycle that a female is most fertile. These estimations range from 2 days (Bongaarts, 1978), to 10 days. In an extensive study measuring conception likelihood across naturally cycling women, Wilcox et al (1995) identified the 6 days prior to ovulation as constituting the fertile window. The gradual increase in fertility as the day of ovulation approaches (day 14) suggests that it may not necessary pay to restrict testing to the day of ovulation (Wilcox et al., 1995; 2001). Fertility rapidly drops after day 14, and so missing opportunities for testing in these prior 6 consecutive days may result in missed opportunities to test fertile women during a narrow time frame. Adopting this method would also lessen the need for hormonal assays to confirm ovulation.

Furthermore, there are also natural limitations when adopting measures of subjective participant responses. Variation in these kinds of methods used may weaken the sensitivity of tests used to identify cyclic changes in female perception (Puts, 2013; Puts, 2006). Instead, perhaps further research may benefit from using measures of implicit behaviours. Methods including eye tracking devices or measures of autonomic nervous system response such as pupil dilation in response to psychophysical stimuli may provide an interesting insight into the spectral properties of stimuli that become more visually "interesting" to fertile women.

4.3 End note

Despite the lack of significant findings of cyclic effects occurring within low-level visual processing, it is important to view these results in relation to the wider body of evidence that together provides evidence for sexual selective processes occurring in modern women. Evidence of these exists across both a range of sensory modalities and within studies of non-human primates (see Gildersleeve et al., 2013 for a review). The very nature of these aspects of female perception is such that they are subtle and nuanced features of the female visual system. The way in which these exist within an array of societal and cultural influences is therefore an important factor to consider when measuring such phenomena. Ultimately, a general consensus across many evolutionary accounts of behaviour posits that as it is the case that our bodies have been shaped by natural selection, how then, as such a social species, should our behaviour have not also been subjected to the same selective processes (Buss, 1999). It is important to consider here that the absence of evidence does not equate to evidence of absence (Gildersleeve et al., 2013). This in particular is true when considering findings from the present experiments in relation to the value in adopting a mechanistic approach when investigating the cycle shift hypothesis. Here, these findings highlight the importance of further adopting novel scopes through which to address the same question. Research within this area will undoubtedly continue to grow, in investigations of significant stimulus properties and their relative processes that may underpin aspects of face perception. The value in using psychophysical tools and methods for identifying proximate mechanisms in visual perception is becoming increasingly apparent. These have a highly important value when adopting a mechanistic approach to measuring visual perception.

This thesis therefore concludes that despite findings from the present study, the importance and value remains in the continuation of investigations of the way in which low-level perceptual processes may be influenced by female reproductive hormones.

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Appendix

Pre-screening questionnaire for female participants, used in experiment 1 (Contrast sensitivity across the menstrual cycle) and experiment 2 (emotion recognition across the menstrual cycle).

1. Which sex are you?
   a) Male
   b) Female
2. What is your age (in years)?
3. Are you currently taking any medication (other than hormonal contraceptives)? If yes, please specify below.
4. Are you currently using hormonal contraceptives?
   a) Yes (hormonal contraceptives include: combined pills such as Microdynon, Brevinor, Cilest, Logynon, progesterone-only pills such as Femulen, Cerazette, Micronor, contraceptive implants, contraceptive injections, IUDs)
   b) No
5. If yes, please specify the kind of hormonal contraceptive that you use
6. What is the usual length of your cycle (in days)? I.e. the number of days between the first day of your period through to the first day that your next period will begin.
7. Are your menstrual cycles regular? I.e. are you able to reliably predict when the onset of your next period will be?
   a) Yes
   b) No
8. Have your previous 3 menstrual cycles been on time and been "normal" for you?
   a) Yes
   b) No
9. When was the first day of your last period (dd/mm/yyyy)?
10. When is the first day of your next period due (dd/mm/yyy)?
11. How certain are these estimates dates (for the onset of your previous and next period)?
    a) Certain
    b) Fairly certain
    c) Uncertain/guessed dates
12. In the past 3 months have you:
    a) Stopped using hormonal contraceptives
    b) Experienced pregnancy or breastfeeding
    c) None of the above
13. In the last month have you taken the emergency contraceptive pill ("morning after pill")?
    a) Yes
    b) No
14. To the best of your knowledge, do you think that you may currently be pregnant?
    a) Yes
    b) No
15. Thank you very much for completing this questionnaire. If you are happy to submit your information and to later take part in the lab experiments, please

leave your University of Essex email address in the space below and you will be contacted shortly to arrange a convenient time to participant in the study.