Factors Influencing the Motivational Salience of Faces

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I, *Amanda Hahn*, hereby certify that this thesis, which is approximately 47,000 words in length (excluding references), has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2009 and as a candidate for the degree of Doctorate of Philosophy in July 2010; the higher study for which this is a record was carried out in the University of St Andrews between 2009 and 2013.

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- The data presented in Chapter 2 is currently being prepared for submission to a peer-reviewed journal. Publication of this data and/or the corresponding theoretical interpretations would prohibit submission to a journal on the grounds that the work would be considered published elsewhere.

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- The preliminary data discussed in Chapter 6 is from on going projects that will be written up for publication upon completion of data collection.

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Acknowledgments

I would like to dedicate this work to my Grandfather, Eugene Walsh who first sparked my interest in the sciences. It is a love that will last a lifetime.

The work presented here would not have been possible without the tireless guidance of my supervisor, Dave Perrett. I owe him a world of thanks for the many hours spent battling over control of the mouse and the highlighting color scheme of data files. I would not be where I am today if it weren't for him. This work also would not be possible without the wonderful Lesley Ferrier whose organizational wizardry keeps the lab running!

Thanks to the technical gurus who made this research possible – Bernie Tiddeman, Davis Bulls, David Hunter, and especially Dengke Xiao for all his work programming the key-press paradigm.

To the vast network of past and present Perception Lab members, my friends and colleagues, thank you for your support/assistance/comradery/etc. throughout the PhD process – especially to Carmen Lefevre for many hours spent in pseudoscientific discussion over countless cups of coffee.

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Lastly, to my family and friends – you know who you are – I 'lurve' you all. Johnson, thanks for being there (vitamin water in hand) through all the highs and lows. Dad, this literature gives a whole new meaning to your personal mantra "lookin' good, feelin' good"!

Collaboration Statement

Throughout the experimental chapters in this thesis, I have used the pronoun 'we' in addition to 'I'. This work is my own in terms of hypotheses, design, analyses and conclusions; however, the Perception Lab is an inherently collaborative environment and such collaborative effort must be acknowledged. The plural pronoun reflects the fact that, if/when published, the following experiments would carry multiple authorship and is used in keeping with intellectual honesty.

This thesis is based partly on works submitted to and accepted for publication in peer-reviewed academic journals. These articles (and the journals in which they have been published) are identified at the beginning of the chapter in which they are featured. As my secondary supervisor, Dr Reiner Sprengelmeyer contributed to the work regarding the incentive salience of infant faces (as presented in Chapter 3, published in the *Quarterly Journal of Experimental Psychology*). Dr Sprengelmeyer contributed to discussions/planning of the experimental design (due to his supervisory role) and contributed to revisions of the manuscript presented in Chapter 3.

As the key-press paradigm in relatively novel in design, the efforts of Dr Dengke Xiao must be recognized here. Dr Xiao constructed the computer program designed to run the key-press task as defined by the adapted specifications from Aharon et al. (2001). Dr Xiao is listed as a co-author on the work presented in Chapter 3, however his program was an essential component of this thesis and he is credited with the programming for the task used in Chapters 2-5 (although the design and implementation of this programming was my own).

Note to the Reader

This thesis presents multiple studies using an adapted neuroscientific technique. This key-press paradigm builds on classic animal-based reward studies from the neuroscientific literature on reward and addiction. Although I introduce and discuss the neuroscience behind this technique, it should be noted that this thesis is written with a focus on evolutionary psychology not neuroscience. The review provided of the neuroscientific basis of reward is, by no means, all inclusive of the wide array of literature on this topic.

Additionally, please note that when the terms 'men/male' and 'women/female' are used in this work, it is in reference to the heterosexual population (for the sake of brevity, the term heterosexual may not be included each and every time). The evolutionary literature regarding mate preferences and mate choice, to date, has focused on the heterosexual population. Although the homosexual population can provide interesting new insight, it is difficult to obtain large enough sample sizes to complete such an analysis without special recruitment.

Lastly, it should be noted that the terms 'beauty' and 'attractiveness' are used relatively interchangeably throughout this work. Many evolutionary psychologists prefer not to use the term 'beauty' when referring to male appearance, as 'beauty' and 'attractiveness' may hold different connotations. However, the literature on the reward value of appearance has used the term 'beauty' relatively exclusively. Throughout this work, I will use both 'beauty' and 'attractiveness' to refer to male and female facial appearance.

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“The passions dispose the soul to desire those things which nature tells us are of use, and to persist in this desire, and also bring about that same agitation of spirits which customarily causes them to dispose the body to movement which serves for the carrying into effect of these things.

Nature has given us attraction to represent, to the soul, the enjoyment of something…and so makes us ardently desire this enjoyment. It is true that there are different sorts of attraction, and that the desires they give rise to are not all equally powerful.”

-René Descartes (1649)

Abstract

My research utilizes a behavioral key-press task adapted from the classic bar-press technique employed in many rodent studies of reward to explore the incentive salience of beauty among humans. In Chapter 2, I replicate previous findings indicating that gender differences exist for the incentive salience of beauty. I extend past findings with regard to the incentive salience of heterosexual beauty by investigating the role of additional aspects of facial appearance. Here, I find that apparent health holds incentive salience. This may serve an adaptive function by driving motivation to seek out healthy potential mates while avoiding infectious individuals.

In Chapter 3, I explore gender differences in the incentive salience of adult and infant faces. I show that women demonstrate greater motivation, overall, to view infant faces while both men and women differentiate between the high-cute and low-cute versions of infant faces, suggesting that infant cuteness may hold incentive salience for both men and women but that infants in general have higher incentive salience for women.

In Chapters 4 and 5, I investigate individual differences and variation across the menstrual cycle for women viewing adult faces. Women's own attractiveness was found to influence motivation to view attractive individuals, especially same-sex individuals. Within-subject variations in motivation across the menstrual cycle were apparent for the incentive salience of same-sex beauty. Taken together, the results of these experiments suggest that the incentive salience of same-sex faces among women may be partially driven by intrasexual competition – a novel explanation for women’s motivation to view same-sex individuals. Overall my research has indicated that infant cuteness, adult attractiveness and apparent health influence the motivational value of faces, while individual differences also exist among women with respect to own attractiveness and fertility. The key-press paradigm offers an exciting new method for exploring inter- and intra-sexual behavior in humans.

Chapter 1 The Incentive Salience of Faces

Facial perception is an extremely well developed skill among humans. We garner a wealth of socially relevant information from the face – information such as emotion, health, and familiarity. Among one of the most researched topics of face perception is that of attractiveness. What makes a face attractive? Does attractiveness honestly signal quality? How does the brain perceive beauty? In this Chapter, I will review the current literature on facial attractiveness and the neural correlates of the perception of beauty. Section 1.1 focuses on how we define beauty, or attractiveness. In Section 1.3, I review the evidence for beauty acting as a reward stimulus. Motivation to obtain rewards is essential for survival – we seek out food when hungry, water when we are thirsty, and we are motivated to obtain mates and reproduce. The evolution of reward-related motivation may extend beyond these drives to obtain food, water and sex and it is this extended adaptation that may explain how beauty can, in and of itself, be rewarding.

1.1 What is Beauty?

For the past 30 years, evolutionary psychologists have worked to determine what beauty is. There is a high level of agreement between individuals as well as across cultures, age-groups, and sexes as to which faces are attractive and which are not (see Langlois et al., 2000 for meta-analysis). While we tend to agree on which faces are attractive, the specific characteristics that make one face more attractive than another are still not fully understood. Early research into what drives perceptions of attractiveness focused on three key aspects of facial appearance: symmetry, sexual dimorphism and averageness (see Rhodes, 2006 for review), while more recent work has expanded to investigate the relationship between attractiveness and cues to health (such as skin color and texture).

Preferences for each of these aspects of facial appearance can be explained by the “good genes” theory, which purports that individuals with greater disease resistance and heritable immunity are more likely to be selected as mates due to their ability to pass on genes that will increase the survival and/or reproductive success of future offspring (Andersson, 1994;

Gangestad & Simpson, 2000; Thornhill & Gangestad, 1993, 1999). The term “good genes”, although widely used in the field to refer to innate immune system competence and disease resistance, is a bit of a misnomer. Realistically, a “good gene” is any gene that improves reproductive success, not only those that directly impact genetic quality or health. For example, genes that impact paternal behavior may increase offspring survival and contribute to reproductive success, making them “good”. However, for the purposes of this review, the term “good genes” will refer to only to those genes that impact an individual’s own health, reproductive fitness and heritable immunity.

The three most widely studied aspects of facial appearance with respect to their influence on facial attractiveness are: symmetry, averageness, and sexual dimorphism. Each of these aspects of facial appearance may reflect an individual’s genetic quality. The relative impact of each of these factors, and their link to underlying genetic quality are detailed below.

1.1.1 Symmetry

Three types of asymmetry exist in living organisms: directional asymmetry (DA), fluctuating asymmetry (FA) and antisymmetry (Van Valen, 1962). Directional asymmetry occurs when one side of the plane of symmetry shows greater development than the other. Common examples include the human heart as well as the testes in many species (van Valen, 1962). The second form, antisymmetry, occurs when an asymmetry is normally present but the dominant side is variable. For example, handedness in humans can be right, left or ambidextrous (VanValen, 1962). Studies investigating the relationship between facial symmetry and facial attractiveness typically focus on the third type of asymmetry, known as fluctuating asymmetry[1] (FA). Fluctuating asymmetry refers to individual variation in bilateral symmetry for traits that are symmetric across the population, such as having one eye that is slightly larger than the other (Ludwig, 1932; van Valen, 1962). Environmental challenges, such as toxins or parasite, encountered during growth/development can act to increase levels of FA. Because symmetry

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[1] For the purpose of this report, any discussion of symmetry will refer to fluctuating asymmetry (FA).

reflects the ability to undergo stable development in the face of such environmental challenges, it is considered to be a reflection of genotypic quality (i.e. a reflection of "good genes") and may influence perceived attractiveness (Gangestad & Simpson, 2000; Møller, 1997; Møller & Swaddle, 1997; Møller & Thornhill, 1997; Parsons, 1992).

A number of early studies investigating the relationship between symmetry and facial attractiveness surprisingly found preferences for asymmetrical faces (Kowner, 1996; Samuels, Butterworth, Roberts, Graupner, & Hole, 1994), although later studies have demonstrated preferences for symmetrical faces (Baudouin & Tiberghien, 2004; Grammer & Thornhill, 1994; Jones, Little, Tiddeman, Burt, & Perrett, 2001; Little, Apicella, & Marlowe, 2007; Penton-Voak et al., 2001; Perrett et al., 1999; Rhodes, Proffitt, Grady, & Sumich, 1998; Scheib, Gangestad, & Thornhill, 1999). It has been suggested that differences in the methodology used when creating symmetrical faces could be the underlying cause of this discrepancy. Early studies used chimeras as symmetrical stimuli. Chimeras are created by taking one half of the face and mirroring it (bilaterally) to create a full, symmetrical face. These perfectly symmetrical chimeric faces can appear quite unnatural or strange looking because mirror reflections of facial hemispheres can make faces appear abnormal, especially if any blemishes or marks are apparent on the face (see Figure 1.1).

Later studies that used computer graphic techniques to systematically manipulate faces, rather than chimeras, have consistently demonstrated that more symmetrical faces are perceived as being more attractive than less symmetrical faces. Perrett et al. (1999) were able to morph/re-map individual faces to create symmetrical versions by measuring distances between bilaterally paired points on a given face. These new symmetrical faces did not have the odd appearance or textural problems seen with chimeric faces. Pairs of faces (original and perfectly symmetrical) were presented in a forced choice task and symmetrical faces were consistently chosen as more attractive than were the original faces (both when analyzing by rater and by face). Preferences for symmetry were further tested when using a set of faces that all had constant, synthetic coloration ('average' texture and color was obtained from composite images and then mapped onto the normal and symmetrical faces). Again, more symmetrical faces were considered more attractive. Lastly, they presented sets of normal and symmetrical images to raters. Each group of faces was composed of half normal and half symmetrical versions, but no one face appeared twice in the same group (i.e. if group 1 contained the symmetrical version of a given face, its normal counterpart was placed in group 2). They found that symmetrical faces received higher attractiveness ratings than non-symmetrical faces.

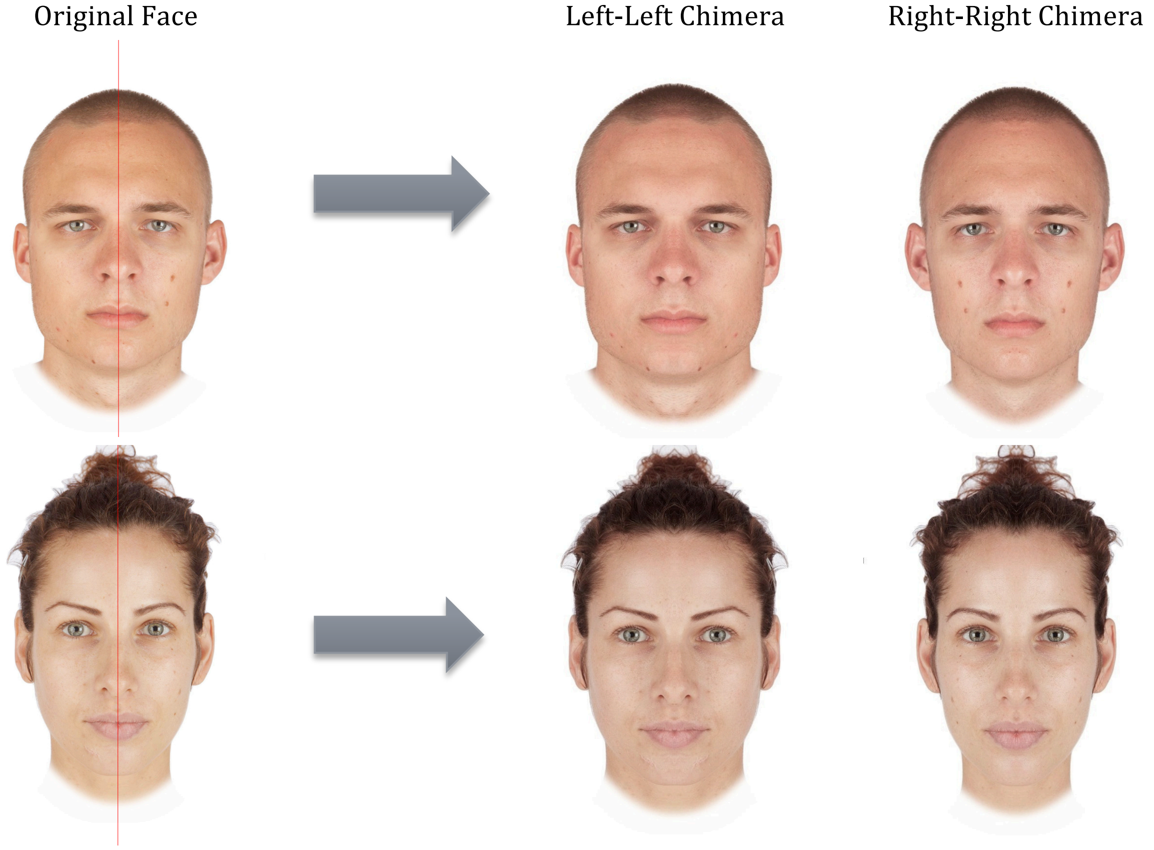

Figure 1.1 *Example of the strange appearance that often occurs in chimeric faces. To create chimeric faces, a normal face is bilaterally intersected. Each half of the face is then mirrored to create left-left and right-right faces that are perfectly symmetrical. Asymmetries in shape and color in the original face will be exaggerated in the chimeric versions. Additionally, skin texture can be affected by the mirroring process (Perrett et al., 1999). The number of blemishes often increases with the mirroring process. In this example, asymmetries in size of the left and right side of the face are apparent in both the male and female examples. In the male example, blemishes that were evident on the right side of the face (based on observer perspective) are duplicated in the right-right symmetrical version adding to the odd appearance.*

The link between symmetry and attractiveness appears to be quite robust to rater and face sex. Scheib et al. (1999) found that measures of facial symmetry in male faces were positively correlated with women's attractiveness ratings of the faces. Interestingly, women were not able to accurately rate the symmetry of the faces, suggesting that perceptions of symmetry may not consciously influence perceptions of attractiveness. The relationship between symmetry and attractiveness is also present when men rate female faces (Fink, Neave, Manning, & Grammer, 2006). In addition to being rated as more attractive, more symmetrical faces were also rated as healthier and less anxious than their less symmetrical counterparts. When both men and women rate both same- and opposite-sex, the link between facial symmetry and perceived attractiveness persists (Jones et al., 2001). Jones et al. (2001) further demonstrated that the relationship between symmetry and attractiveness was mediated by a link between apparent health and facial symmetry – individuals with highly symmetrical faces were rated as more attractive and, separately, healthier than individuals with asymmetrical faces. Although the symmetry-attractiveness link is robust to observer and face sex, there is an opposite-sex bias in sensitivity to facial symmetry (Jones et al., 2001). This finding may be the result of a greater need to attend to perceptual cues of genetic quality in potential mates (i.e. opposite-sex individuals) as compared to non-mates (i.e. same-sex individuals).

Overall, research over the past several decades has provided strong evidence for symmetry preferences. In addition to being rated as more attractive, more symmetrical faces are also perceived as healthier than less symmetrical faces (Grammer & Thornhill, 1994; Penton-Voak et al., 2001). In a sample of University-aged men and women, Milne et al. (2003) found that FA was associated with the number of reported medical conditions (i.e. less symmetric subjects were more likely to report multiple medical conditions such as heart problems, kidney/bladder infections, major surgery, etc.) and BMI (in women only, less symmetrical women tended to be heavier). Surprisingly, no link was observed FA and a set of direct health measures including: blood pressure, cholesterol, and cardiovascular fitness. However, in a larger sample, Thornhill and Gangestad (2006) observed a link between FA and reported number of respiratory infections, duration of infection, and antibiotic use. Together, these results suggest that facial symmetry may be indicative of underlying health.

Many researchers have argued that the symmetry component of facial appearance provides an honest signal regarding an individual's genetic quality. Indeed, a study of symmetry among men in rural Belize indicated that more symmetrical men (i.e. those with lower levels of FA) had lower morbidity rates as well as a higher number of offspring and more lifetime sexual partners than less symmetrical men (Waynforth, 1998). With symmetry linked to underlying health and attractiveness, facial symmetry may act as a reliable cue of health – which may act, in turn, to inform mate selection.

1.1.2. Averageness

Fascination with the relationship between averageness and attractiveness began nearly 150 years ago when Francis Galton (1879) developed a new technique known as composite photography. This technique involves overlaying several individual images to create a composite, or average, face. Galton noticed that composite faces appeared more attractive than the individual faces of which they were comprised because any individual abnormalities were eliminated with the averaging process (see Figure 1.2). The *Averageness Hypothesis*[2] purports that facial attractiveness is simply facial averageness (Langlois & Roggman, 1990; Perrett, May, & Yoshikawa, 1994; Valentine, Darling, & Donnelly, 2004). Facial averageness may reflect genetic heterozygosity, which provides an individual with stronger immune response capabilities than those with genetic homozygosity (Thornhill & Gangestad, 1993). Because individuals nearest the population midpoint for any given trait are often the most fit (Symons, 1979), preferences for facial averageness may have evolved in order to draw us to individuals of high genetic quality.

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[2] It has been noted that in addition to averageness of facial features, facial symmetry also increases when composite images are created. The *Symmetry Hypothesis* claims that increased symmetry, rather than averageness, is responsible for the increased attractiveness of composite faces (Rhodes, Sumich, & Byatt, 1999; Valentine, Darling, & Donnelly, 2004). Several studies have attempted to systematically parse out the effects of averageness and symmetry. Grammer and Thornhill (1994) found that averaged facial images were not rated as more attractive when controlling for changes in symmetry. However, Rhodes, Sumich and Byatt (1999) created composites of high-, normal- and low-averageness versions of faces (based on ratings of facial distinctiveness) and then created a perfectly symmetrical version of each of these faces. They found that as averageness increased, attractiveness ratings increased and that attractiveness ratings increased with symmetry, but no interaction was observed for averageness and symmetry, suggesting that averageness has an independent impact of perceptions of attractiveness.

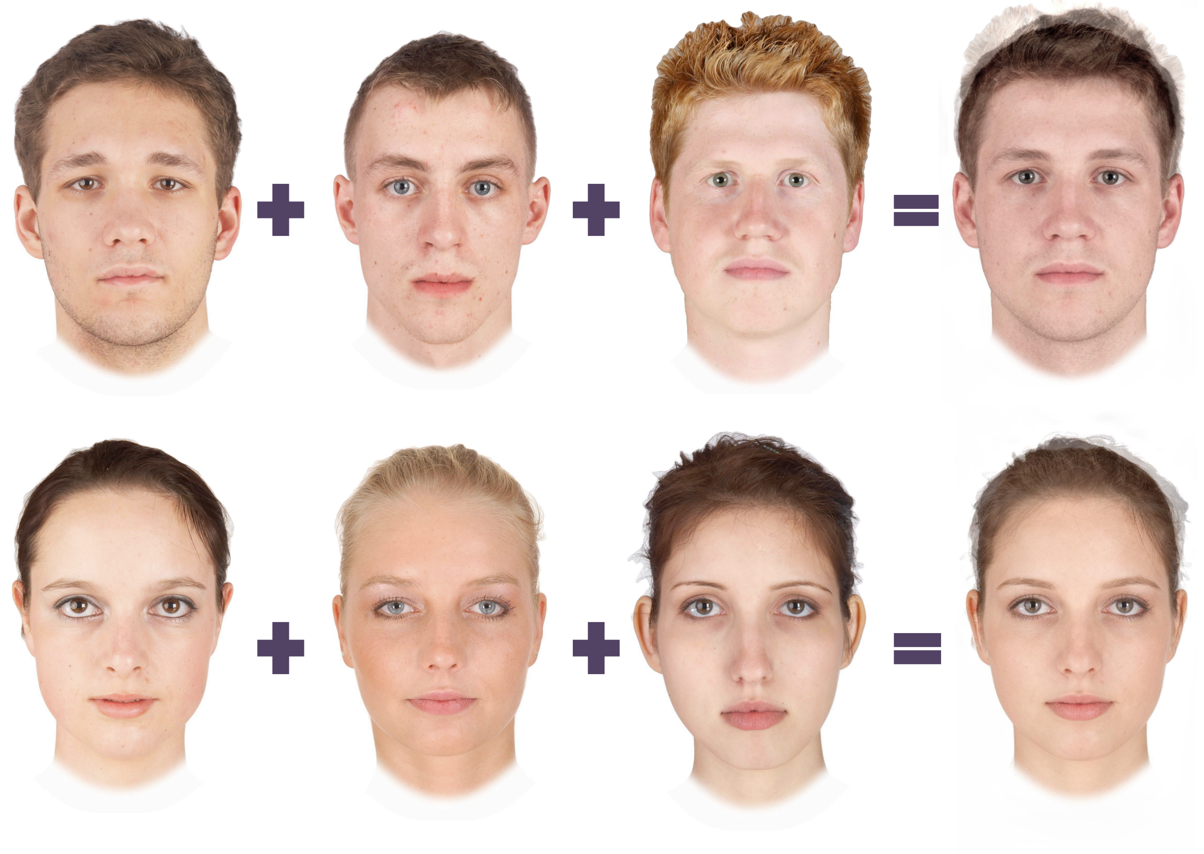


Figure 1.2 Example of facial averages or composites. By mapping the facial structure of each individual, it is possible to determine the average shape and create the corresponding average face. As seen above, the average man and average woman made from three individual identities are more attractive than the individuals that went into that average.

Since Galton's original finding, a number of studies using composite images, mathematical averages, and systematic manipulations of averageness have demonstrated that averageness is positively correlated with perceived attractiveness (Bronstad, Langlois, & Russell, 2008; Komori, Kawamura, & Ishihara, 2009; Langlois & Roggman, 1990; Langlois, Roggman, & Musselman, 1994; Little & Hancock, 2002; O'Toole, Price, Vetter, Bartlett, & Blanz, 1999; Rhodes, Roberts, & Simmons, 1999; Rhodes, Sumich, & Byatt, 1999; Rhodes & Tremewan, 1996). Grammer and Thornhill (1994) found that composites made from several images of the same individual were rated as more attractive than the individual images – although this pattern of results was only seen for female faces. Langlois and Roggmann (1990) empirically tested the relationship between facial averageness and perceived attractiveness. They created mathematical averages of several faces (averages of 2, 4, 8, 16 and 32 faces were used). Average and original faces were rated for attractiveness. Average images made from a high number of faces (i.e. the 16 & 32 face groups) were rated as significantly more attractive than the original face images for both male and female faces. These findings are consistent even when individual features are aligned/averaged in size (Rhodes, Sumich, & Byatt, 1999; Rhodes & Tremewan, 1996), as well as when an identical skin condition is applied to each face (Little & Hancock, 2002; Rhodes & Tremewan, 1996).

A major issue that arises with the use of composite images is that these averaged faces have smoother skin texture than the originals, which can impact perceived attractiveness independently of averageness (Penton-Voak & Perrett, 2001). However, when normal/unmanipulated faces are used, those that have an appearance which is closer to the population average face are rated as more attractive than distinct faces (Morris & Wickham, 2010; Rhodes & Tremewan, 1996) although the averageness-attractiveness relationship seen with natural faces is smaller than that seen with manipulated faces (see Rhodes, 2006 for meta-analysis).

Perrett et al. (1994) have argued strongly against the averageness hypothesis – proposing instead that attractiveness is dependent on both the distance from average *and* the direction of the difference (known as the *Contrast Hypothesis*). To test the A*verageness* and *Contrast Hypotheses*, they created an overall-average face shape based on a sample of 60 female faces. High-attractive and low-attractive average face shapes were then created using the 15 highest and lowest rated faces, respectively. These high/low shapes were then exaggerated by 50% of the difference between high/low and overall average. They found a strong preference for the high-attractive average face as compared to the overall average face (this finding persisted cross-culturally). Caricaturing the shape differences between the average composites and the attractive composites in the direction of the attractive group resulted in faces that were less average yet more attractive. These findings, they argue, explicitly dismiss the *Averageness*

Hypothesis; if attractiveness were simply averageness, then there should not have been any differences in preference among the high-, low- and overall average face shapes.

Follow up studies have failed to replicate these findings, however, and some researchers argue that the *Averageness Hypothesis* may actually explain Perrett et al.'s findings – if faces that are attractive are more mathematically close to average, then composites of highly attractive faces should be closer to mathematical average than composites of "normal" or unattractive faces. In a series of studies designed to empirically test the *Averageness* and *Contrast Hypotheses,* DeBruine et al. (2007) found consistent evidence that attractiveness and averageness are dissociable aspects of facial appearance. Using symmetrical composite images, DeBruine et al. manipulated faces along a continuum from the average of the set to the average of the 15 most attractive faces in the set. They demonstrated that the faces which were perceived as most typical or average were not those that were perceived as most attractive, the direction of the deviation from average impacts perceptions of attractiveness, and that deviation from average along the attractiveness dimension only increases attractiveness up to a certain point – further deviations from averageness then give the face an unnatural appearance which results in decreased attractiveness.

Although there remains some debate among researchers as to the importance of averageness in perceptions of facial attractiveness, the evidence to date would suggest that faces that are closer to the population average may be more attractive than many that deviate from this average, but are not necessarily "the best" or most attractive in that certain deviations from average actually increase perceived attractiveness.

1.1.3 Sexual Dimorphism

Sexual dimorphism refers to the systematic variation in form between males and females of a given species (see Figure 1.3). Sexually dimorphic physical features (i.e. secondary sex characteristics) develop in response to increased levels of sex hormones (estrogen and testosterone) that occur at the onset of puberty (Farkas, 1987). In humans, sexual dimorphism is apparent in shape cues (in the face and body) and color cues. Male and female typical face shape differs as the result of sexually dimorphic bone growth in response to increased levels of sex hormones. In males, increased levels of testosterone stimulate lateral facial bone growth (including the mandibles, brow ridge and chin; Enlow & Hans, 1996; Fink & Penton-Voak, 2002). In women, the high levels of estrogen during puberty inhibit these effects of testosterone. The female face, therefore, retains a neotenous (childlike) appearance. Because the nose and forehead do not become more prominent during development, the cheekbones appear much more protrubent in the female face (Enlow & Hans, 1996). Additional estrogen-markers in the face include fat deposits in the lips and upper cheek (Perrett et al., 1998). Dimorphic cues also exist for body shape. High estrogen-to-testosterone ratios in women cause breast development and widening of the hips and pelvis resulting in the stereotypical female hourglass figure. In addition to these shape cues, skin color is also sexually dimorphic; higher levels of melanin give

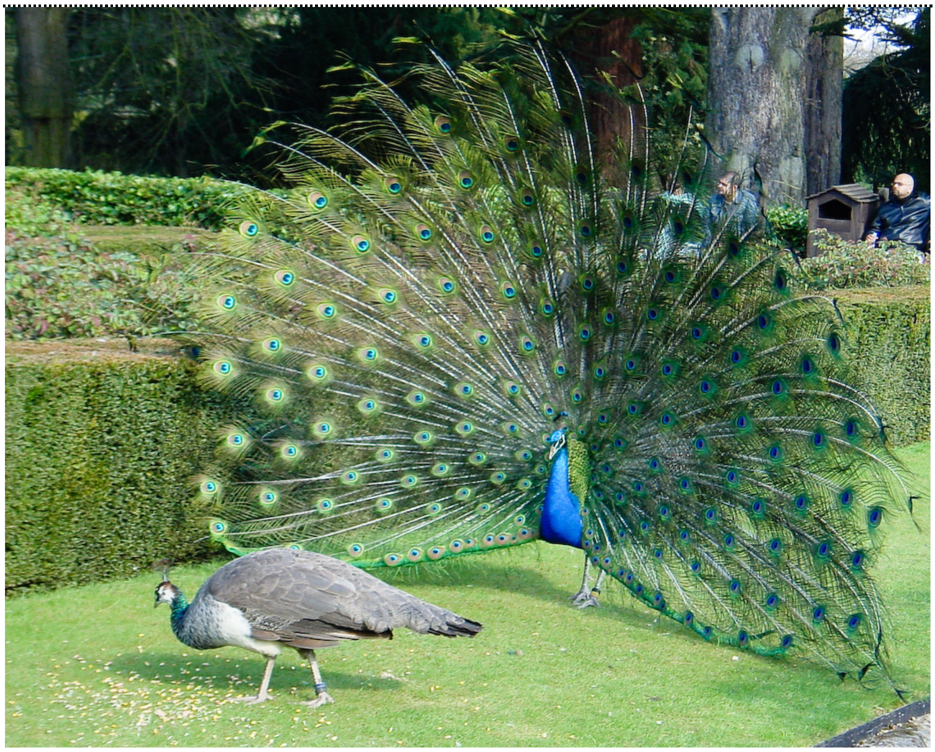


Figure 1.3 *The colorful plumage of the male peacock in comparison to the muted coloration of the female peahen is a common example of sexual dimorphism*

men darker skin, hair and eyes than females (Jablonski & Chaplin, 2000). Sexually dimorphic facial features are detailed in Figure 1.4.

MASCULINE MALE

- Prominent brow ridge
- Flat forehead
- Large jaw
- Thin lips
- Nose: wide, convex shape, downward facing tip

FEMININE FEMALE

- Bulbous forehead
- Protrubent cheekbones
- Small Jaw
- Full lips
- Nose: narrow, concave shape, turn-up at the tip

Figure 1.4 A comparison of facial characteristics typical of the highly masculine male face and the highly feminine female face. For a detailed overview of gender differences in face shape, see Enlow & Hans (1996).

The good genes theory purports that sexually dimorphic features are an indicator of high genetic quality. In males especially, sexually dimorphic features may provide indication of health. According to the Immunocompetence Handicap Hypothesis (ICHH; Folstad & Karter, 1992), the immune system and developing sex characteristics compete for resources. Because masculine features develop in response to high levels of testosterone, which acts as an immunosuppressant (Ahmed & Talal, 1990; Wyle & Kent, 1977), exaggerated secondary sexual characteristics provide an honest cue about the bearer's heritable immunocompetence. The immunological challenge of developing exaggerated dimorphic (i.e. highly masculine) characteristics “handicaps” the individual (Zahavi, 1975) and only the healthiest males are able to cope with the cost of developing such features (Hamilton & Zuk, 1982; Thornhill & Gangestad, 1993). Penton-Voak and Chen (2004) have observed a direct correlation between testosterone levels and ratings of facial masculinity in humans. Studies investigating the relationship between facial masculinity and health (current, long-term, or apparent health) have yielded conflicting results – with some studies suggesting facial masculinity is positively correlated with health (Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006), while others find no link between these two factors (Boothroyd et al., 2005).

Rhodes et al. (2003) found that facial masculinity was correlated with perceived and actual health in males. Detailed health records were obtained from a set of college-aged males. Each male’s image was rated for attractiveness, masculinity and perceived health. Masculinity had a positive relationship with actual health and perceived health, but not with attractiveness (a positive but non-significant correlation was found). Similarly, using measured rather than rated masculinity, Thornhill and Gangestad (2006) found that more masculine men reported fewer instances of respiratory infections, shorter duration of infection and less antibiotic use than more feminine men. In addition to signalling health, masculinity may also act as a social signal; specifically, masculinity signals dominance and status, which are indicative of high resource levels and may enhance mate value (Mazur & Booth, 1998; Neave, Laing, Fink, & Manning, 2003; Perrett, 2011).

Because sexually dimorphic features become exaggerated post-puberty, they can act as cues to sexual maturity, signalling that an individual is at reproductive age (Johnston & Franklin, 1993; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Symons, 1979, 1995). Sexual dimorphism may be a particularly salient cue of female reproductive potential. Men are capable of reproducing for a greater portion of the lifespan than women – a commonly cited example is that of Charlie Chaplin, who had children well into his 70’s. Women, on the other hand, are only able to bear children from the onset of puberty (average age 12-13) through menopause (typically occurs age 49-50) with peak fertility occurring at age 25 (Nichols et al., 2006). Ratios of estrogen-to-testosterone decrease as women age; a by-product of this change is facial masculinization. A feminine face can, therefore, be indicative of fecundity (Enlow, 1990).

In addition to providing cues of reproductive potential, dimorphic features can also supply information about the reproductive *fitness* of a potential mate. For females, estrogen's blocking effects on testosterone are responsible for a more dimorphic appearance. Along with progesterone, estrogen is one of the main hormones governing female reproduction. Several studies have indicated that these trait hormones are accurate predictors of conception success (Baird et al., 1997; Baird, 1999; Lipson & Ellison, 1996; Lu, Bentley, Gann, Hodges, & Chatterton, 1999; Stewart, Overstreet, Nakajima, & Lasley, 1993). Baird et al. (1997) measured levels of estrogen and progesterone across the menstrual cycle in over 200 women who were trying to conceive. They found that women with lower baseline progesterone levels (i.e. less progesterone overall, regardless of cycle stage) were more likely to achieve conception. They also found that higher post-ovulatory estrogen and progesterone levels at the early-luteal stage (i.e. stage when implantation can occur) were associated with increased conception rates. Similarly, Lipson and Ellison (1996) demonstrated that high levels of mid-follicular (i.e. ovulatory phase) estrogen were highly correlated with conception success.

Estrogen levels also impact facial attractiveness. Law-Smith and colleagues (2006) directly measured levels of estrogen in female participants and assessed the relationship between hormone levels and perceived facial attractiveness. Both individual and composite faces with high levels of estrogen were consistently rated as more feminine, more attractive and healthier than those with low levels of estrogen. Together, these finding indicate that sexually dimorphic traits act as indices of female reproductive fitness and potential in women.

In humans, there is an overwhelming contention that high femininity is considered attractive in female faces (Cunningham, Roberts, Barbee, Druen, & Wu, 1995; Cunningham, 1986; Dunkle & Francis, 1990; Johnston & Franklin, 1993; Johnston et al., 2001; Koehler, Simmons, Rhodes, & Peters, 2004; Law Smith et al., 2006; O'Toole, Deffenbacher, Valentin, McKee, & Huffabdi, 1998; Penton-Voak & Chen, 2004; Perrett et al., 1998; Rhodes et al., 2003; Rhodes, Hickford, & Jeffery, 2000). Female faces that possess more feminine features are consistently rated as more attractive than those with more masculine features (Cunningham et al., 1995; Cunningham, 1986; Jones & Hill, 1993; Perrett et al., 1994). Systematic exaggeration of femininity (i.e. morphing a face towards a highly feminine protoype) also increases attractiveness (Perrett et al., 1998; Rhodes et al., 2000). Meta-analytical data (Rhodes, 2006) indicates that feminine faces are attractive when either natural or manipulated images are used. The clear relationship between femininity and attractiveness may be due to the fact that female reproductive potential is easily assessed based on physical appearance due to the age-related decline in fertility (Penton-Voak & Perrett, 2001).

The relationship between masculinity in male faces and perceived attractiveness is much less straightforward. Women must consider the trade-offs between negative aspects of masculinity (low paternal investment, negative personality traits; Gangestad & Simpson, 2000; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Mazur & Booth, 1998) and positive aspects (high immunocompetence; Folstad & Karter, 1992; Rantala et al., 2013; Rhodes et al., 2003). A number of studies have indicated that individual masculine facial features/traits are considered attractive (Cunningham, Barbee, & Pike, 1990; Grammer & Thornhill, 1994; Keating, 1985; Scheib et al., 1999). Keating (1985) found that masculine schematic male faces were preferred to feminine ones. Similarly, studies using natural (i.e. unmanipulated) male faces have demonstrated that masculinity is positively correlated with attractiveness (Cunningham et al., 1990; Gillen, 1981; Grammer & Thornhill, 1994; Koehler et al., 2004; Neave et al., 2003; Rhodes et al., 2003; Scheib et al., 1999). However, several studies using photographs of male faces manipulated on a masculinity continuum (i.e. individual face can be transformed by varying degrees of dimorphism based on high masculinity/femininity prototype faces) demonstrated preferences for feminised faces or no overall masculinity preference (Penton-Voak et al., 1999, 2001; Perrett et al., 1998; Rhodes et al., 2000; Swaddle & Reierson, 2002). Although it has been suggested that methodological differences in image creation are the cause of discrepancies in the literature, DeBruine et al. (2006) examined masculinity preferences using multiple common manipulation techniques (altered sexual dimorphism, perceived masculinity and pubertal development) and found that women's masculinity preferences were similar across all three methods. DeBruine suggests that individual differences in preference for masculinity may account for inconsistencies in past findings. Factors such as ideal masculinity preference and actual partner masculinity impacted the observed masculinity preferences, suggesting that variability exists in the masculinity-attractiveness relationship among individual women.

1.1.4 Cues to Health

Andersson (1994) proposed an adaptive theory of Darwin's sexual selection, positing that the traits that come to be preferred in a potential mate are those that indicate high genetic quality or fitness, or "good genes". Hamilton and Zuk (1982) extended this notion, proposing their parasite model which states that the characteristics considered attractive in potential mates are those that indicate low parasite load and high resistance to infection. Choosing a healthy mate can provide both direct and indirect benefits in that one is less likely to be exposed to pathogens when with a healthier mate and offspring health may be improved assuming immunocompetence is heritable (see Section 1.1.3 for discussion of the Immunocompetence Handicap Hypothesis). Gangestad and Buss (1993) found that people living in areas with higher pathogen prevalence do indeed show stronger preferences for attractiveness, suggesting a link between health and attractiveness could relate to cues of pathogen resistance.

Both current and long-term health can be indicators of genetic quality; those with "good genes" are more likely to be healthy now and in the future. Cues that are associated with apparent health, such as pallor (Roujeau, 2001) and MHC-similarity/dissimilarity (Roberts et al., 2005), adiposity (Tinlin et al., 2013), and symmetry (Jones, Little, Feinberg, et al., 2004; Thornhill & Gangestad, 1993) can signal current health status. Shackelford and Larsen (1999) explored the link between current health and facial attractiveness in 100 individuals (66 women). Participants reported physical health symptoms daily over four weeks and had their cardiovascular health assessed in the lab using cardiac recovery time. Facial photographs of the participants were rated for attractiveness. They found that more attractive men reported fewer instances of illness (runny nose, sore throat and cough) and had greater cardiovascular health than unattractive men. Similarly, attractive women reported fewer instances of headaches than their less attractive counterparts.

Gray and Boothroyd (2012) explored the link between attractiveness and more extensive past health (12 months and 3-years) in a set of University-aged women. Over 100 women aged 18-20 were photographed under standardized conditions. These women were also asked to report on the number of cold/flu bouts and stomach bugs, as well as antibiotic use, and pre-existing immune system disorders in the past 12 months and 3 years prior to participation. Participants returned to the lab at the end of the year and answered these health questions for a second time, with respect to how frequently they had experienced symptoms since their first visit. Photographs of the participants were rated for femininity, mood, health, and attractiveness. Women who were rated as more feminine and more attractive reported fewer colds (past 12 months) and less antibiotic use (past 12 months and 3 years) than less attractive/feminine women. Surprisingly, rated health did not correlate with actual health measures in this sample. However, in a similar study where participants provided self-ratings of health (measured via current cold and how frequently in the past 12 months did they suffer from a cold) and photographs of these individuals were rated by others for apparent health, Little et al. (2011) found that self-ratings and observer-ratings were positively correlated, although these results failed to reach significance (p-values of .07 and .08 for women and men, respectively).

In an attempt to uncover the link between attractiveness and long term health, Henderson (2003) had a set of images (25 male, 25 female) from the 1920s rated for attractiveness and perceived health. Longevity was assessed using census data; these data were correlated with ratings of perceived health and perceived attractiveness. They found that perceived attractiveness predicted future longevity and ratings of perceived attractiveness and perceived health were highly correlated. Interestingly, ratings of perceived health did not predict future longevity. It may be the case that the loss of color information due to black and white images obscured detection of health cues.

Although these studies would suggest a link between health and attractiveness, an additional longitudinal study failed to find a relationship between attractiveness and actual health (Kalick, Zebrowitz, Langlois, & Johnson, 1998). Health data were collected during adolescence, middle adulthood and later adulthood. Facial photographs taken at the age of 17 were assessed for attractiveness. These attractiveness ratings were not correlated with actual health scores at any time point. However, those individuals who received higher attractiveness ratings were perceived as healthier than their less attractive peers. A number of methodological issues with this study may explain the lack of observed relationship between actual health and attractiveness. Firstly, all photographs were black and white slides of images taken in the 1930s. As previously mentioned, accurate health judgements may be harder to make when using black and white images due to the loss of color cues to health. Secondly, the measures of actual health utilized in the dataset involved a single yearly rating of health on a 5-point scale ranging from “no illness” to “severe illness”. Although this assessment was made by a physician and included detailed medical histories, collapsing health measures to a single yearly assessment may not be a truly accurate measure of actual health.

While the evidence for a link between attractiveness and actual health may be somewhat equivocal, a number of studies have shown high correlations between judgements of facial attractiveness and perceived health – faces that look healthier receive higher attractiveness ratings and attractive faces tend to receive higher ratings of perceived health (Henderson & Anglin, 2003; Jones et al., 2001; Kalick et al., 1998; Krupp, DeBruine, & Jones, 2011). Grammer and Thornhill (1994) have shown that men and women judge attractive opposite-sex faces as healthier than unattractive faces. Kalick et al. (1998) have extended these findings to show that both men and women judge attractive individuals of the opposite-sex and same-sex as healthier than unattractive individuals. These assessments of health extend to perceptions of fertility. Cunningham (1986) found that men judge attractive women to be more fertile and less likely to experience medical problems than their unattractive counterparts. Similarly, Singh and Young (1995) found that female figures with slender bodies and low waist-to-hip ratio were rated as most attractive, healthy, and feminine looking. Interestingly, women with low waist-to-hip ratio *actually* report fewer health problems than those with higher ratios, providing additional evidence for the link between apparent and actual health (Singh, 1993).

A number of factors have been found to influence perceptions of health. Specific to the face, skin condition and color as well as levels of facial fat can influence how healthy an individual appears to be. The effects of these factors on perceived health and attractiveness are outlined below:

Skin condition/texture, a cue to health, has been implicated as a key factor in perceptions facial attractiveness, particularly for females (Fink, Grammer, & Thornhill, 2001; Fink & Penton-Voak, 2002; Frost, 1994; Matts, Fink, Grammer, & Burquest, 2007). Skin infections (acne, lesions, etc.) negatively impact male's assessments of female beauty (Fink et al., 2001). Similarly skin homogeneity acts as an indicator of age and ultraviolet damage which provides cues to health and impacts attractiveness judgements (Matts et al., 2007). Using skin patches, several studies have suggested that skin condition can influence perceived attractiveness (Jones, Little, Burt, & Perrett, 2004) and health (Roberts et al., 2005) independently of shape cues. Indeed, there is a strong correlation between the attractiveness ratings of skin patches and whole-face ratings (Jones et al., 2004).

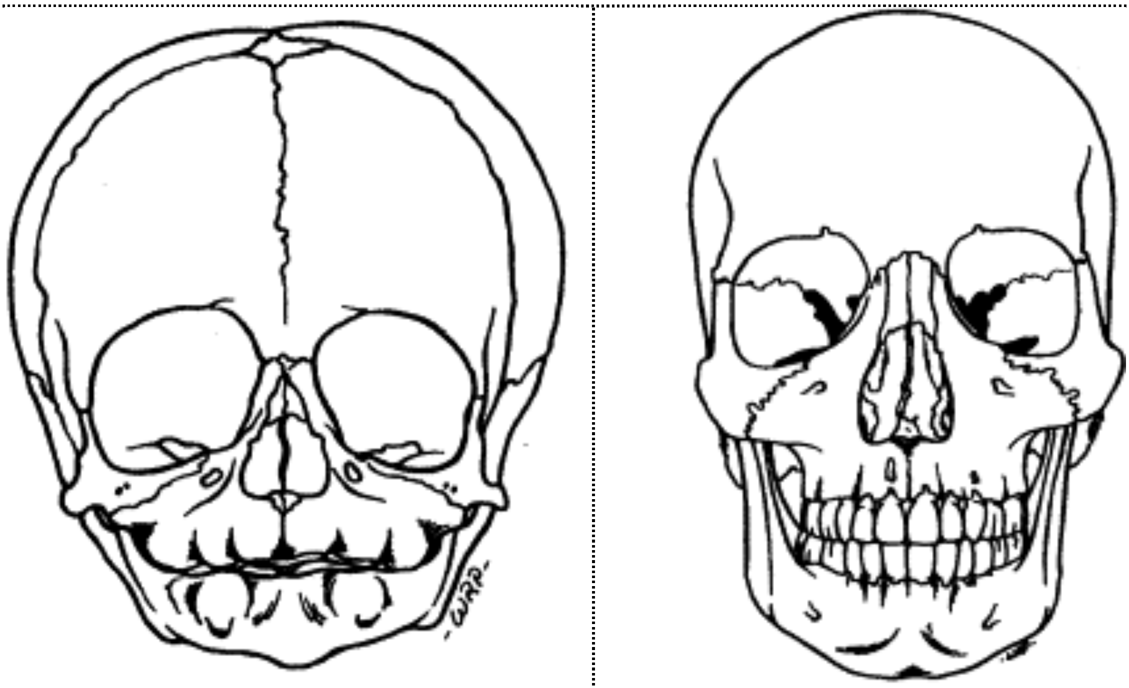
Skin color can affect perceived attractiveness in a number of ways. Homogeneous skin color is perceived as more attractive and healthy (Fink, Grammer, & Matts, 2006). Skin pigments that hold specific biological relevance also impact perceived attractiveness. Skin redness may be indicative of higher blood circulation in peripheral vessels (Fink et al., 2001). Using computer graphic manipulation techniques, studies have shown that faces increased in redness are perceived as healthier (Stephen, Coetzee, Law Smith, & Perrett, 2009; Stephen, Smith, Stirrat, & Perrett, 2009) and more attractive (Re, Whitehead, Xiao, & Perrett, 2011). When able to alter skin color directly, participants have been shown to consistently increase oxygenated blood coloration (i.e. skin redness) to make faces appear healthy (Stephen, Coetzee, et al., 2009). Increased skin yellowness, which is the result of carotenoids (a pigment obtained from eating fruits and vegetables) and indicative of dietary quality and health, has also been shown to positively affect perceived attractiveness (Stephen, Smith, et al., 2009; Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012).

Facial adiposity, or facial 'fat' may act as a cue to health, and thus impact judgements of attractiveness. Weight is a heritable feature (Elks et al., 2012) and may reflect genetic quality. As such, it is not surprising that preferences related to body weight have been observed, particularly for women. In Western populations, heavier women (i.e. those with a higher BMI) are judged as less attractive (Hume & Montgomerie, 2001; Thornhill & Grammer, 1999; Tovée, Reinhardt, Emery, & Cornelissen, 1998). Similarly, women with lower waist-to-hip ratios are considered to be more attractive (Singh & Young, 1995; Singh, 1993). Importantly, cues to weight are present in the face and can impact perceptions of attractiveness. Tinlin et al. (2012) found that ratings of facial adiposity are predicted by body weight, suggesting that body size can accurately be assessed from facial cues. Facial adiposity in women was shown to be correlated with various indices of poor health and physical condition – women with higher levels of facial fat report more past health problems, and greater psychological issues (i.e. stress, depression, and anxiety). In addition to the link between facial adiposity and health, Coetzee, Perrett and Stephen (2009) found that facial adiposity predicted ratings of attractiveness as well as ratings of apparent health. Importantly, facial adiposity was also an accurate predictor of actual health (measured via cardiac health), suggesting that facial adiposity may provide an honest cue to genetic quality.

1.2 Beautiful Babies

1.2.1 Infant Facial Morphology

Infant facial morphology is fundamentally different from adult facial morphology (Bergersen, 1966; Enlow & Hans, 1996). As seen in Figure 1.5, the lower half of the face is proportionately smaller in infants than it is in an adult face. Infants and young children have a characteristically short and wide face due to skeletal differences between infancy and adulthood; infants have a broad basicranial template, with an otherwise vertically short face because the nasal and mandibular regions are small due to their small body size and minimal pulmonary requirements.



INFANT FACE

- Large, bulbous skull
- Large eyes
- Close-set features
- Features low on face
- Short chin

ADULT FACE

- Skull is more proportional
- Proportional eye size
- Features spread out
- Vertical distribution of features
- Larger chin and jaw

Figure 1.5 *A comparison of the craniofacial structure of infants and adults. For a detailed overview of skeletal growth from infancy to adulthood, see Enlow & Hans (1996).*

Image adapted from Enlow & Hans (1996)

Facial growth occurs in three principle regions during development: the brain, the nasal passage, and the oral region (Enlow & Hans, 1996). Brain development is very important in utero – during fetal development, the brain takes precedent over the other two aspects of facial growth – resulting in the disproportionately large skull in relation to body size among infants. It is also interesting to note that the eye sockets are at their full size at birth. This contributes to the typical infant facial configuration: large eyes, large bulbous forehead, and close-set features positioned low on the face. During adolescence, vertical nasal enlargement occurs in pace with growing body and lung size; the mandibular arch is also lowered by increasing vertical ramus length. As seen in Figure 1.5, during growth the maxilla (top of the jaw) and mandible (bottom of the jaw) begin to protrude away from the face giving a longer, more ovular head shape. Overall, these vertical changes result in the face losing its wide appearance in adulthood – and the top of the skull looks proportional to the rest of the face.

In addition to these stereotypical baby facial features infants tend to have short, thick limbs and a plump body shape. High levels of fat, or pudginess, act as a sort of fatty "insurance policy" for development. Baby fat is a large fuel storage in the form of fatty acids (i.e. triglycerides) which are precursors to ketone bodies, the key substrates for brain lipid synthesis necessary for normal brain development (Cunnane & Crawford, 2003). If the infant were to experience a period of hardship, such as food shortage, this fat repository can be utilized to ensure that brain development progresses normally.

The young of many mammal and avian species undergo similar facial development from birth to maturation. As Figure 1.6 demonstrates, many newborn or young animals share the same skull shape and baby-face appearance as human infants; especially a bulbous forehead, large eyes and close-set internal features.

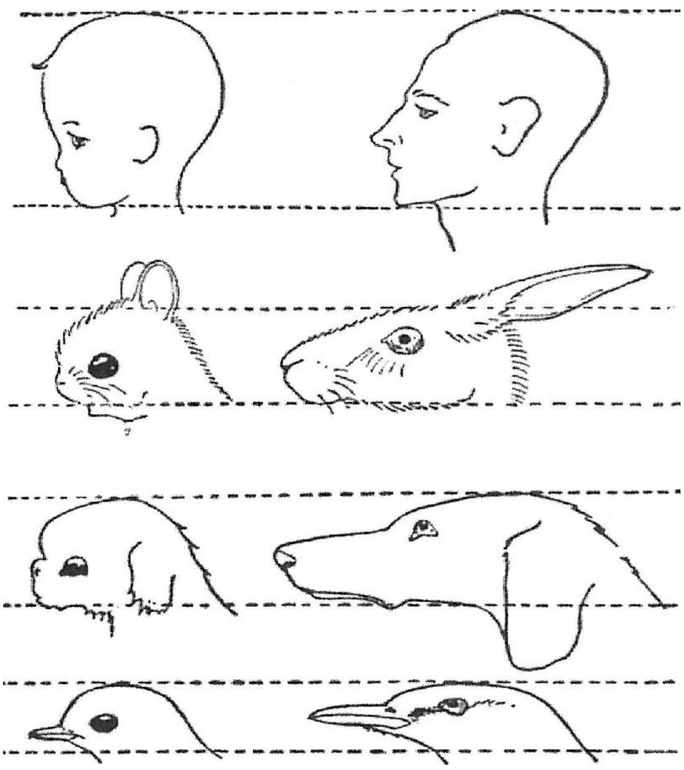


Image from Lorenz (1943)

Figure 1.6 *The craniofacial differences between infants and adults across multiple species.*

1.2.2 Perceptions of Cuteness

The more an infant's face displays the stereotypical features outlined in Section 1.2.1 (the 'baby schema': large, bulbous forehead, large eyes, close-set features positioned low on the face, small chin), the cuter the infant is considered to be (e.g. Alley, 1981; Boukydis, 1981; Brooks & Hochberg, 1960; Glocker et al., 2009; Hess & Polt, 1960; Hildebrandt, 1978; Little, 2012; Lobmaier, Sprengelmeyer, Wiffen, & Perrett, 2010; Sprengelmeyer et al., 2009; Sternglanz, Gray, & Murakami, 1977). Early studies sought to determine the specific infantile features that influenced perceptions of cuteness. Line drawings of infant faces with manipulated forehead height and forehead curvature where shown a set of over 300 raters; faces with more exaggerated encelaphatic shape were rated as more pleasing (Hückstedt, 1965). Similarly, systematic variation was applied to facial configurations in another series of black and white line drawings to determine which features influence cuteness perceptions. Features manipulated included: vertical position of the features within the face space, eye width, eye height, eye width and height simultaneously, and iris size. Each of these features was found to impact perceptions of attractiveness. Overall, the most attractive infants were those with large eyes, a large forehead, and a slightly low vertical feature position (Sternglanz et al., 1977).

Studies that have directly measured various ratios of infant facial features and dimensions (see Figure 1.7) have empirically demonstrated that baby schema is linked to perceptions of cuteness. In the first of these studies, specific feature combinations were predictive of perceived cuteness; a cute infant is likely to have short and narrow features, large eyes and pupils, and a large forehead (Hildebrandt & Fitzgerald, 1979). Similarly, Parsons et al. (2011a) calculated proportional indices relative to overall face width or length for: nose length/face length, nose width/face width, eye length/face length, eye width/face width, mouth width/face width and forehead length/face length. They then used Z-scores of these measures to quantify the extent of the baby schema in each face (3 groups: high baby schema, average baby schema, low baby schema). Across a sample of 71 raters, infant faces with high baby schema were rated as cuter than average baby schema, which were in turn rated as cuter than faces with low baby schema.

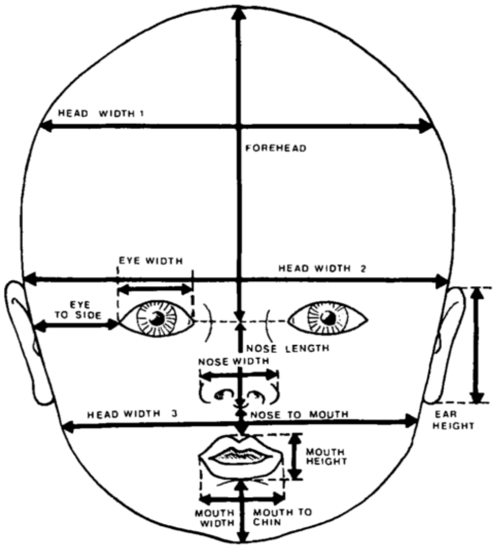


Image adapted from (Maier, 1984)

Figure 1.7 *The facial ratios used to measure baby schema in faces.*

Based on these findings, newer studies have used these high baby schema and low baby schema facial ratios to systematically manipulate baby schema within an individual identity and determine the effects of these subtle manipulations on perceptions of cuteness. Glocker and colleagues (2009) demonstrated that faces manipulated to increase baby schema received higher cuteness ratings than unmanipulated faces or those with decreased baby schema. These high baby schema faces also received higher ratings for caretaking motivation. Follow up work has indicated that there are detectible differences in cuteness perception with even extremely subtle manipulations of the baby schema, however women may be better at detecting these very subtle changes than men (Lobmaier et al., 2010; Sprengelmeyer et al., 2009).

The impact of the baby schema extends to the media, toy companies, and advertising. For example, teddy bears have changed in appearance over the past several decades – from long snouted, long-limbed bears to more baby-like bears with big eyes, short-snouts, and chubbier bodies. Hinde and Barden (1985) suggest that the teddy bear has evolved in this way by means of artificial selection due to customer preference. People prefer baby-like characteristics and the bear makers cater to the tastes of their customers – bears that look more like infants sell better.

This baby schema preference is also apparent in house pets. Lorenz first pointed out that many dog breeds have retained their infantile features into adulthood (Lorenz, 1950). Indeed, there appears to be a strong selection for neotenous features in many breeds of domesticated dogs and cats (Serpell, 1986; Tuan, 1984). It's likely that we are drawn to infantile traits in other animal species due to their resemblance to human infants. Archer and Monton (2011) explored preferences for the baby schema using images of dogs, cats, humans, and teddy bears. Each stimulus type had a version with infantile features (high baby schema) and a version without infantile features (low baby schema). When participants rated the attractiveness these images, faces with the infant features were rated as more attractive than those without. There were no differences in ratings given to the human, dog, or cat faces with infantile features (i.e. babies, puppies, kittens). And women showed higher ratings than men for animals with infant features, but not for human infants or animals without infant features. Little (2012) conducted a similar study using human adult faces, human infant faces, and cat faces. Baby schema was experimentally manipulated (using the shape difference between a prototypical adult and infant face). Across all three face types, faces with higher baby schema were rated as cuter, however infants and cats were cuter overall while adults were less cute. These data demonstrate that the baby schema has a powerful influence on human perception.

1.2.3 The Kindchenschema

Darwin (1872) posited that the natural inclination humans have towards infants might have evolved to increase individual fitness (by increasing reproductive success through increased offspring survival rates as infants are relatively helpless and dependent on parental care for survival). Lorenz argued that infantile features (i.e. baby schema) activate an innate releasing mechanism for positive affective orientation, caretaking behavior, and decreased aggression – a mechanism he coined as the '*Kindchenschema*' (Lorenz, 1943). These behavioral outcomes would have obvious advantages for infant survival rates and, thus, survival of the species. The *Kindchenschema* is triggered by the neotenous features that are typical of an infant including: a large/bulbous forehead, large eyes, small mouth, chubby cheeks and close-set facial features as well as a number of body features (e.g. soft skin, short limbs, chubbiness) and helpless behaviors such as crying and clumsy, awkward movement. Interestingly, the *Kindchenschema* can even be triggered by non-human stimuli; cars with "faces" that are manipulated in accordance with the baby-schema can trigger more positive affective responses (Miesler, Leder, & Herrmann, 2011). The *Kindchenschema* also acts across species; humans show preferences for infantile images of both humans and other animal species (Cann, cited in Hess & Polt, 1960; Hückstedt, 1965; Sanefuji, Ohgami, & Hashiya, 2006).

1.3 The Beauty Premium

There is a well-documented "beauty premium" whereby what is attractive is considered to be good (Dion, Berscheid, & Walster, 1972; Hamermesh & Biddle, 1994). This beauty premium is prevalent in many aspects of daily life, from the labor market to the dating market. In the labor market, strong hiring preferences for attractive individuals have been documented (Cash, Gillen, & Burns, 1977; Cash & Kilcullen, 1985; Gilmore, Beehr, & Love, 1986; Hosoda, Stone-Romero, & Coats, 2003; Marlowe, Schneider, & Nelson, 1996). Cash and Kilcullen (1985) empirically investigated hiring preferences based on appearance by asking college students to evaluate fictitious resumes and make hiring decisions. Applicant gender, qualifications, and physical attractiveness varied (this information was available to participants via applicant resumes). Their results demonstrated hiring preferences for attractive applicants over unattractive applicants despite equal qualifications. In real world situations, employers often consider attractive workers to be “more able” than their less-attractive counterparts (Mobius & Rosenblat, 2006), increasing their likelihood of being promoted. Additionally, attractive people tend to have higher earnings. Hamermesh and Biddle (1994) investigated salary rates of workers in the US and Canada and found that attractive people earned on average 10-15% more money than their average-looking co-workers – it quite literally “pays to be good looking”. An even larger “plainness penalty” was discovered in their analysis (i.e. unattractive workers earned significantly less), suggesting that the ‘punishment’ for being unattractive is even greater than the ‘reward’ for being attractive.

Attractive individuals also experience more social success. Studies on the relationship between physical attractiveness and social interaction have shown that attractiveness is related to the amount of interaction one has with members of the opposite sex. Attractive people are more likely to be chosen from dating ads (Harrison & Saeed, 1977; Lynn & Shurgot, 1984; Woll, 1986), are considered more popular and are more likely to be approached (Prestia, Silverston, Wood, & Zigarmi, 2002; Riggio & Woll, 1984), have higher levels of dating experience than their less attractive counterparts (Berscheid, Dion, Walster, & Walster, 1971; Walster, Aronson, Abrahams, & Rottman, 1966) and are more likely to have had sex (Mazur, Halpern, & Udry, 1994). Using computerized dating settings, Walster et al. (1966) demonstrated that both men and women liked attractive potential dates better than unattractive ones (regardless of the participant's own level of attractiveness), and that they were more likely to seek additional dates with the more attractive individuals. In addition to the amount of social contact, physical attractiveness is also positively correlated with the *quality* of social interactions (Reis et al., 1982; Reis, Nezlek, & Wheeler, 1980). Attractive individuals are often assumed to possess more positive personality traits (i.e. social stereotyping, Berscheid & Walster, 1974; Snyder, Tanke, & Berscheid, 1977; Zebrowitz, Hall, Murphy, & Rhodes, 2002; the "attractiveness halo", Feingold, 1992; Langlois et al., 2000). Berscheid and Walster (1974)found that physically attractive people were perceived to be interesting, sociable, sexually warm/responsive and outgoing. These traits were assigned to attractive individuals much more frequently than unattractive individuals. Similarly, Snyder et al. (1977) demonstrated that when primed to believe they would be interacting with an attractive woman, men predicted that she would be sociable, poised and humorous. When anticipating an unattractive woman, however, men expected that she would be awkward, serious, and socially inept.

1.3.1 Is There a Baby Beauty Premium?

As described in section 1.2.3, the facial features that influence perceptions of infant cuteness trigger the *Kindchenschema* mechanism, which acts to elicit care-taking responses and inhibit aggressive responses from adults. This would suggest that a cuteness premium exists for infants (and young children). Indeed, experimental evidence supports this theory. In a series of studies, Hildebrandt and colleagues have shown that infant cuteness impacts positive affective responses from adults. Using photographs of actual infants, they found that cuter infants are looked at for longer periods of time and elicit more smiling responses, as measured by facial electromyography (Hildebrandt, 1978; Power, Hildebrandt, & Fitzgerald, 1982). Mothers of cuter infants have also been shown to be more playful and affectionate towards their baby than mothers of less cute infants (Langlois, Ritter, Casey, & Sawin, 1995). Perceptions of infant competence are also contingent on cuteness. Cuter babies are perceived as smarter, more likeable, well behaved, and less likely to cause their parents problems as compared to less cute babies (White, Langlois, & Stephan, 2011).

Negative responses also appear to be modulated by infant cuteness. Mothers of less cute infants report more negative attitudes towards their child than do mothers of cute infants (Langlois et al., 1995). Similarly, the cries of babies that are less cute (based on adult ratings of facial photographs) are considered more aversive than those from cute babies (Frodi, 1978); this pattern was true when participants were presented with the auditory stimuli alone as well as when the auditory stimuli were paired with a photograph of the infant, suggesting cuteness can suppress aggressive responses.

A number of researchers have explored how these affective responses may impact real world behavior. Alley (1983) tested the impact of infantile head shape on the likelihood of receiving protective care across four studies (half used line drawings, half used outlines of actual heads). Participants ranked or rated how compelled they would be to defend the infant if they saw someone striking it. Across all four experiments, protective responses decreased as the stimulus head shape changed in accordance with growth/age (i.e. became less "babyish"). These findings suggest that the more infantile a child appears, the more likely adults will be to protect or defend the child indicating that cues to cuteness can directly affect behavioral outcomes. Similarly, adults report being more willing to babysit, take care of, be close to, or take home babies that are perceived as cuter (Maier, Holmes, Slaymaker, & Reich, 1984). Staff in neonatal units even report being more attentive to cuter pre-term infants (Badr & Abdallah, 2001).

Infant cuteness may be indicative of underlying health or viability. Infants suffering from low birth weight or other health defects, such as cleft palate or fetal alcohol syndrome, are perceived as less cute (Volk, Lukjanczuk, & Quinsey, 2005; Waller, Volk, & Quinsey, 2004). In normal infants, perceptual ratings of cuteness have been found to correlate with perceptual ratings of health (Volk & Quinsey, 2002). As such, the link between cuteness and caregiver behavior may serve an adaptive function – that is, to optimize allocation of parental resources according to perceived offspring quality or viability as a sick infant simultaneously increases the cost of parental investment and decreases the chances of investment payoff (see Volk &

Quinsey, 2002). Indeed, apparent health abnormalities have been found to negatively influence adoption rates in hypothetical adoption tasks (Volk et al., 2005; Volk & Quinsey, 2002; Waller et al., 2004) and real world adoption (Weiss, 1994). Facial appearance, and specifically facial deformities, directly influences motivation to care for children. In a sample of 1,450 adopted or abandoned children nearly 70% of the abandoned children carried a conspicuous appearance flaw that was neither life threatening nor did it affect intellectual development; only 7% of the abandoned children had a serious internal organ (e.g., heart and kidneys) disease. Additionally, the non-abandoned babies with an appearance flaw were commonly abused and isolated from their siblings by the caregivers (Weiss, 1994).

That physical appearance can impact likelihood of being hired (adults) or adopted (infants), perceived aptitude (adults and infants), and influence social success (adults) emphasizes the importance of better understanding just what beauty is. The literature reviewed here demonstrates that beauty can influence behavior, which suggests that there may be a motivational aspect of facial appearance.

1.4 Is Beauty Rewarding?

Reward processing has fundamental biological importance and is a necessary component of motivation and goal-directed behavior. These behaviors likely evolved to aide in survival (Nicholson, 1997) - they ensure that we breathe when air is required, eat when hungry, and seek out mates for genetic propagation. The nature of the stimuli capable of eliciting a reward-related neural response has been divided into two categories: primary rewards and secondary rewards. Primary (or natural) rewards, such as food and sex, are necessary for survival and do not require pairing to function as reinforcing stimuli (hence the term 'natural'). Secondary rewards, such as money, derive their value from their association with primary rewards. Both categories of rewarding stimuli have been used to explore the psychological, neuroanatomical, and neurochemical aspects of reward. Although originally, reward was considered a unitary process, more recent theories suggest that there are multiple psychological components of reward. These include learning, pleasure ('liking'), and motivation ('wanting'). In the next few sections, I will introduce these reward components and their relevant neural correlates. This thesis is a collection of behavioral studies employing a key-press paradigm that mimics traditional lever pushing paradigms used in non-human animal studies of the neural correlates of reward. Although this thesis does not include neuroimaging data and is written from an evolutionary perspective, it is important to discuss the fundamental reward literature. This introduction is brief in nature and by no means encompasses a full review of the reward literature. The following sections will focus on Robinson and Berridge's incentive salience theory of reward.

1.4.1 The Incentive Salience Theory of Reward

The incentive salience hypothesis, parses reward into three distinct states: (1) learning – the process by which knowledge of the relationships among stimuli is gained, (2) liking – the hedonic consequences of reward consumption, and (3) wanting – the motivation to learn and act in order to gain rewards (Berridge & Robinson, 2003; Robinson & Berridge, 1993; see Figure 1.8). Neuroscientific research indicating that it is possible to alter liking responses without influencing wanting (and vice versa) has demonstrated that these states are dissociable aspects of reward that have distinct neural substrates (Berridge & Robinson, 1998, 2003; Peciña & Berridge, 2000; Peciña, Cagniard, Berridge, Aldridge, & Zhuang, 2003). These three components, and evidence of their dissociability, are discussed individually below.

1.4.1.1 Learning

Learning is a key aspect of reward and is required for goal-directed action, reward prediction, anticipatory responses, and cue guidance (Berridge & Robinson, 2003). Learning involves forming associations, representations, and predictions about future reward based on knowledge obtained from past experiences. Thorndike argued that these connections are formed whenever a response is followed by a reward (Thorndike, 1898). This process is responsible for the reward value of secondary rewards – without learning, these stimuli would not be associated with the primary rewards they come to represent. Consider the example of Pavlov's dogs; when they were initially presented with the bell stimulus, they did not salivate. It was only through the bell being continuously paired with food (a natural reward) that the bell itself eventually was able to elicit salivation. It is this learning process that connects a secondary reinforcer (the bell) to a primary reinforcer (the food).

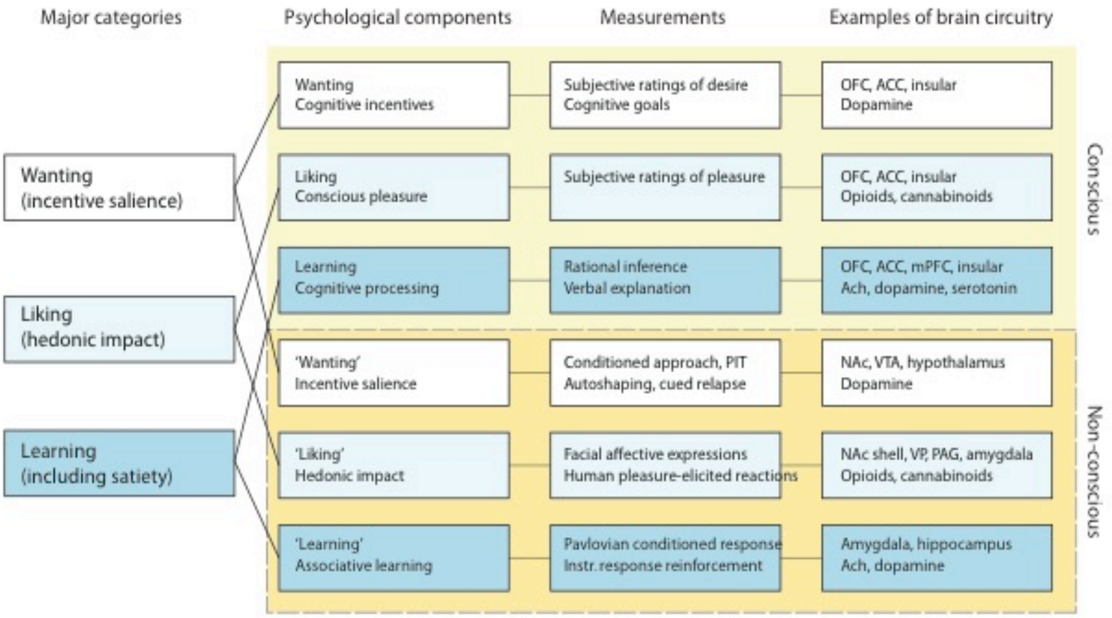


Image adapted from: Kringelbach & Berridge (2009)

Figure 1.8 *Components of reward according to the incentive salience hypothesis. These include conscious and non-conscious forms of learning, liking, and wanting.*

Learning can be associative or cognitive and the products of this learning can be procedural (i.e. habits) or declarative (i.e. memories; Berridge & Kringelbach, 2008; Berridge, Robinson, & Aldridge, 2009; Berridge & Robinson, 2003). Associative learning involves conditioning (Pavlovian or instrumental), while cognitive learning is more complex and may involve rational inference and higher-order rule-based predictions. Cognitive learning involves encoding multiple relationships between stimuli and actions and is a much more complex form of learning than associative learning. This form of learning requires an understanding of the causal links between an action and an outcome and a mental representation of the value of the outcome which act to influence goal-directed behaviors (Dickinson & Balleine, 2000).

Associative learning can take the form of Pavlovian incentive learning or instrumental incentive learning. In the case of Pavlovian incentive learning, a conditioned stimulus is repeatedly associated with an appetitive or aversive reinforcer (e.g. a food reward or a shock) referred to as an unconditioned stimulus. Initially, encountering the conditioned stimulus does not produce any particular response; however after continual pairing with the unconditioned stimulus, a conditioned response emerges, which is learned over time (Pavlov, 1927).

Instrumental incentive learning, on the other hand, involves strengthening or weakening a voluntary behavior in response to consequences such as reward or punishment. This form of learning determines the incentive value of a given action, which must be learned through experience (Dickinson & Balleine, 2002). This form of learning is illustrated by work utilizing an operant conditioning chamber, classically known as a "Skinner Box" (Ferster & Skinner, 1997). A Skinner Box is a small chamber with a lever that will deliver food (or another reward) when pressed. When animals are placed into the box, they will typically press the bar by accident while exploring. When they press the bar, a food pellet is delivered. The behavior (i.e. lever pressing) is then reinforced with a reward (i.e. a food pellet). Skinner observed that the frequency of lever pressing increased dramatically once the rat learned that the behavior elicited a reward. Similarly, by pairing a behavior such as lever pressing with an aversive or punishing outcome such as an electric shock, an animal will learn to avoid the behavior to prevent a negative outcome. In both Pavlovian and incentive learning, an association is formed between a stimulus or behavior and the reward value of the outcome.

Although learning is a widely studied, key aspect of reward it is not the focus of this review. The processes of wanting and liking, which are much more germane to the present work, are discussed in greater depth below. It is essential, however, to emphasize the necessity of learning for motivated behavior. It is only through learning that we like a given stimulus that the stimulus gains incentive salience and is 'wanted'.

1.4.1.2 Liking

The liking, or pleasure, component of reward refers to the hedonic quality of the stimulus. According to the incentive salience theory, pleasure is represented by two psychologically distinct aspects: **liking** (explicit, i.e. conscious pleasure) and **'liking'** (implicit, i.e. hedonic impact; see Figure 1.9). The unconscious 'liking' aspect of reward involves sensory pleasure and is typically reflected by a positive affective reaction. It is important to note that the conscious experience of pleasure is dissociable from the implicit 'liking' response to hedonic stimuli. For example, Winkielman et al. (2005) have shown that subliminal presentation of affective primes can influence consumption behavior and subsequent reports of feelings of enjoyment even though they produce no change in subjective feelings at the time of presentation. Participants were primed using subliminal facial expressions – either happy or angry – prior to completing a beverage-rating task. Participants did not report any awareness of having seen an emotional expression, yet priming with happy faces resulted in participants consuming more of the fruit drink as well as assigning higher ratings of pleasantness and monetary value to the beverage. Conversely, priming with frowns resulted in less consumption and lower ratings of pleasantness and monetary value for the beverage. Because explicit liking responses can only be measured when the subject can provide explicit ratings, this aspect of reward is difficult to study (with the exception of human subjects). As such, the majority of studies regarding liking responses focus on non-conscious, implicit 'liking'.

1.4.1.3 Measuring Liking

Perhaps the most commonly assessed measure of implicit 'liking' is that of facial expressions in response to taste stimuli – specifically, tongue protrusions in response to 'liked' stimuli and gapes in response to 'disliked' tastes, which are thought to reflect positive and negative affective responses, respectively (Berridge, 2003). Grill and Norgren (1978) first demonstrated these affective responses using sweet, salty and bitter gustatory stimuli in rats. They found that sweet tastes (i.e. sucrose) elicit rhythmic smacking as well as lateral and frontal tongue protrusions, accompanied by a relaxed expression (including a slight upturn at the corners of the mouth). Bitter (i.e. quinine), sour, and salty tastes elicit a grimace, gapes, rearing, shakes of the head or turning away, wiping of the face and shaking of the paws. Often these responses are accompanied by a gagging movement – as though to push out the offending taste. A number of studies using sweet and bitter tastes have demonstrated that affective facial responses are consistent across species, including: humans, chimpanzees, monkeys, rats and mice, suggesting that these affective expressions likely developed from the same evolutionary source (see Figure 1.9; Ganchrow, Steiner, & Daher, 1983; Rosenstein & Oster, 1988; Steiner, Glaser, Hawilo, & Berridge, 2001).

Hedonic Reactions (sweet)

Aversive Reactions (bitter)

Image adapted from: Kelley & Berridge (2002)

Figure 1.9 *Sweet and bitter tastes result in positive and negative affective reactions, respectively. These affective reactions are similar across species, suggesting a common evolutionary mechanism.*

Because it is not possible to assess conscious liking in animals and non-human primates, much of the reward literature has focused on the implicit 'liking' response to rewards. However, studies using human subjects offer the unique ability to assess the conscious experience of pleasure in addition to implicit 'liking' responses – we can simply ask participants to report how much they enjoy a given stimulus. These subjective ratings of conscious pleasure act to measure explicit liking. Throughout this thesis, I will refer to attractiveness ratings as liking responses in humans. To this end, I am describing conscious liking responses rather than implicit 'liking', as measured through attractiveness ratings.

1.4.1.4 Wanting

The final component of reward is motivation, which is also represented by two distinct psychological components: **wanting** (explicit, i.e. cognitive desires, incentives, or goals) and **'wanting'** (implicit, i.e. incentive motivation or salience). Explicit wanting refers to conscious or subjective desires. According to Berridge (2004) the explicit, cognitive form of wanting involved declarative memories of the valued goal, explicit predictions for the outcome based on that knowledge, and a cognitive understanding of the causal relationships between potential actions and future goal attainment. By contrast implicit 'wanting', or incentive salience, does not need to be a conscious process and is mediated by relatively simple brain mechanisms rather than complex cortical circuits (Berridge et al., 2009). Rather, 'wanting' refers to the underlying implicit and objective motivational processes that drive behavior (Berridge & Robinson, 2003).

Rewards that are liked (or 'liked') are usually also 'wanted', and it is the attribution of incentive salience to a stimulus makes it a target of motivation (i.e. approach toward and consumption of the reward stimulus). The notion of an implicit 'wanting', or incentive salience, was first proposed by Berridge and Robinson who define incentive salience as "a psychological process that transforms the perception of stimuli, imbuing them with salience making them attractive, wanted, incentivized stimuli" (Berridge & Robinson, 1998, 2003; Robinson & Berridge, 2003). More simply put, incentive salience refers to the motivational power of a given stimulus. Stimuli with high incentive salience are more 'wanted' and motivate behavior to a greater extent. Berridge and Robinson (2003) suggest that 'wanting' likely evolved as a separate function of reward as an early form of stimulus-guided goal-directed behavior (mediating the pursuit of stimuli related to food/sex). Much like the classic bar press paradigm utilized in rodent studies of reward, the key-press paradigm employed throughout the studies described in Chapters 2 – 5 taps this subconscious 'wanting' or incentive salience of a given stimulus.

1.4.1.5 Measuring Wanting

As with liking, it studying human behavior offers the unique opportunity to assess both explicit wanting (i.e. cognitive goals or desires) and implicit 'wanting' (i.e. incentivized behavior). Implicit 'wanting' behaviors have been assessed in a number of interesting ways in both animals and humans. Reaction times have been used in human studies to measure 'wanting' (e.g. Finlayson, King, & Blundell, 2008), while similar measures of speed and approach trajectory to a reward stimulus have been used in runway tasks when studying 'wanting' in rodents (e.g. Peciña et al., 2003). Measures of effort can also be used across human and non-human animal studies of 'wanting'. For example, the classic lever press paradigm used to assess motivation in many animal species (e.g. Wyvell & Berridge, 2000) has recently been adapted in interesting ways to measure human behavior.

A number of studies have used the "pay-per-view" key-press task that will be utilized in the present work, which allows participants to exert effort via key-pressing to prolong exposure to rewarding stimuli (e.g. Aharon et al., 2001). Similarly, Ferrey et al. (2012) have used a progressive ratio key-pressing task to measure 'wanting' responses to sexual stimuli whereby the number of key-presses required to see a given stimulus category doubles each time the participant selects that category. In another effort-based task, participants were able to gain access to rewarding or neutral stimuli by clicking on a moving target (Waugh & Gotlib, 2008). Treadway and colleagues have also developed the Effort Expenditure for Rewards Task, or EEfRT, in which participants are able to select either an easy task or a hard task during which they must repeatedly press a button to raise a bar to a certain level within a restricted amount of time. If they successfully complete the task in the time limit, they receive a monetary reward on some trials (trials were either “win” or “no win” to manipulate reward expectancy). The hard task pays out a higher monetary reward, but requires more effort per unit of time (Treadway, et al. 2009; 2011; 2012a; 2012b). In humans, there is the unique ability to assess conscious wanting; feelings of wanting (desire) and craving (needing) have been measured for drug rewards (Childress et al., 1999; Evans, Haney, & Foltin, 2002; Jaffe, Cascella, Kumor, & Sherer, 1989) and food rewards (Volkow et al., 2002).

The explicit wanting and implicit ‘wanting’ components of motivation are dissociable and can be measured in distinct ways. For example, Finlayson et al. (2008) assessed the impact of hunger on implicit and explicit wanting. Participants were first asked to view a series of savory and sweet food images and report how much they wanted to eat the food item at that moment using a visual analogue scale. This task measured their conscious (or explicit) motivation for the food. They also completed a forced-choice task whereby they were asked to select the image of the food they would most like to eat. The speed with which they made their decision was analysed as a measure of the implicit motivation or ‘wanting’ they felt for each food item. Hunger caused explicit ratings of wanting to increase for all food categories, while implicit ‘wanting’ measures differed based on hunger level only for the sweet food category.

1.4.1.6 Is Liking Different Than Wanting?

Although rewards that are liked/’liked’ are usually also wanted/‘wanted’, these aspects of reward are dissociable. Behavioral evidence for the dissociability of these components comes from a number of studies utilizing food as a reward stimulus (for a review see Mela, 2006). One such example comes from work comparing wanting and liking responses to food in obese and lean women. Saelens and Epstein (1996) used a progressive ratio computer task (which functions much like a slot machine) in which participants could work to earn points for either snack foods or time to engage in sedentary activities such as fun computer games. Although both obese and lean women did not differ in their explicit ratings of liking snack foods, obese women put greater effort into earning food points than game points as compared to lean women. These findings suggest that the two groups of women liked the food rewards equally, but obese women have greater ‘wanting’ responses than lean women. Similarly, food deprivation has been shown to influence ‘wanting’ but not liking responses. Using the same progressive ratio computer task, Epstein et al. (2003) demonstrated that food-deprived participants and fed participants rated the pleasantness of various foods similarly, but food-deprived individuals invested greater effort in obtaining food points than fed participants. Further evidence for the dissociability of these components of reward based on neuroscientific studies aimed at determining the underlying neural mechanisms associated with each component is discussed in Section 1.3.3.

1.4.2 The Brain’s Reward Circuitry

In their pivotal study on reward, Olds and Milner (1954) found that rats would lever-press to the point of physical exhaustion to receive electrical stimulation in septal and other brain areas, including the nucleus accumbens (NAcc). This finding led to the notion of ‘reward centers’ in the brain – that is, a set of structures that encode the pleasure associated with obtaining ‘rewards’.

The mesocorticolimbic dopamine system is widely believed to be the main component of the brain’s reward circuitry. While dopamine’s specific role in reward is currently debated (Berridge & Robinson, 1998; Berridge, 2007; Spanagel & Weiss, 1999; Wise & Rompre, 1989), a number of studies have provided strong evidence that this system is involved in reward-related behavior such as motivation and addiction (e.g. Kelley & Berridge, 2002; Miner, Drago, Chamberlain, Donovan, & Uhl, 1995; Sellings & Clarke, 2003; Wise & Rompre, 1989; Wise, 1987, 1988, 2004; Yokel & Wise, 1975). For example, amphetamine-induced conditioned place preferences (i.e. preference for a location previously paired with an unconditioned stimulus or reward, see Prus, James, & Rosecrans, 2009) have been shown to be abolished following 6-hydroxydopamine (6-OHDA) lesions, which selectively destroy dopaminergic neurons, in mesocorticolimbic brain regions such as the NAcc (Spyraki, Fibiger, & Phillips, 1982).

The mesocorticolimbic dopamine system (see Figure 1.10) is composed of dopaminergic projections that originate in the medial forebrain bundle of axons in the ventral tegmental area and substantia nigra (Schultz, 1997). These dopaminergic neurons extend to the nucleus accumbens (Nestler & Malenka, 2004), amygdala (Baxter & Murray, 2002), hippocampus (Nestler & Malenka, 2004), and forebrain regions (Nestler & Malenka, 2004), as well as the ventral striatum (Koepp et al., 1998) and midbrain and thalamic regions (Thut et al., 1997). Dopamine levels in this system increase when rewards are obtained – including natural rewards such as food, water and sex (Young, Joseph, & Gray, 1992), while dopamine blockade in these areas (via antagonists such as spiperone, pimozide, or flupenthixol) attenuates the rewarding effects of both primary and secondary reinforcers, as demonstrated by decreased display of conditioned place preferences (Cervo & Samanin, 1995; Di Ciano, Cardinal, Cowell, Little, & Everitt, 2001; Wise, 2004; Yokel & Wise, 1975).

This system originates at the ventral tegmental area (VTA), which is located near the midline on the floor of the midbrain. The primary function of the VTA is reward, but it may also be involved in emotional processing due to connectivity with the amygdala. Dopaminergic projections from the VTA reach the nucleus accumbens (NAcc), located in the ventral striatum. The NAcc is composed of two subdivisions: the shell and the core. The shell is involved in regulation of motivation and reward; the core is involved in sensory-motor integration, reward and goal-directed behaviors. The nucleus accumbens has reciprocal connectivity with the insular cortex, hippocampus and frontal regions (medial frontal cortex and orbitofrontal cortex; Heimer et al., 1997). Activation of the NAcc structure occurs during anticipation of rewards (Knutson, Fong, Adams, Varner, & Hommer, 2001), and release of dopamine into this structure increases reinforcement behaviors that can lead to addiction after a secondary reinforce is paired with a primary reinforcer (Berridge & Robinson, 1998; Walton, Bannerman, & Rushworth, 2002; Wyvell & Berridge, 2000, 2001). Dopaminergic projections continue to the forebrain regions, such as the orbitofrontal cortex (OFC), prefrontal cortex (PFC) and medial frontal cortex (MFC). These frontal regions are involved in higher-order aspects of reward, such as signalling expected reward/punishment, reward value coding and decision making, and are sensitive to abstract reinforcers such as winning or losing money (Elliott, Friston, & Dolan, 2000; Peters & Büchel, 2010; Sescousse, Redouté, & Dreher, 2010).

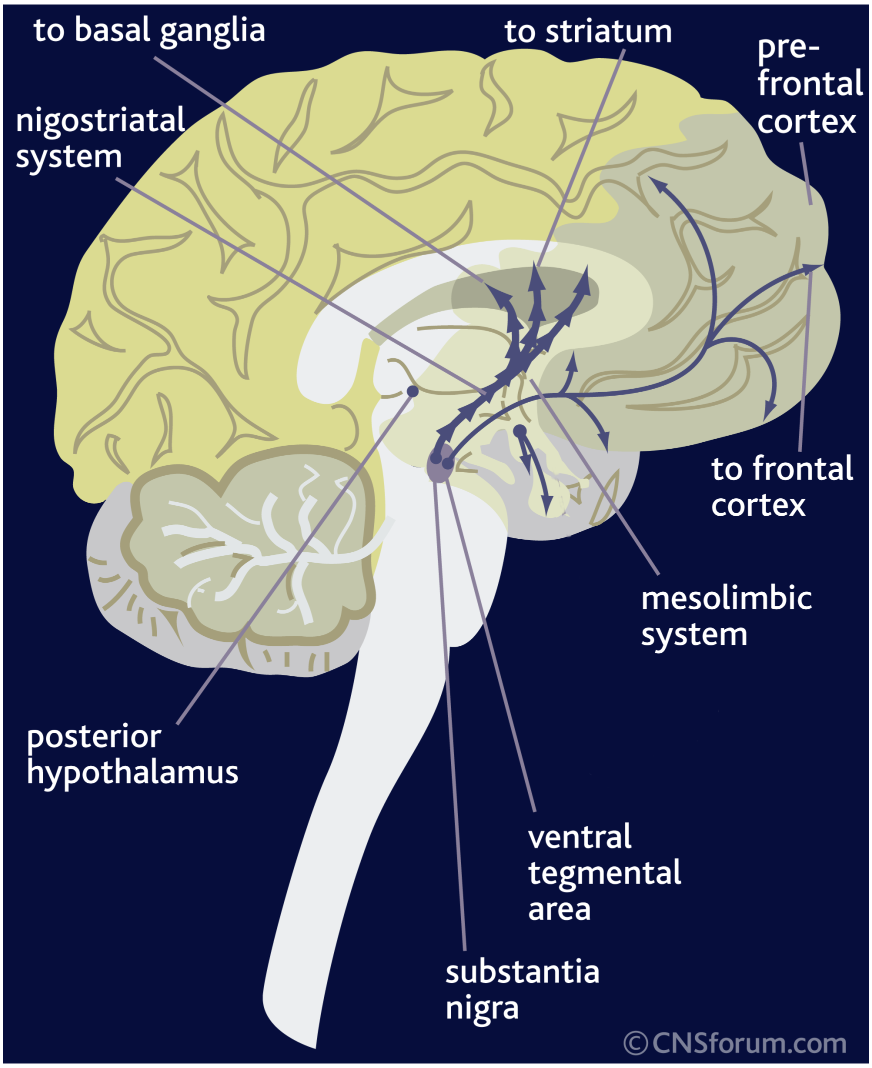


Image from: CNS forum

Figure 1.10 *Dopamine pathways in the brain. The mesocorticolimbic dopamine system, pictured here, is theorized to be at the core of reward-related behavior.*

1.4.3 Neural Correlates of the Incentive Salience Theory

According to the incentive salience theory of reward, although 'liking' and 'wanting' are typically activated together, these components of reward have distinct neural correlates, which can be parsed out using various neuroscientific techniques. 'Liking' is mediated via l-opioid neurotransmission within the scattered network of subcortical and brainstem nuclei, whereas the mesocorticolimbic dopaminergic system described in section 1.3.2 is responsible for learning and 'wanting' or the incentive/motivational aspects of reward function.

Although original theories of reward posited that dopamine was the key neural substrate underlying reward-related behaviors, dopamine does not appear to be involved in the process of 'liking' (Berridge & Robinson, 1998; Brauer, Cramblett, Paxton, & Rose, 2001; Brauer, Goudie, & de Wit, 1997; Wyvell & Berridge, 2000, 2001). For example, manipulations of dopamine systems have been shown not to impact taste 'liking' (Berridge & Robinson, 1998). To this end, Berridge and Robinson (1998) conducted a series of studies exploring the impact of dopamine blockade on 'liking' in rats. They found that dopamine-depletion did not impact hedonic 'liking' responses to sucrose versus quinine (as measured by affective facial reactions) suggesting that dopamine is not the primary correlate of 'liking behaviors'. Rather, this aspect of reward is mediated by opioid, endocannabinoid, and GABA-benzodiapine neurotransmitter systems active at "hedonic hotspots" (Barbano & Cador, 2007; Peciña & Berridge, 2000; Peciña, Smith, & Berridge, 2006; Smith, Mahler, Peciña, & Berridge, 2010; Smith & Berridge, 2007). These hedonic hotspots are areas of the brain that, when activated, cause pleasure enhancement (e.g. increase 'liking' responses to sucrose as measured by increased tongue protrusions and positive affective facial responses). Opioid hotspots have been located in the NAcc (specifically in the shell) and ventral pallidum (VP). Opioid-agonist microinjections into the hotspot within NAcc increase the 'liking' reactions to sweet rewards, while injections into the remaining area of the NAcc do not seem to impact 'liking' responses (Peciña & Berridge, 2005). An endocannabinoid hotspot has also been located in the NAcc shell. These hotspots are extremely small, thought to encompass only 1 cubic centimetre in the human brain (Peciña & Berridge, 2005).

Brain regions involved in 'liking' include: the cingulate cortex, frontal regions (OFC, PFC), NAcc, and the hypothalamus. The cingulate cortex is thought to be involved in the process of reward prediction and the reinforcement of adaptive behaviors (Holroyd & Coles, 2002; Holroyd et al., 2004). Frontal regions, such as the OFC and PFC have been found to respond to psychostimulant drugs (i.e. the pleasurable aspect of drug consumption; Breiter & Rosen, 1999; Breiter et al., 1997). These regions also respond to pleasant sensory input such as tastes and odors (Doyle, Berridge, & Gosnell, 1993; Zald, Lee, Fluegel, & Pardo, 1998; Zald & Pardo, 1997; Zald, Hagen, & Pardo, 2002), pleasant touch (Francis et al., 1999), and the receipt of money (Thut et al., 1997) suggesting their involvement in liking aspects of reward. Activation of opioid circuitry in the NAcc (specifically in the shell region) increases the affective response to sweet tastes as measured by facial expressions (Peciña & Berridge, 2000). Finally, in monkeys neurons in the hypothalamus have been shown to fire intensely when food is viewed, suggesting hypothalamic involvement in liking responses to pleasant stimuli (Nishijo, Ono, & Nishino, 1988; Ono, Nishino, Fukuda, Sasaki, & Nishijo, 1984; Ono, Nishino, Sasaki, Fukuda, & Muramoto, 1981; Rolls, 2000; Wauquier & Rolls, 1976).

While dopamine does not appear to be the primary component of liking as was once thought, much evidence for the role of dopamine in both learning and wanting responses has been found (see Berridge, 2007). Dopamine transporter (DAT) knockdown mice do not produce normal amounts of dopamine transporter; as a result, these DAT knockdown mice have higher extracellular dopamine than normal control mice and are considered to by hyperdopaminergic. When given a runway task, hyperdopaminergic mice were found to display enhanced acquisition and incentive performance for a sweet reward compared to control mice, as measured by time to reach the goal object (Peciña et al., 2003). Importantly, no differences were observed in speed between the hyperdopaminergic mice and normal mice prior to training, or after extended training. It was only during the learning phase that differences emerged, suggesting that dopamine facilitates learning.

Microinjections of amphetamines and 6-hydroxydopamine (6-OHDA) lesions in the NAcc have been shown to impact 'wanting' without affecting 'liking', with exposure to amphetamines (dopamine agonists) increasing ‘wanting’ behaviors and exposure to 6-OHDA lesions or other dopamine antagonists decreasing ‘wanting’ behaviors (Peciña et al., 2003; Wyvell & Berridge, 2000, 2001). For example, in the same runway learning experiment described above, Peciña et al. (2003) observed greater ‘wanting’ behavior in hyperdopaminergic mutant mice as compared to normal mice. However, these mice did not show enhanced ‘liking’ responses to sucrose (as measured by affective facial reactions). Similarly, increased cue-triggered ‘wanting’ in response to dopamine agonists (Wyvell & Berridge, 2001) and decreased conditioned place preferences (i.e. reward-seeking behavior) in response to dopamine blockade/lesions (Spyraki et al., 1982) have been observed in rodents. Notably, the anticipation phase of reward has higher dopamine release than the consumption phase suggesting that an incentive can drive behavior to obtain a reward even if there is no hedonic quality derived at reward acquisition (i.e. we can ‘want’ without ‘liking’; Berridge & Robinson, 1998). Key brain regions involved in the ‘wanting’ component of reward include the NAcc (particularly the spiny neurons), amygdala and basal forebrain (Kelley & Berridge, 2002; Parkinson et al., 2002; Reynolds & Berridge, 2002, 2008; Sarter & Bruno, 2000).

1.4.4 Faces as Natural Rewards

With facial attractiveness potentially signalling higher mate quality, it would be evolutionarily advantageous for attractive individuals to be both ‘wanted’ and ‘liked’. Behaviorally, facial attractiveness has been shown to elicit affective responses (liking/’liking’) as well as influence behavior (wanting/’wanting’). As discussed in section 1.1.5, attractive individuals receive higher subjective appraisal (i.e. liking). Facial electromyography data[3] suggests that unconscious ‘liking’ responses may also be affected by facial attractiveness – facial movements associated with disgust responses have been found when viewing unattractive faces that are not exhibited when viewing attractive faces (Proverbio & Langlois, 2011). Conscious wanting behaviors are subject to attractiveness effects. As discussed in section 1.1.5, people are

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[3] As measured via the *corrugator supercilii* (pulls eyebrows), *levator labii superioris* (raises nostrils), and *zygomaticus major* (pulls corner of lips into smile) muscles.

more likely to actively seek out dates with attractive individuals (Walster et al., 1966; Woll, 1986). Similarly, unconscious 'wanting' responses are impacted by facial attractiveness. Wilson and Daly (2004) demonstrated that beautiful women lead men to discount higher future rewards against smaller immediate rewards (measured as choice between specified sum of money given immediately versus a larger sum given after a delay of 7-236 days). Viewing attractive faces can also unconsciously motivate sexual behavior and the formation of same-sex bonds (Berscheid & Reis, 1998; Rhodes, Simmons, & Peters, 2005; Welling et al., 2007, 2008).

Research using neuroimaging techniques has demonstrated that beauty can activate the reward circuitry outlined in sections 1.3.2 and 1.3.3. Specifically, activation in the brain systems for assessing reward-value, such as: the ventral striatum, prefrontal cortex, and nucleus accumbens has been shown in response to viewing beautiful faces (Aharon et al., 2001; Cloutier, Heatherton, Whalen, & Kelley, 2008; Ishai, 2007; Kampe, Frith, Dolan, & Frith, 2001; Nakamura et al., 1998; O'Doherty et al., 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). Additional areas that have been found to respond to beauty include the cingulate cortex, thalamus, superior temporal sulcus (STS) and the amygdala. The cingulate cortex preferentially responds to attractive faces, which may reflect an increase in internal monitoring of autonomic state (Cloutier et al., 2008). The amygdalar response to attractiveness appears to be non-linear – with greater activation in response to highly attractive and unattractive faces as compared to middle-ranked faces (Winston et al., 2007).

A number of imaging studies have provided evidence that frontal regions associated with reward respond to facial beauty. The prefrontal cortex has been shown to have dissociable regions that respond independently to attractiveness for same- and opposite-sex faces (O'Doherty et al., 2003); medial regions of the PFC and OFC respond to attractive faces while lateral regions of the OFC and PFC as well as the insula (bilaterally) respond to unattractive faces. Similarly, when using opposite-sex faces alone, Cloutier et al. (2008) observed increased activation in the medial PFC and OFC for attractive faces as compared to unattractive faces of the opposite-sex (although OFC activation was only observed in men), and increased activation in the lateral OFC with decreasing attractiveness. These findings are in line with previous results indicating that the medial OFC responds to reward-stimuli while the lateral PFC responds to punishing stimuli (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). An interesting finding is that the OFC was activated by attractiveness even when the viewer is performing an unrelated task (i.e. gender discrimination task) and not consciously attending to facial appearance (O'Doherty et al., 2003).

The evidence for striatal responses to facial beauty is somewhat less clear. Kampe et al. (2001) found that activation in the ventral striatum (a region associated with reward prediction) increased in response to beauty (i.e. attractive-unattractive) when eye gaze was directed at the viewer, suggesting that eye contact with attractive individuals is more "rewarding" than eye contact with less attractive individuals. Evidence for NAcc activation in response to beauty is somewhat equivocal. O'Doherty et al. (2003) failed to demonstrate NAcc activation to attractive faces, while Aharon et al. (2001) observed an increase in NAcc activity when men viewed attractive opposite-sex faces. More recently, Cloutier et al. (2008) observed an increase in NAcc activity in both men and women in response to attractiveness for faces of either sex. Sex-differences in experimental paradigms across these studies suggest the reward-value of beauty may context- or stimulus-dependent.

1.4.5 'Wanting' and 'Liking' Beauty

Beauty can stimulate separate reward and aesthetic assessments, much like Berridge and Robinson's 'wanting' and 'liking'. Aharon et al. (2001) showed three groups of men beautiful and average-looking faces of the same- and opposite-sex. One group performed an attractiveness rating task and were found to rate beautiful faces of both genders highly on the attractiveness scale, suggesting that beautiful faces receive equally high aesthetic assessments – or are 'liked' equally – regardless of sex of the face. The second group underwent fMRI scanning while passively viewing the images. Six regions of interest were analyzed: the NAcc, sublenticular extended amygdala (SLEA) of the basal forebrain, amygdala, hypothalamus, OFC, and VTA. Significantly greater levels of activation were seen when viewing beautiful females (as compared to activation for beautiful males) in the NAcc, VTA and SLEA. Activation in the OFC was similar for same- and opposite-sex beauty and greater for attractive faces than unattractive faces of either sex. The final group completed a novel key-pressing task whereby the viewing time of each stimulus could be changed by pressing a set of alternating keys. The amount of work or effort exerted to change viewing time (as measured by key-pressing) was considered an operational measure of the motivational value (or incentive salience) of the stimulus. Men key-pressed to increase the viewing time of beautiful female faces, but not beautiful male faces demonstrating that opposite-sex beauty holds incentive salience while same-sex beauty does not (at least among men).

That men rated attractive male and female faces equally attractive (i.e. like male and female faces equally), but only worked to view female faces (i.e. 'want' female faces more than male faces) suggests that a dissociation exists between the aesthetic value of beauty (i.e. its hedonic quality, or 'liking') and its reward value (i.e. its incentive salience, or 'wanting'). This work was extended in a study by Elman et al. (2005) using men suffering from posttraumatic stress disorder (PTSD). This disorder is associated with deficits in reward mechanisms and is characterized by a general anhedonia (Kashdan, Elhai, & Frueh, 2006). Using Aharon et al.'s key-press task on a group of male veterans suffering from PTSD and an age-matched control group, Elman et al. found that PTSD sufferers showed a significant reward deficit with regard to the incentive salience of beauty (for beautiful female faces). No group differences were apparent for beautiful male faces, or unattractive faces of either sex. Importantly, there were no differences in the liking responses (i.e. attractiveness ratings) between PTSD sufferers and the control group; it was only in the incentive salience of female beauty (as measured by effort on the key-press task) that was impacted in PTSD sufferers. This work suggests that disorders that impact reward processing (i.e. PTSD, depression, addiction, etc.) may impact the incentive salience of beauty in a measureable fashion.

The literature on mate preferences has focused on rating and forced choice paradigms to explore human preferences. While such tasks may illuminate what we *like* in a mate, do they accurately portray what we *want* or seek out in a potential mate? That is to say, do mate preferences match actual mate choices? To date, few studies have addressed this issue. Those that have explored the link between preference and choice for facial masculinity indicate that women's mate preferences do, indeed, match their actual mate choices. DeBruine et al. (2006) have shown that stated preferences for facial masculinity can be predicted by reported ideal masculinity in a partner, as well as actual partner's rated facial masculinity. Additionally, for both men and women levels of sex-typicality in their actual partner's face predicted preferences for sex-typical shape cues when evaluating faces in long-term but not short-term contexts (DeBruine, Fincher, Watkins, Little, & Jones, *under review*). Similarly, Burriss, Welling and Puts (2011) found that women's short- and long-term masculinity preferences are correlated with ratings of their actual partner's masculinity (as rated by the women and the men themselves) but not with independent ratings of the partner's masculinity or facialmetric masculinity.

Conversely, a study that addressed the relationship between preferences and choice in body size found gender differences in the link between preference and choice; women show similar preferences and choices while men show increased preference for small body size than is reflected in their actual choice of partner (Courtiol, Picq, Godelle, Raymond, & Ferdy, 2010). Using a speed-dating paradigm, Todd et al. assessed men and women's stated preferences for wealth/status, family commitment, physical appearance, attractiveness (self-perceived and observer-rated) and health. They then used their behavior in the speed-dating task to measure how frequently these qualities were chosen in a potential mate. They found a positive correlation for women's preference and choice for the physical appearance factor, but negative correlations for preference and choice for men concerning physical appearance and healthiness. No other relationships were detected between stated preferences and actual choices (Todd, Penke, Fasolo, & Lenton, 2007).

Taken together, these studies suggest that the relationship between what we claim to like in a mate and what we actually chose in a mate may not be straightforward. The key-press paradigm may offer a new way to bridge this gap in our understanding. While preferences for averageness, health and sexual dimorphism have been established in the literature, we have yet to determine how these factors drive behavior. Are we motivated to seek out mates with these qualities? The work presented throughout this thesis will utilize the key-press paradigm to measure factors that influence the motivational salience of faces. The initial work by Aharon and colleagues (2001) demonstrates that this key-pressing task can act as a behavioral measure of the motivational value (or incentive salience) of various rewarding stimuli – much like a rat pushing a lever receive food rewards – and offers an exciting new avenue to explore the topic of mate preferences and mating behavior among humans.

Chapter 2 Incentive Salience of Beauty in Adult Faces

Abstract

Beauty (or attractiveness) holds incentive salience in that it can motivate behavior. Previous work (discussed in section 1.2.5) has indicated that beautiful women hold high incentive salience among men, and that neurological disorders that disrupt reward-functioning, or cause anhedonia, can result in diminished incentive salience for beauty. These pivotal studies exploring the incentive salience of beauty were conducted using male participants only. Only one study has explored the incentive salience of beauty for women. This work indicates that while the aspects of liking and 'wanting' beauty can be dissociated for men, this dissociation may not exist for women. This chapter comprises two experiments; the first follows previously reported methodology to replicate and further explore gender differences in the incentive salience of beauty. Using highly attractive and unattractive male and female faces, I show that men are motivated by opposite-sex beauty alone, whereas women are motivated by beauty for same- and opposite-sex faces. Three possible explanations for this behavior among women are discussed: (1) women are more motivated by beauty in general, (2) women are engaging in social comparison behavior, and (3) women have a less stringent sexual preference. I further explore the link between attractiveness and motivation using a larger range of attractiveness in a regression analysis that shows that the relationship between these two factors is linear. In Experiment 2, I extend these findings to explore additional factors of facial appearance that may influence the motivational salience faces using path analysis. The relative impact of apparent health, facial adiposity, facial averageness, and sexual dimorphism are explored for opposite-sex faces (men and women), and for same-sex faces (women only). Results indicate that apparent health influences motivation independently of its effect on perceived attractiveness for both men and women when viewing opposite-sex faces, as well as for women when viewing same-sex faces. Sexual dimorphism in male faces also influenced key-pressing behavior independently among women. Motivation to seek out healthy mates or avoid unhealthy individuals would be evolutionarily advantageous as it would reduce the risk of contracting an illness and could act to increase reproductive success.

2.1 Introduction

When considering a potential mate both sexes place some importance on physical attractiveness; however men place much greater importance on attractiveness, while women tend to be more concerned with status and wealth (Buss & Barnes, 1986; Buss & Schmitt, 1993; Buss, 1987, 1989; Hill, 1945; Li, Bailey, Kenrick, & Linsenmeier, 2002; Mcginnis, 1958). This would suggest that attractiveness might, in general, be more rewarding for men than it is for women. Men and women selectively focus on different aspects of erotic stimuli, specifically in terms of erotic versus contextual information (Lykins, Meana, & Kambe, 2006; Lykins, Meana, & Strauss, 2008). Lykins et al. (2008) showed heterosexual men and women identical erotic images, consisting of male-male, female-female and male-female interactions, and tested the time spent viewing same- and opposite-sex components. Women spent equal amounts of time looking at same- and opposite-sex individuals, whereas men spent more time viewing the opposite-sex figures. Similarly, Chivers et al. have shown that the stimuli required to elicit a genital response are much less specific for women than they are for men (Chivers & Bailey, 2005; Chivers, Rieger, Latty, & Bailey, 2004). Women (both heterosexual and homosexual) experience similar levels of genital arousal when viewing sexual stimuli containing male-male and female-female interactions. Men on the other hand, only experience arousal when viewing sexual stimuli of the preferred sex (i.e. homosexual men are aroused by male images, heterosexual men are aroused by female images). Chivers' findings suggest that women have an automatic arousal response to sexual stimuli that is not preference specific, whereas men's responses are specific to their sexual interests.

This pattern of gender differences in physical arousal is apparent in terms of brain activation as well; neuroimaging studies have provided evidence that gender differences in the incentive salience of beauty exist (Ishai, 2007; Kampe et al., 2001; Kranz & Ishai, 2006; Levy et al., 2008). Cloutier et al. (2008) investigated sex differences in neural activation patterns when viewing attractive faces. They showed male and female participants a set of opposite-sex faces and found BOLD signal differences (attractive-unattractive) in the NAcc, the medial PFC (mPFC), and the dorsal anterior cingulate in response to attractiveness regardless of participant gender. The only notable sex-difference found was in the OFC, which preferentially responded to attractive faces over unattractive faces only for male participants. Although Cloutier et al. did not observe gender differences in mPFC activation, O'Doherty et al. (2003) observed preferential mPFC responses to attractive faces (over unattractive faces) of the opposite-sex only in males. The sex differences in frontal brain responses likely reflect differences in the importance of physical attractiveness when evaluating a potential mate.

If beauty acts as a signal of mate quality, it would be adaptive for opposite-sex attractiveness to be rewarding because it would increase motivation to seek out high-quality mates. Lesser activation in reward regions in response to same-sex beauty (Aharon et al., 2001, note: only heterosexual males were studied) may indicate that this type of beauty is not as rewarding because same-sex faces do not have reproductive salience (Senior, 2003). However, recent work using heterosexual female participants and homosexual individuals have suggested that same-sex faces can actually activate reward-related regions.

Kranz and Ishai (2006) showed male and female images to heterosexual and homosexual men and women to determine the influence of sexual orientation on responses to faces. They found that the OFC and the mediodorsal nucleus of the thalamus (mdT) were preferentially activated by male faces in heterosexual women and homosexual men. The OFC and mdT were preferentially activated by female faces in groups of homosexual women and heterosexual men. These findings suggest that the OFC may represent the reward value of possible sexual partners regardless of their reproductive significance and that sexual preference may drive reward circuitry activation (note: the reverse may also be true, i.e. reward circuitry activation drives sexual preference). An interesting finding in this study was that the difference in activation in the OFC and mdT for same- versus opposite-sex faces was quite small in the group of heterosexual women, perhaps indicating that beauty in both sexes provides a source of interest and reward. Diamond (2008) has argued that female sexual orientation is much more "fluid" than that of males. As such, women's sexual desire may be more broadly directed towards attractive individuals in general.

Levy et al. (2008) investigated gender differences in the motivational salience of beauty, with the aim of determining if opposite-sex beauty holds stronger incentive salience for men than it does for women. Heterosexual men and women were given the key-press task and asked to rate a set of attractive and average male and female faces. Women gave equally high attractiveness ratings to male and female faces, and exerted equal amounts of effort to prolong viewing attractive faces of both sexes. In contrast to Aharon's (2001) findings that men gave equal aesthetic ratings to same- and opposite-sex faces, Levy found that men actually rated beautiful female faces significantly higher than beautiful male faces (although beautiful male faces were rated significantly higher than the average male faces). They also saw corresponding increases in key-pressing behavior for beautiful female faces as compared to beautiful male faces. In another study exploring the impact of anhedonia on motivation, Elman et al. (2005) presented heterosexual men (control group and PTSD sufferers) with attractive and average male and female faces. Although the authors do not report statistical analyses on the rating data, reports of the means for each face category indicate that beautiful male faces were rated lower than beautiful female faces (although, again they were rated higher than the average group of male faces). While Aharon et al. found a strong dissociation between men's aesthetic beauty ratings of male faces and their corresponding reward value using independent groups of raters and key-pressers, subsequent work utilizing the same men for both tasks indicate that this dissociation may not be as clear as previously assumed[4].

The majority of mate preference studies, to date, have used aesthetic ratings to assess face preferences. Data from these rating studies is interpreted as reflecting preferences for actual mate choice, yet studies utilizing the motivational key-press paradigm have shown that

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[4] Note: Dai et al. (2010) used the same men in the key-press task and aesthetic assessment task. Their aesthetic assessment task was an evaluation movement assessment (EMA) in which they are asked to quickly respond to a stimulus using one of two keys. One moves the image closer to the participant's name (which appears on the screen during the trial) and the other moves the image away. This is interpreted as a measure of likability for the stimulus. Using this task, they found that men responded equally quickly to attractive male and attractive female faces.

aesthetic judgements may or may not parallel incentivised behavior. In cases where these do not parallel one another, judgements using Likert scale ratings may not be accurate predictors of mate preferences or mating behavior. The relationship between mate preferences and actual mate choice is a crucial, and somewhat underexplored, aspect of Evolutionary Psychology (see Section 2.3 for discussion of the literature on mate preferences versus mate choice). In light of this issue, I aimed to explore the relationship between motivated behavior and aesthetic ratings for facial attractiveness.

The first aim of the work presented in this chapter was to replicate and extend previously published findings regarding the incentive salience of facial attractiveness. I hypothesized that men and women would both work to increase the viewing time of opposite-sex attractive faces, but only women would work to increase the viewing time of same-sex attractive faces. I also hoped to clarify the slight discrepancy seen in rating behavior between Aharon's (2001) study and the results of subsequent work on motivation (Elman et al., 2005; Levy et al., 2008). Both Elman and Levy found that men rated attractive male faces significantly lower than they did attractive female faces (although still higher than unattractive faces of either gender). Aharon, however, found no differences in the attractiveness ratings men gave to attractive male and female faces. This may be due to different participant expectations. Aharon used a separate set of raters and key-pressers; whereas Elman and Levy had the same men perform both tasks. It may be that men who performed the key-press task and worked hard for female faces but not male faces subsequently rate attractive male faces lower than attractive female faces because they have incorporated their previous behavior into the current rating task. Additionally, because Aharon used only male participants, it remains unclear whether a similar pattern of results would be seen in women.

2.2 Experiment 1: Gender Differences

2.2.1 Pilot Study: Determining Attractiveness Groups

2.2.1.1 Stimuli

The facial stimuli used in the studies reported in this chapter included 120 adult faces (60 male). Because student faces often do not yield highly attractive stimuli, the set of faces used here were obtained from various online modelling/acting websites in order to ensure a range of facial attractiveness (including highly attractive) across the stimulus set. Although this results in an unstandardized image set, preventing certain types of analyses (i.e. calculation of symmetry), it was necessary for the present study, which aims to explore the motivational salience of facial attractiveness. Each image used was a head-on shot, where the individual was looking directly at the camera and did not have any visible body jewellery. The facial stimuli varied in attractiveness, and were masked with a black background to remove any additional visual cues from the images.

2.2.1.2 Independent Ratings of Stimuli Attractiveness

Independent ratings of attractiveness were obtained for each of the 120 stimuli in order to classify the faces into high- and low- attractiveness groups (these groups will be used in the analysis reported in section 2.2.3). Each face was rated for attractiveness on a 7-point Likert scale (where 1=Very Unattractive, 7=Very Attractive). Presentation order of the faces was randomized across participants. Attractiveness ratings were obtained from 76 raters (36 female). These raters ranged in age from 16-42 (M = 22.16, SD = 4.402). Of the 76 raters, 35 completed the online task in the lab and were remunerated with 1 course credit; the other 41 raters completed the online task via the Perception Lab webpage and were not remunerated in any way for their time. There were no differences in the stimulus ratings between those who participated online and those who participated in the lab ($t(119) = .274$, $p = .784$). All participants provided informed consent prior to beginning the experiment (see Appendix B.1 for ethical approval).

Before sorting the stimuli into high- and low- attractiveness groups, correlational analyses were performed on the rating data to determine if male and female raters agreed on which faces were attractive. Overall, there was a high level of inter-rater reliability for individual evaluators in general ($\alpha = .97$). As seen in Figure 2.1, there was a high agreement between men and women on the attractiveness of female faces ($r_{60} = .95$, $p < .001$). There was a high level of inter-rater reliability among male raters ($\alpha = .95$) and female raters ($\alpha = .97$) for the set of female faces. Although the male faces were not, overall, rated as highly as the female faces, there was still a significant level of agreement across raters of both gender ($r_{60} = .95$, $p < .001$, see Figure 2.2). Again, high levels of inter-rater reliability were seen for both male ($\alpha = .96$) and female ($\alpha = .97$) raters.

The facial stimuli were then sorted into high- and low-attractiveness groups. These groups were comprised of the 15 faces of each gender with the highest and lowest ratings. T-tests confirmed that the female faces in the high attractiveness group were rated significantly higher than those in the low attractiveness group ($t(22.4) = 20.8$, $p < .001$). The same was true for the male faces ($t(22.7) = 21.7$, $p < .001$). There were no differences in rating scores between the male and female faces in the attractive groups ($t(28) = -.087$, $p = .931$) or the average (unattractive) groups ($t(28) = 1.07$, $p = .293$). Example images from each group can be seen in Figure 2.3.

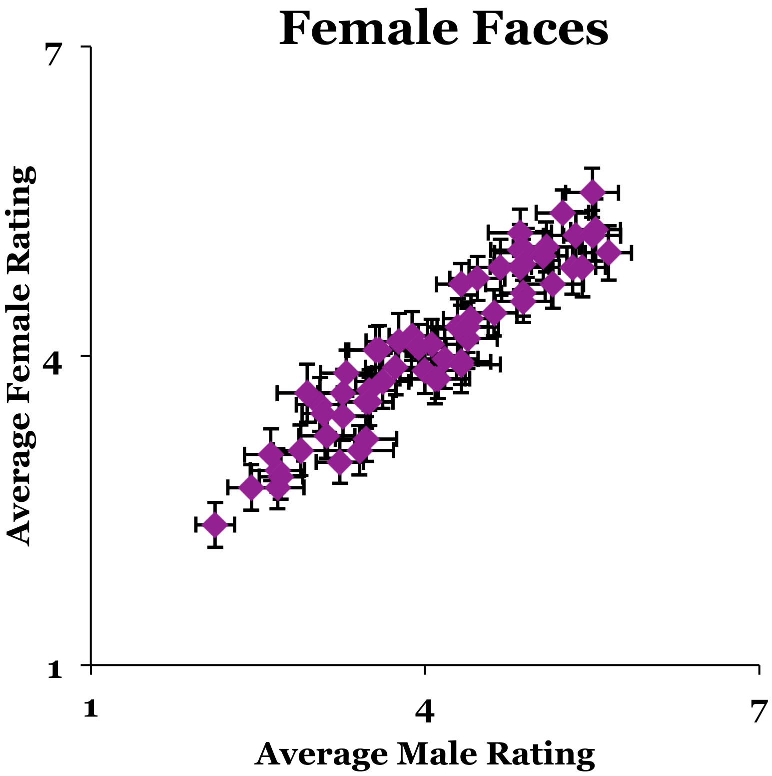

Figure 2.1 *Average rating given to each of the 60 female faces by male (x-axis) and female (y-axis) raters. Error bars represent SEM.*

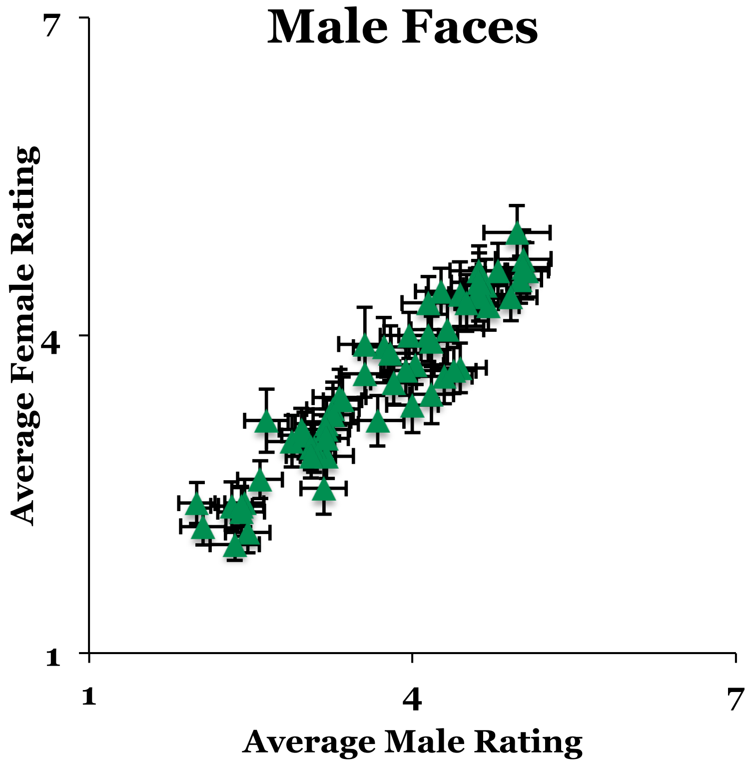

Figure 2.2 *Average rating given to each of the 60 male faces by male (x-axis) and female (y-axis) raters. Error bars represent SEM.*

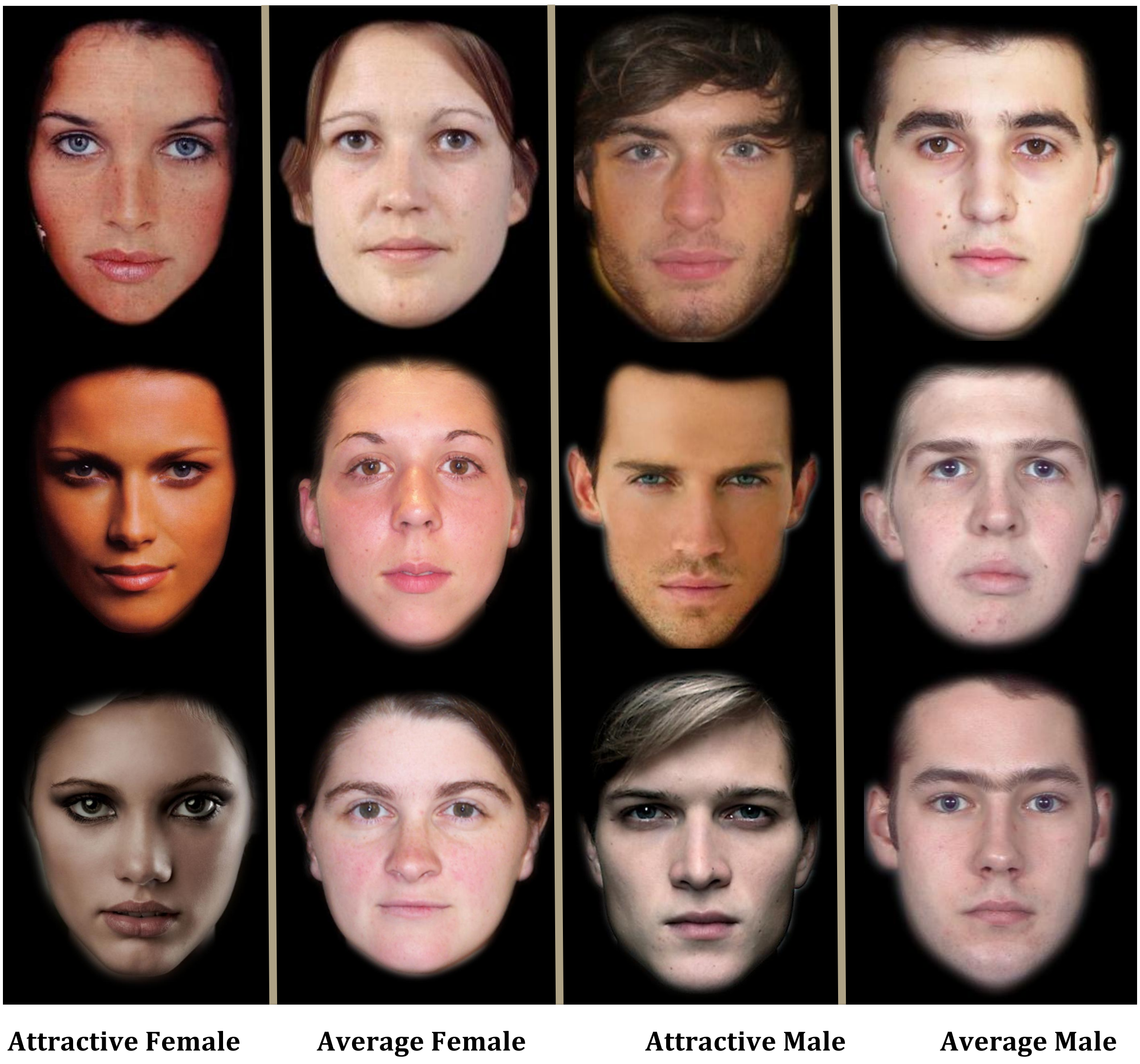

Figure 2.3 *Example images from each of the 4 face categories: Attractive Female, Average Female, Attractive Male, and Average Male.*

2.2.2 Method

2.2.2.1 "Pay-per-view" Key-press Task

Participants were first given a "pay-per-view" key-press task. This key-press task, adapted from Aharon et al. (2001), presents participants with images at a default rate of 1 image every 4 seconds. However, the participant directly controls the presentation time of each image. Participants were told that they could "keep a picture on the screen longer" by pressing

"N" & "M" alternately, or "remove an image faster" by pressing "Z" & "X" alternately. Each pair of key-presses changed the overall presentation duration according to the formula:

$$\text{Viewing Duration} = \frac{\text{Default} + (\text{ExtremeTime} - \text{Default})}{\text{Scaling Constant}}$$

$$\text{Where: ExtremeTime} = 0\text{s for key} - \text{presses decreasing the viewing time and 16s}$$

$$\text{for key} - \text{presses increasing the viewing time. The scaling constant was set to 40.}$$

Visual feedback was given via a timer bar presented on the left-hand side of each image (see Figure 2.4). If the participant did nothing, this timer would "run out" after 4 seconds[5] and a new image would appear on the screen. Pressing to increase image presentation time was coded as positive key-presses and would halt the timer or reverse its direction, while pressing to decrease image presentation time was coded as negative key-presses and would cause the timer to "run out" more quickly. One key-press unit was coded each time a key-pair was pressed alternately (i.e. pressing N-M coded as 1 key-press, pressing N-N repetitively or N-only was not counted). The amount of increase or decrease to the overall viewing time was dependent on the frequency and duration of key-pressing (i.e. total viewing time was a direct reflection of key-press activity). This key-pressing task operationalizes motivation by measuring amount of effort/work exerted to view an image and can be used to evaluate the reward value (or incentive salience) of stimuli.

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[5] Note: the use of 4 seconds as the default, with 0s and 16s as ExtremeTime values results in an unbalanced increase versus decrease 'allowance'. However, when 0s and 8s were used as ExtremeTime values, the resultant visual feedback from increase key-presses was not sufficient. Because all results reported utilize number of key-presses as the dependent variable, this unbalance is not considered to be an issue.

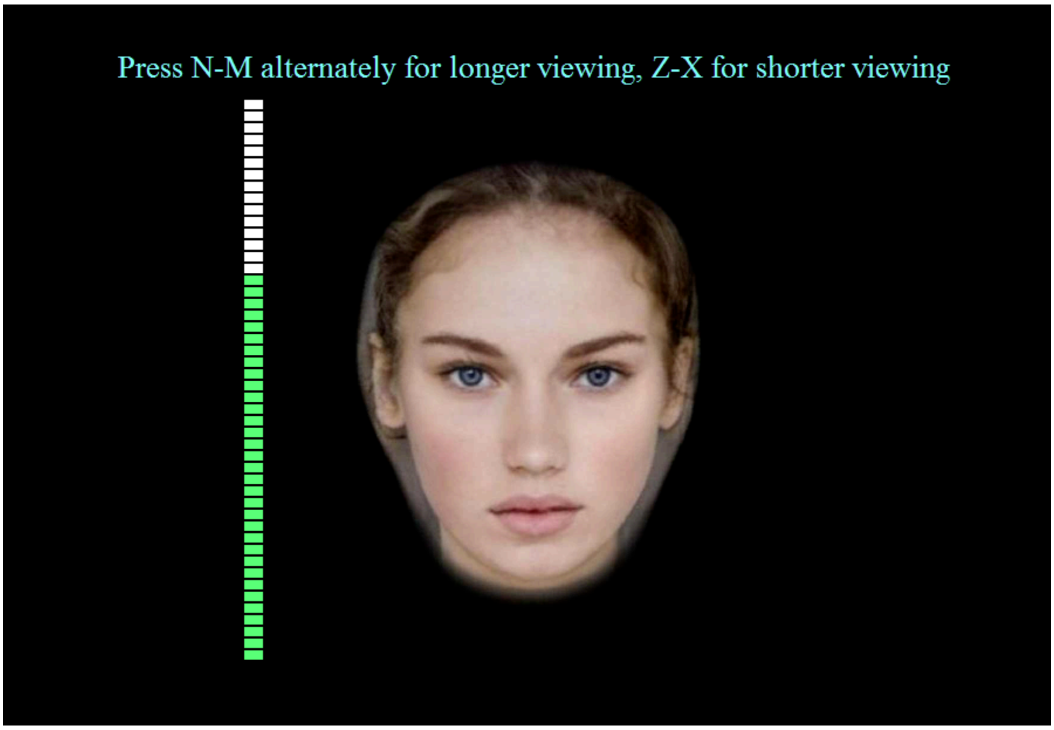
Press N-M alternately for longer viewing, Z-X for shorter viewing

Figure 2.4 *Demonstration of the key-press task as it appeared to participants. The timer bar on the left hand side of the image reflects the length of time the image will remain on the screen if no additional key-presses are made.*

Prior to beginning the experiment, each participant was given a training session designed to familiarize them with the key-press procedure. Faces were not presented during this task; rather, images of objects were used. After the training task, participants were given the opportunity to ask questions, or repeat the training if they did not fully understand the procedure.

The set of stimuli faces were presented in two blocks, grouped by gender. The order of presentation was counterbalanced across participants. Participants were informed that the task length was set at 10 minutes (5 minutes per block); although in actuality, the task length was dependent on their behavior. The measured number of key-presses per trial was calculated by subtracting the number of negative key-presses made from the number of positive key-presses made.

2.2.2.2 Rating Task

Following the key-press task, participants rated the perceived attractiveness of each face on a 7-point Likert scale (where 1=Very Unattractive, 7=Very Attractive). Presentation order of the faces was, again, blocked by gender. We chose to present faces blocked by gender in order to maximize participants' ability to judge a given face's attractiveness in comparison to others of the same gender. Faces were presented for rating in the same gender-order as they had been during the key-press task (i.e. if a participant saw male faces first, they also rated male faces first).

2.2.2.3 Participants

Forty-nine Caucasian students (23 women, 26 men) from the University of St Andrews participated and were paid £5 per hour *pro rata*. Participants were recruited from the psychology department participation pool (i.e. SONA), which includes age-, gender-, and ethnicity-screening questions at the time of sign-up. Participants ranged in age from 18-29 (M = 21.2, SD = 2.86). There were no significant differences in age between the two genders ($t(40)$ = 1.16, p = .25). All participants read and signed a statement of informed consent prior to beginning the study. Participants also completed a demographic questionnaire regarding sexual orientation and relationship status. Sexual orientation was assessed on a 7-point Likert scale where 1 = completely homosexual, 4 = bisexual, and 7 = completely heterosexual. Participants reporting non-heterosexual orientation (i.e. scores of 5 and below) and those failing to complete the key-press task were excluded from the data analysis. "Failure to complete the key-press task"[6] was defined as any participant who had an average total number of key-presses (regardless of increase versus decrease) that was less than 1.0. The final analysis consisted of 42 participants (23 men, 19 women).

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[6] *Note:* this elimination criterion was applied to all experimental studies described in this thesis.

2.2.3 Results

Although participants viewed all 120 faces, only 60 of these were used in the analysis reported in this section (additional analyses utilizing all 120 faces will be presented in Experiment 2). To follow previous methodology (essential for replication), four face-classes were used in the analysis reported below: Attractive Female, Attractive Male, Average Female and Average Male (each comprised of 15 images, as detailed in section 2.2.1.2). Separate 2x2x2 repeated measures ANOVAs were run on the rating data and the key-press data. Stimulus gender and attractiveness group were used as within-subject factors in the analysis, and participant gender was used as a between-subject factor.

2.2.3.1 Rating Task

A main effect of stimulus gender was found in the rating data ($F(1,40) = 9.70$, $p = .003$, $\eta_p^2 = .20$). Pairwise comparisons indicated that female faces received higher ratings, overall, than male faces ($M_{\text{Female}} = 3.74$, $SEM_{Female} = 0.09$; $M_{\text{Male}} = 3.32$, $SEM_{Male} = 0.11$). As expected, there was a main effect of attractiveness on the rating data ($F(1,40) = 362.1$, $p < .001$, $\eta_p^2 = .90$). Faces from the attractive groups were rated much higher than those from the average groups. There was also a significant interaction between stimulus gender and attractiveness ($F(1,40) = 13.28$, $p = .001$, $\eta_p^2 = .25$). Paired comparison t-tests indicated that attractive females were rated higher than attractive males ($t(41) = 3.78$, $p < .001$), but no differences were apparent in the ratings of average male and female faces ($t(41) = 1.68$, $p = .10$).

There was no significant effect of subject gender on attractiveness ratings ($F(1,40) = .327$, $p = .571$, $\eta_p^2 = .01$). A significant interaction between stimulus gender and subject gender was found ($F(1,40) = 4.52$, $p = .040$, $\eta_p^2 = .10$). Figure 2.5 displays the average ratings for each category based on subject gender. Women did not differ in their attractiveness ratings based on stimulus gender, whereas men rated female faces much higher than they did male faces. There was also an interaction between attractiveness and subject gender ($F(1,40) = 5.90$, $p = .020$, $\eta_p^2 = .13$). Women appeared to be more sensitive to facial attractiveness. They tended to rate the low-attractiveness group lower than males did, while they rated the high-attractiveness group much higher than males did.

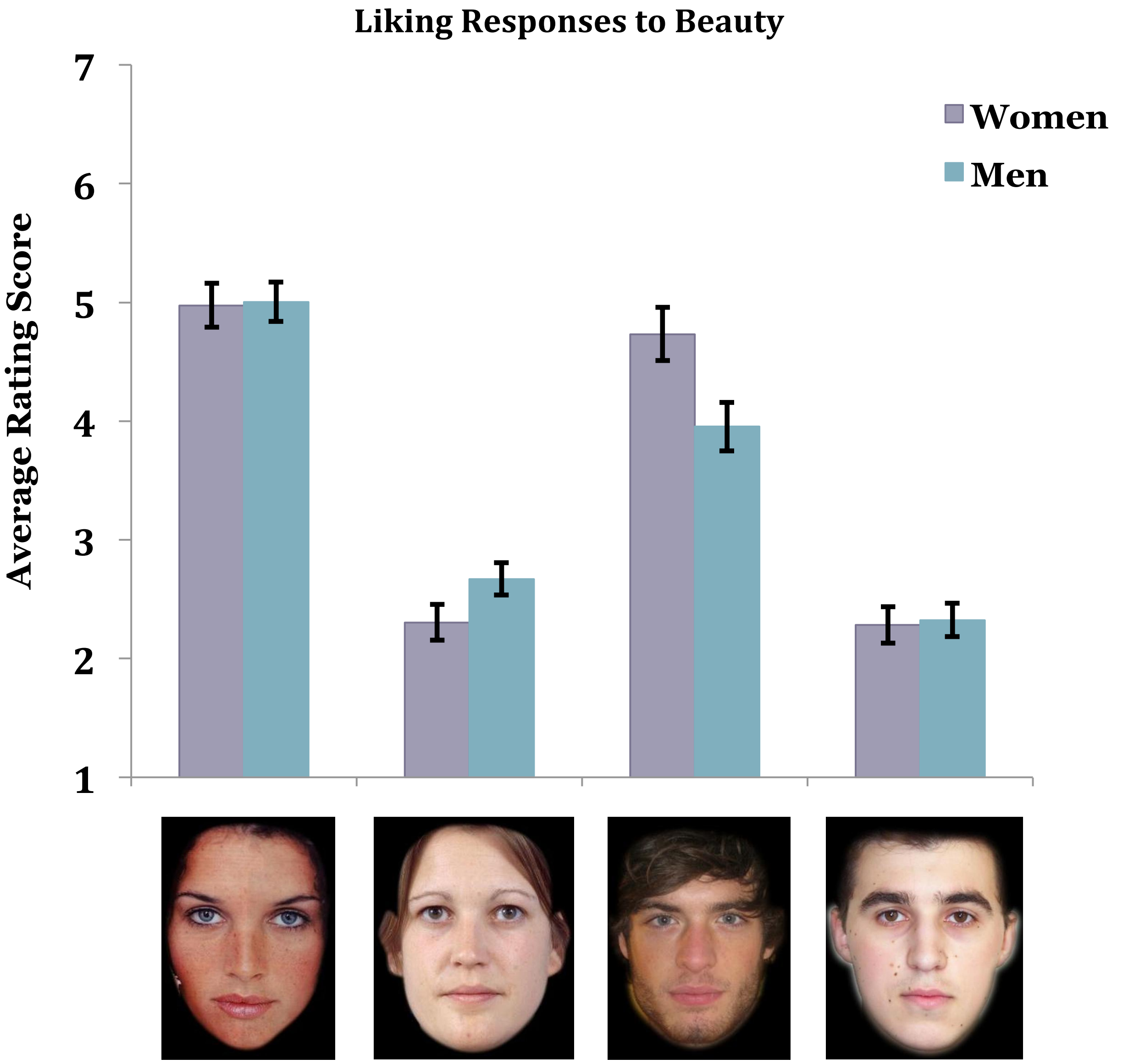

Figure 2.5 Average attractiveness ratings for each facial category. Face categories were formed using the set of independent ratings, while the data presented above reflects the ratings given to each face category by the set of in-lab raters who also completed the key-press task. Error bars represent SEM.

The three-way interaction between stimulus gender, attractiveness and subject gender was marginally significant ($F(1,40) = 3.65$, $p = .063$, $\eta_p^2 = .08$). Women tended to give similar ratings to same- and opposite-sex faces within each attractiveness category, whereas men rated opposite-sex attractive faces higher than they rated same-sex attractive faces. *Post-hoc* t-tests revealed no gender differences in the ratings of attractive female faces (p = .95) or of opposite-sex attractiveness ratings (i.e. men rating attractive female faces and women rating attractive male faces; p = .60).

2.2.3.2 Comparing Raters

To explore the impact of task demands, and attempt to clarify the discrepancies seen between previous studies, I next compared the ratings from these participants to those of the independent raters from Section 2.2.1.2. The independent raters performed the rating task alone, whereas the participants in this study previously saw all faces in the key-press task. It is possible that memory of their performance for a face on the key-press task could influence their subsequent ratings (i.e. if a participant key-pressed to remove a face from the screen, this behavior could influence their judgement when they are later asked to rate the attractiveness of that face). An independent samples t-test for the attractive male face group indicated that the sample of independent raters did, indeed, rate attractive male faces significantly higher than men who had completed the key-press task prior to rating the faces ($t(55) = 2.92$, $p = .005$).

It is not the case that completing the key-press task prior to rating faces impacted all men's ratings because this discrepancy between types of rater was not seen for any other face group (i.e. the average male faces, attractive female faces, or average female faces; all *p-values* between 0.16 – 0.34). Nor is it the case that this discrepancy is true of all raters (regardless of sex) because among women, no differences were found for the attractive male face group ($t(52) = 0.60$, $p = .56$). Additionally, this finding cannot be explained in terms of an effect on judgements of attractive same-sex faces because among female raters, there were no group differences for the attractive female faces ($t(52) = 0.51$, $p = .61$).

2.2.3.3 Key-press Task

A main effect of stimulus gender was found for number of key-presses ($F(1,40) = 11.19$, $p = .002$, $\eta_p^2 = .22$). Pairwise comparisons indicated that female faces received slightly positive key-presses overall (i.e. the key-press pattern required to *increase* viewing duration), whereas male faces tended to receive more negative key-presses (M_{Female} = 0.80 key-presses, SEM_{Female} = 0.72; M_{Male} = -2.16 key-presses, SEM_{Male} = 0.62). There was a main effect of attractiveness on the key-press data, as was expected ($F(1,40) = 69.49$, $p < .001$, $\eta_p^2 = .64$). Faces from the attractive groups received positive key-presses, while faces from the average group received negative key-presses. Additionally, a significant interaction between stimulus gender and attractiveness was found ($F(1,40) = 12.39$, $p = .001$, $\eta_p^2 = .24$). The number of positive key-presses in response to attractive versus average faces was larger for the set of female faces than it was for the set of male faces.

There was no significant main effect of subject gender on key-pressing behavior ($F(1,40) = .392$, $p = .535$, $\eta_p^2 = .01$), indicating that men and women were equally likely to key-press, overall. Figure 2.6 displays the average number of key-presses for each face category based on subject gender. A significant interaction between stimulus gender and subject gender was found ($F(1,40) = 14.14$, $p = .001$, $\eta_p^2 = .26$). Women did not differ in the number of key-presses based on stimulus gender, whereas men used significantly more positive key-presses for female faces than they did for male faces. No interaction was found between attractiveness and subject gender ($F(1,40) = .283$, $p = .598$, $\eta_p^2 = .01$). The three-way interaction between stimulus gender, attractiveness and subject gender reached significance in the key-press data ($F(1,40) = 12.53$, $p = .001$, $\eta_p^2 = .24$). Women exerted similar effort (measured in units of key-presses) to view attractive male and female faces, whereas men only exerted effort to view attractive female faces. *Post-hoc* t-tests revealed strong gender differences in the number of key-presses for attractive female faces ($p = .03$) and attractive male faces ($p = .001$). Differences in the number of negative key-presses for average male faces did not quite reach significance ($p = .08$), however it appears that men tended to key-press more to remove average male faces than females did (although both key-pressed to remove the faces). There were also gender differences in the number of key-presses spent to view attractive opposite-sex faces (i.e. men looking at attractive female faces and women looking attractive male faces; $p = .002$), with men key-pressing more for opposite-sex attractive faces than women did.

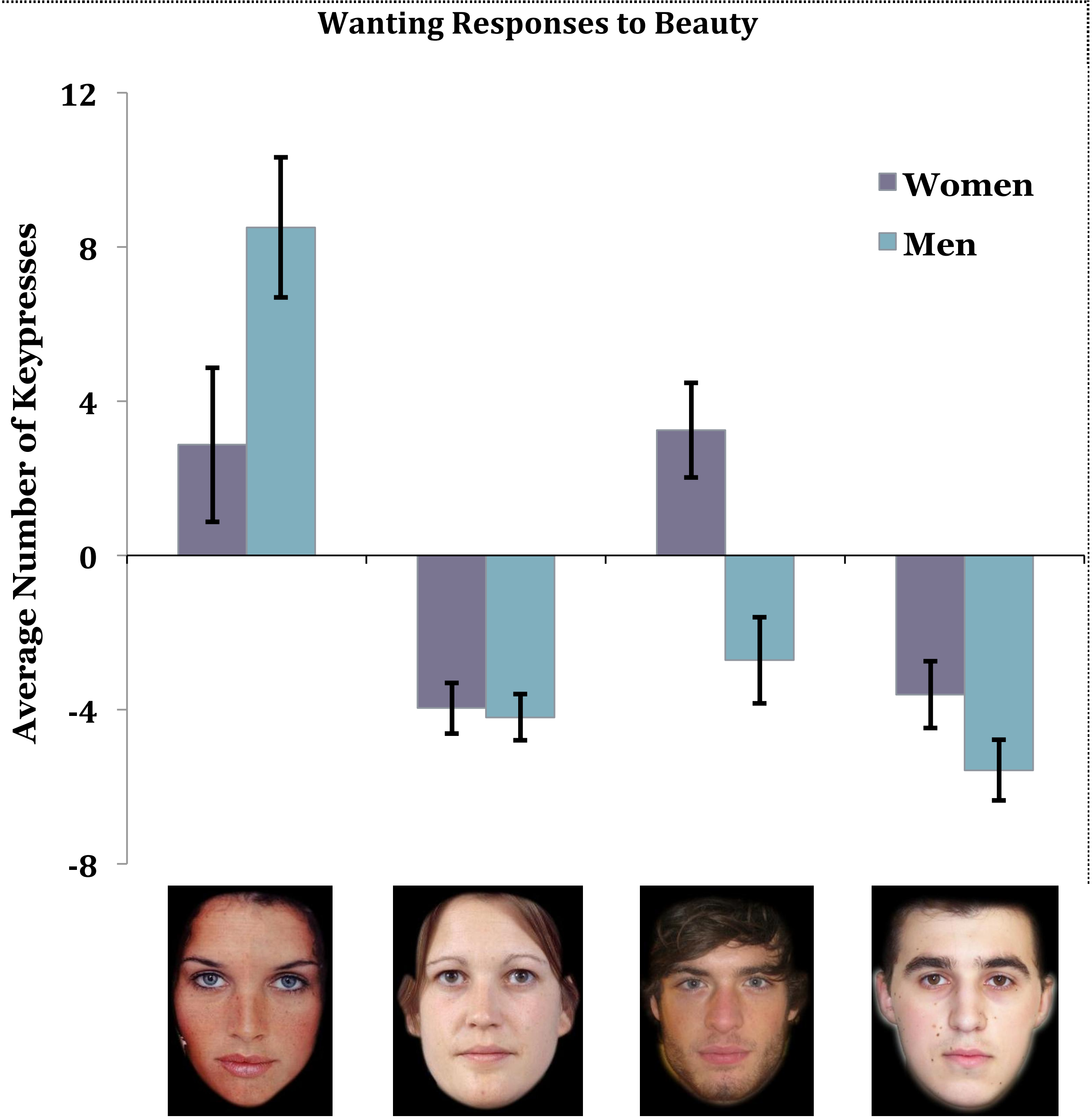

Figure 2.6 *Average number of key-presses exerted by men and women for each facial category. Error bars represent SEM.*

2.2.3.4 Does Attractiveness Predict Motivation?

The previous analyses replicate the findings from Aharon et al. (2001) and Levy et al. (2008) with regards to the motivational salience of beauty and gender differences in motivation, respectively. However, a shortcoming of these studies is that they treat attractiveness as a categorical variable rather than a continuous variable. Here, I report the results of regression analyses using data from all 120 stimulus faces that range in attractiveness. For each of the 120 faces, key-presses were used as the dependent variable and the independent attractiveness rating and face sex were used as predictor variables. Because gender differences exist in terms of the motivational salience of facial attractiveness, separate regression analyses were conducted for men and women.

For women, the overall model was significant ($R^2 = 0.47$, $F(2,117) = 51.0$, $p < .001$). Facial attractiveness ($\beta = 0.70$, $p < .001$) but not face sex ($\beta = 0.07$, $p = .314$) significantly predicted key-press behavior, indicating that same- and opposite-sex beauty hold equal incentive salience among women (see Figure 2.7a). This relationship is linear – the more attractive a face, the more incentive salience it holds. For men, the model was significant ($R = 0.53$, $F(2,177) = 64.5$, $p < .001$) and both facial attractiveness ($\beta = 0.495$, $p < .001$) and face sex ($\beta = 0.43$, $p < .001$) significantly predicted key-press behavior. As seen in Figure 2.7b, opposite-sex beauty holds stronger incentive salience among men than same-sex beauty, although again the relationship between attractiveness and motivation is linear. In the case of men viewing same-sex faces, it appears that more attractive faces are less aversive[7] (i.e. yield less *negative* key-pressing).

2.2.4 Discussion

The present study yielded a number of interesting findings. Firstly, I was able to replicate previous work exploring the incentive salience of beauty. Here, I show that opposite-sex beauty holds high incentive salience among men (Aharon et al., 2001), while among women opposite-sex beauty holds less incentive salience (replicating the findings of Levy et al., 2008). Both men and women worked to significantly increase the viewing time for attractive faces of the opposite-sex suggesting that heterosexual beauty has some degree of incentive salience among both sexes. If facial attractiveness is a reflection of an individual's underlying genetic

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[7] Note: That attractive faces yield positive key-presses while unattractive faces yield negative key-presses may be an artifact of default presentation time rather than a reflection of reward versus aversion. This theory has yet to be empirically tested (I am currently running a methodological study testing various default presentation times and increment changes in response to key-pressing to determine the optimal settings for studies utilizing the key-press paradigm as a behavioral task). See Section 6.1.3 for further discussion.

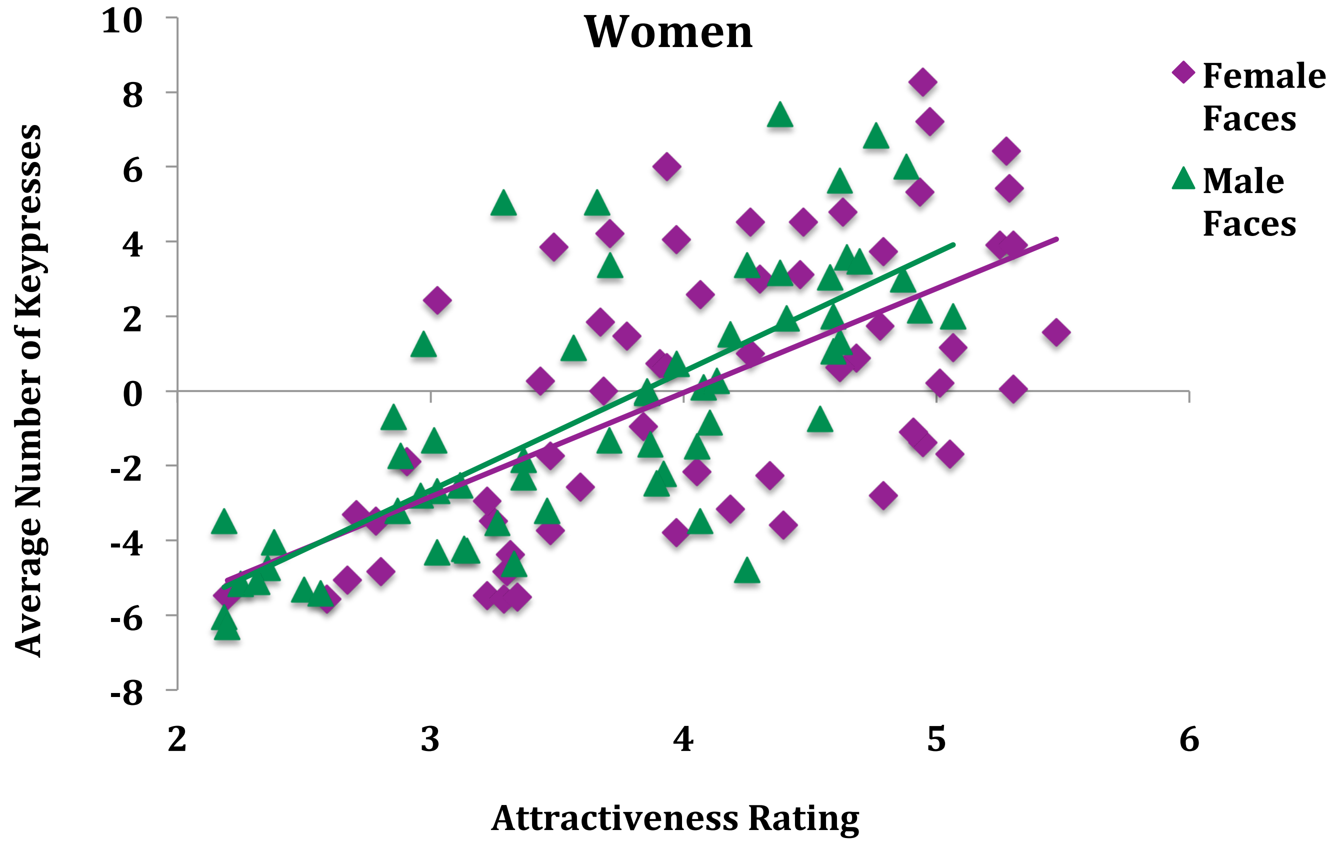

Figure 2.7 (a) Average number of women's key-presses regressed against the attractiveness for each male and female face.

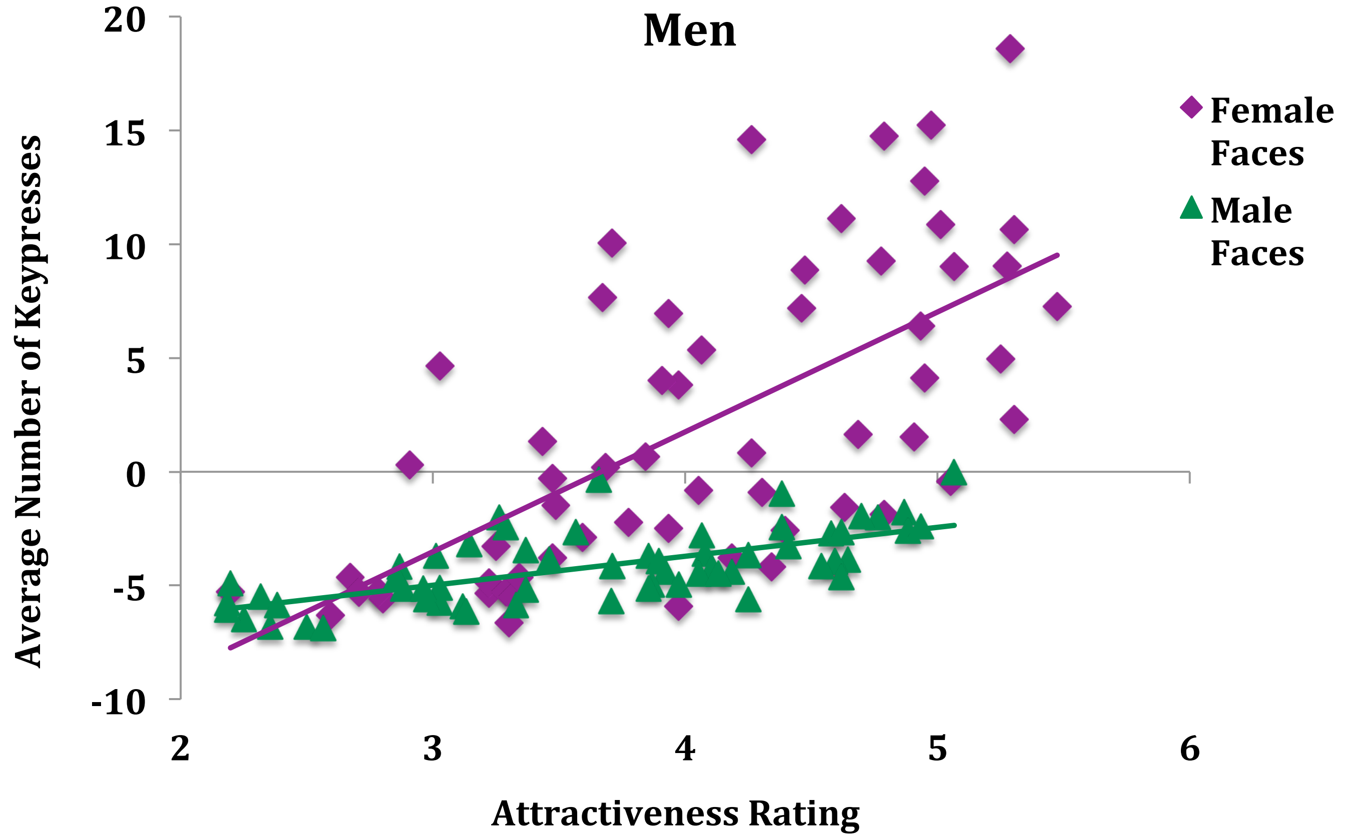

Figure 2.7 (b) Average number of men's key-presses regressed against the attractiveness for each male and female face.

quality, it makes sense that both men and women would want to maximize their potential interactions with more attractive individuals, as they would be higher quality mates and produce healthier, more viable offspring; although this is only true when socialization leads to unprotected sex.

Interestingly, there were noticeable differences in the *amount* of effort (as measured by number of key-presses) expended between men and women to view attractive faces of the opposite sex. On average, women exerted moderate effort to view attractive male faces, while men worked extremely hard to view attractive female faces (some even upward of 25 key-presses for a given face). This gender difference did not exist for the group of unattractive female faces nor was it apparent in the mid-range attractive faces (both sexes show relatively minimal motivation for average faces; see Figure 2.7), so it cannot be the case that men are motivated by female faces in general. Rather, there seems to be something specific about *beautiful women* that drives male behavior. Indeed, Wilson and Daly (2004) found that after viewing pretty women men were more likely to discount larger, future monetary rewards (for smaller, immediate rewards). This reward discounting behavior was not observed after the men viewed unattractive women, or attractive non-face stimuli (i.e. cars). Among women, however, viewing neither attractive nor unattractive men resulted in a significant change in reward discounting behavior (although a non-significant directional shift was seen after women viewed attractive male faces). This finding would suggest that attractiveness has different incentive salience for men and women; attractiveness acts as a more important cue for males and thus can motivate male behavior to a much larger degree than it motivates female behavior.

There are a number of possible explanations for this interesting gender difference. Differences in mating strategies may be the driving force. Triver's (1972) suggested that the sex of a species that requires greater parental investment becomes a limited resource for which members of the opposite sex must compete. According to this theory, in humans it is the case that men must compete for women (i.e. Bateman's Principle, Bateman, 1948; Brown, Laland, &

Mulder, 2009). Men benefit more from short-term relationships/encounters whereby they can maximize their reproductive success by impregnating many different women (males from polygamous societies have greater rates of reproductive success than those from monogamous societies, although serial monogamists have highly variable rates of reproductive success; see Brown et al., 2009). As such, men should seek out a greater number of partners than women. Differential levels in drive to seek out mates may explain the differences in amount of effort seen in the present study. The lack of effort women make, relative to men, for heterosexual beauty suggests that other factors aside from physical appearance may influence female behavior. Attractiveness may act as a cue to physical quality, but with the prevalence of biparental care among humans, cues to male disposition (e.g. kindness) or status (e.g. wealth) may also be influential. Traits that signal paternal investment or quality may motivate women's behavior in much the same way as attractiveness.

Perhaps the most interesting finding in the present study is that women will work just as hard to view attractive *same-sex* faces as they will for attractive opposite-sex faces. A similar result was observed by Levy et al. (2008), however the authors failed to address this finding or provide possible explanations other than a brief mention of women having "greater bisexual interest" in their introduction. The fact that women will expend effort to look at beautiful women suggests that social stimuli that are not specific to mating can also influence behavior. Because all of our participants were heterosexual, it is also the case that something aside from sexual preference is likely responsible for the observed female behavior. There are a number of possible explanations for this finding. Here, I present three potential reasons why same-sex beauty may hold incentive salience among women. These hypotheses are by no means mutually exclusive, and may be acting in conjunction to influence women's motivated behavior.

Firstly, and most simply, women may be motivated by aesthetically pleasing stimuli regardless of their social significance; that is, perhaps women like "pretty things" in general. Another plausible explanation is that women are interested in looking at attractive women due to intrasexual competition or social comparison (Festinger, 1954; Gilbert, Giesler, & Morris, 1995; Vukovic et al., 2008). Buss (1988) has suggested that intrasexual competition is driven by the opposite-sex's mate choice preferences. That is, if men prefer to mate with thin women, women will compete to be thinnest in an attempt to increase their chances of being selected as a mate. With the vast amount of exposure young women have to feminine beauty though the media, it could be the case that women are choosing to increase the amount of time they view attractive female faces in order to learn how to improve their own appearance (i.e. they are making a social comparison of their own appearance against the appearances of the more beautiful women; Martin, Kennedy, & Costa, 1994; Martin & Kennedy, 1994; Richins, 1991).

A third explanation, and the reasoning given by Levy et al., is that women may be aroused by attractive individuals in general rather than solely by heterosexual beauty. This would give attractive female faces a more sexually significant role. As discussed previously, Chivers et al. (2004; 2005) have shown that women experience general arousal rather than category-specific arousal, as is the case with men. Women have been shown to exhibit physiological arousal when viewing sexual stimuli of the same- and opposite-sex. In Kranz and Ishai's (2006) study, the response observed in the mdT to attractive female faces was equal for homosexual and heterosexual women, and level of activation in the OFC in response to attractive female faces was larger for heterosexual women than homosexual women (although the OFC response in heterosexual women was larger for attractive male faces than it was for attractive female faces). It may be the case that although beautiful females do not hold reproductive significance, they are sexually interesting or rewarding to women regardless of their sexual orientation.

In an attempt to clarify discrepancies across previous studies with regards to men's ratings of same-sex beauty, I next explored differences between groups of raters. These results indicated that men who first viewed attractive male faces in the key-press task subsequently rated these faces as less attractive than those men whose only task was to rate the faces. This pattern of results perfectly matches those observed in previous studies. Aharon et al. (2001) found that men rated beautiful male faces as highly as they rated beautiful female faces. These men, however, were tasked only with rating faces. In contrast, the men in Levy et al. (2008) and Elman et al. (2005) were given the key-press task prior to the rating task and were shown to rate beautiful male faces lower than they rated beautiful female faces (although they were still rated as more attractive than the average male faces). Although both groups of men rated the attractive male faces lower than the attractive female faces, the discrepancy between raters was only seen for men rating the group of attractive male faces. Women did not show rater differences for the attractive male faces or the group of attractive female faces. So, it cannot be the case that completing they key-press task first somehow impacts all subsequent rating behavior. There seems to be something specific to men viewing attractive same-sex faces. Perhaps having previously seen these attractive same-sex individuals in the context of attractive female faces impacts men's judgements of their own quality, leading to a more negative affective reaction to attractive male faces during the rating task. There may also be interesting individual differences in aesthetic judgements and motivation yet to be explored.

2.3 Experiment 2: Exploring Beyond Beauty

The secondary goal of the present work was to explore additional facial dimensions that may influence motivation or behavior. As discussed in section 1.1, perceptions of facial attractiveness are influenced by a number of factors, including: perceived health, symmetry, averageness, and sexual dimorphism. Is it through their influence on perceived attractiveness that such factors influence motivation to view faces? Or do certain aspects of facial appearance drive motivated behavior directly? Using path analysis, in this chapter I will explore the impact of facial averageness, sexual dimorphism, health and adiposity[8] on motivated behavior (i.e. wanting) for opposite-sex faces (i.e. potential mates), as well as how these factors impact women's motivation to view same-sex beauty.

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[8] Note: Due to the non-standard format of the images used in this study, it was not possible to conduct symmetry analysis, as measurements of facial symmetry are highly sensitive to head posture.

While the literature regarding the impact of averageness, sexual dimorphism and health was discussed in length in Chapter 1, a brief outline of each of these factors and their likelihood to influence liking and/or wanting responses is described here. The literature on the averageness-attractiveness relationship has yielded conflicting results. While some studies indicate that faces which are closer to average in appearance are more attractive (Langlois & Roggman, 1990; Rhodes & Tremewan, 1996), others have shown that averageness and attractiveness are dissociable aspects of facial appearance (DeBruine et al., 2007; Perrett et al., 1994). Faces that are closer to the population average may be considered more attractive in general, but it is not the case that these are the most attractive faces. As DeBruine et al. (2007) demonstrated, faces that deviate from the population average along the attractiveness dimension are considered more attractive than absolute average faces. As such, it is *possible*, but not necessarily a clear prediction, that facial averageness could influence liking and/or wanting in the present study.

According to the good gene theory, sexual dimorphism is indicative of high genetic quality. Sexually dimorphic features can be costly to develop and are cues to an individual's reproductive potential. As discussed in Section 1.1.3, high sexual dimorphism in female faces is considered attractive (Cunningham et al., 1995; Cunningham, 1986; Law Smith et al., 2006; Perrett et al., 1998) while the relationship between sexual dimorphism and attractiveness in male faces is more contentious (Koehler et al., 2004; Perrett et al., 1998). There appears to be greater variability in preferences for sexual dimorphism in male faces across individual women (DeBruine et al., 2006). If high dimorphism is indicative of genetic quality, it may be that sexual dimorphism influences motivation to seek out high quality mates. As such, sexual dimorphism could impact wanting behavior (i.e. key-pressing) when considering opposite-sex faces (i.e. potential mates) and a strong, positive relationship between facial attractiveness and sexual dimorphism was predicted for female faces.

With regard to male faces, we anticipated that sexual dimorphism may have a direct effect on motivation independent of its impact on attractiveness due to the benefit of seeking out high quality mates, however due to the prosocial connotations of femininity in male faces, it may also be the case that masculinity negatively affects motivation. The link between masculinity and motivation has never been explored, and its impact on perceptions of facial attractiveness has been demonstrated to be highly labile. For this reason, it was essential to perform separate analyses for men and women when considering the incentive salience of opposite-sex faces.

There appears to be a clear link between apparent health and facial attractiveness (Grammer & Thornhill, 1994; Kalick et al., 1998). As such, it was anticipated that apparent health scores would positively influence perceived attractiveness. There is some evidence that apparent health impacts how others respond to us. Krupp et al. (2011) found that people are more likely to reciprocate with individuals who appear healthy in economic games than with those who appear unhealthy. When selecting a potential mate, it would be advantageous for individuals to seek out healthy partners and avoid unhealthy individuals who could be detrimental to current health and offspring viability. In light of the evidence reviewed here, we predicted that apparent health would positively impact both liking and wanting behaviors in the present analysis.

Similar effects were anticipated for facial adiposity. Facial adiposity may act as a cue to health, as weight is a heritable feature (Elks et al., 2012) and may reflect genetic quality. Cues to weight are present in the face and can impact perceptions of attractiveness. Coetzee, Perrett and Stephen (2009) found that facial adiposity predicted ratings of both health and attractiveness. Importantly, facial adiposity was also an accurate predictor of actual health (measured via cardiac health), suggesting that facial adiposity may provide an honest cue to genetic quality. We predicted that facial adiposity would negatively impact liking responses for faces (i.e. higher facial adiposity results in lower perceived attractiveness). Singh and Young (1995) found that men rate heavier women as less desirable for romantic relationships. Based on this evidence, it is possible that facial adiposity could influence motivation to view opposite-sex faces. If trimmer, healthier mates are preferred then facial adiposity scores may negatively impact wanting behavior (i.e. key-pressing).

2.3.1 Method: Face Ratings

The 120 adult faces used in Experiment 1 were assessed on the following aspects of facial appearance:

Distance from averageness was calculated using an adaptation of the methods described in Baudouin and Tiberghien (2004). All stimulus faces were sized to 400 by 300 pixels and aligned based on interpupillary distance. Facial structure for each of the 120 faces was mapped along 38 points (see Figure 2.8) using Psychomorph (Tiddeman, Burt, & Perrett, 2001). The template map this program creates gives the x- and y-coordinates (relative to the top left corner of the image) for each point, which can be viewed as the point's position in a Euclidean two-dimensional orthonormal space. The 38 points were reduced to 36 values by calculating upper and lower lip size (i.e. point 35-36 and point 37-38) to control for any variation in mouth opening. The average face shape (i.e. the average x, y coordinates of each point) was computed for the 60 female faces and, separately, the 60 male faces. Using the x- and y-coordinates for these 36 average values, the distance of each point from the average for the individual faces in the stimulus set was computed using the Pythagorean theorem ($a^2 + b^2 = c^2$). The difference between the face x- and y-coordinate and the average x- and y-coordinate were calculated (a and b, respectively). These difference values were then squared (a^2 and b^2) and the total distance from average for each point was computed by solving for c. The overall distance from average was computed by taking the average deviation across all points. As such, higher scores represent greater deviation from average face shape (sex-specific), while lower scores are indicative of a more average face shape. Among the female faces, averageness scores ranged from 10.3 to 35.7 (mean = 19.1, *SD* = 4.98). Among the male faces, scores ranged from 13.1 to 42.9 (mean = 22.1, *SD* = 6.96).

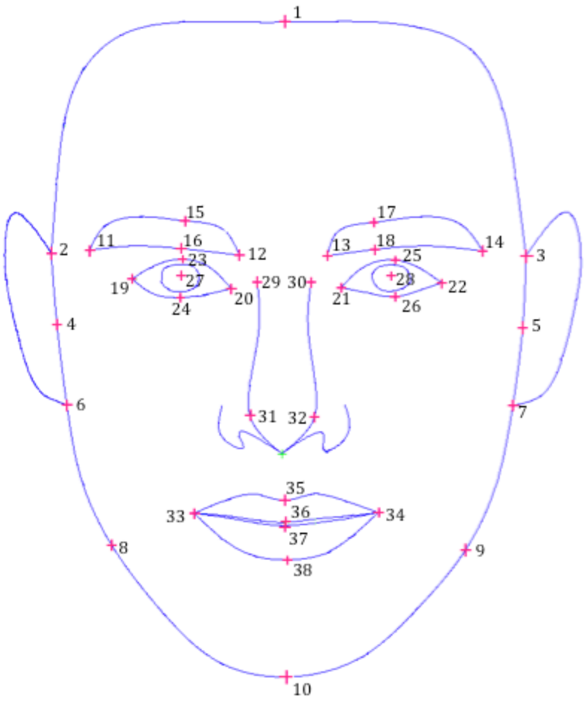

Figure 2.8 A map of the 36 delineation points used in facial averageness calculations.

Sexual dimorphism scores were calculated from masculinity/femininity ratings. Masculinity/Femininity was assessed using a 7-point Likert scale where 1 = very feminine, 4 = androgynous and 7 = very masculine). Because high sexual dimorphism is represented by low scores for female faces but high scores for male faces, the ratings were reverse coded for female faces. The resultant scores range from 1-7, where 1 represents low sexual dimorphism and 7 represents high-sexual dimorphism. Two hundred raters (126 female) completed this task online via the Perception Lab webpage. The average age of these raters was 26.7 years (*SD* = 11.6). High levels of inter-rater reliability were observed for the stimulus set (α = .979). Sexual dimorphism scores ranged from 4.4 – 6.6 for female faces, with high levels of inter-rater reliability for this subset (α = .962). Similarly, for male faces dimorphism scores ranged and from 4.5 – 6.4 and high levels of inter-rater reliability were observed (α = .973).

Apparent health was assessed using a 7-point Likert scale where 1 = very unhealthy and 7 = very healthy. Sixty-nine raters (43 female; mean age = 30.5 years, *SD* = 12.6) completed this task online. High inter-rater reliability scores were seen for the stimulus set (α = .978). Apparent health scores ranged from 2.6 – 5.8 for the female faces (*M* = 4.2, *SD* = 0.8), with high inter-rater reliability within this subset of the stimuli (α = .957). Health scores ranged from 2.4 – 5.7 for the male faces (*M* = 4.1, *SD* = 0.7). Again, high levels of inter-rater reliability were seen for this subset (α = .962).

Facial adiposity was assessed using a 7-point Likert scale where 1 = very underweight and 7 = very overweight. Sixty-nine raters (44 female; mean age = 24.5 years, *SD* = 9.8) completed this task online. A high level of inter-rater reliability was observed for the complete face set (α = .926). Female faces ranged in adiposity ratings from 2.3 – 5.4 with high inter-rater reliability (α = .912). Male faces ranged in adiposity ratings from 2.9 – 6.0 with an acceptable level of inter-rater reliability (α = .877).

Facial attractiveness ratings were obtained from independent raters as detailed in Section 2.2.1.2.

2.3.2 Statistical Analyses

A meditational path analysis was constructed to assess the direct and indirect effects of each of the appearance factors on key-pressing behavior. The analysis was done per face (N_{faces}=120). The average score for each of the 5 appearance factors (distance from average, sexual dimorphism, facial adiposity, apparent health, and facial attractiveness) was calculated for each face. Using the data collected in Study 1, the average number of key-presses exerted by opposite-sex participants was calculated per face (i.e. female participants for male faces and male participants for female faces, N_{female}= 23, N_{male}= 26). Path analyses were conducted using AMOS software (SPSS), which tests the fit of a hypothesized model to the observed variancecovariance matrix using maximum-likelihood estimation. Because studies have shown that sexual dimorphism may have a differential impact on the attractiveness of male and female faces, separate analyses was conducted for men and women when analysing the data. Distance from averageness, sexual dimorphism, apparent health and adiposity were entered as exogenous variables, predicting both the face attractiveness ratings and opposite-sex key-pressing behavior[9]. Attractiveness ratings were also included as a predictive variable for key-pressing. Covariance was calculated between all exogenous variables. An identical model was used to further explore the observed phenomenon of high incentive salience of same-sex faces among women. Because previous studies have indicated that same-sex faces do not hold incentive salience among men, these data are omitted from the analysis presented here[10].

2.3.3 Results[11]

2.3.3.1. Men Looking at Opposite-Sex Faces

Path analysis revealed a positive relationship between facial attractiveness and both apparent health ($\beta = .42$, $p < .001$) and sexual dimorphism ($\beta = .54$, $p < .001$). As predicted, facial adiposity was negatively related to facial attractiveness ($\beta = -.20$, $p < .001$), as was distance from facial averageness although this relationship failed to reach significance ($\beta = -.08$, $p = .085$). Of these factors, only attractiveness and apparent health impacted motivation (as measured by key-pressing). Attractiveness was the strongest predictor of motivation ($\beta = .46$, $p < .001$), while the link between apparent health and motivation tended to be positive ($\beta = .30$, $p = .081$), but

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[9] Note: this results in a saturated model; therefore fit statistics cannot be reported. When using path analysis, model saturation is not a problem as model saturation is only a concern for structural equation models, which attempt to fit the data to latent constructs rather than measured/observed variables.

[10] Although these data are not reported for the purpose of this thesis, the analysis was run. Results indicate that there were no significant predictors of key-pressing for men looking at same-sex faces beyond attractiveness.

[11] The results reported here utilize path analysis, which is a more sophisticated form of linear regression that allows for multiple dependent variables. An additional feature of path analysis is that it allows for both direct and indirect effects between predictive variables and the dependent variables to be assessed. It is worth noting that when more traditional statistical methods typically utilized in evolutionary psychology such as: partial correlations, ANCOVA, and linear regression are employed the pattern of results reported here (i.e. direct effect of apparent health on key-pressing) is consistently observed.

was not quite significant. Sexual dimorphism, facial adiposity and facial averageness did not significantly affect key-pressing. The path model can be seen in Figure 2.9.

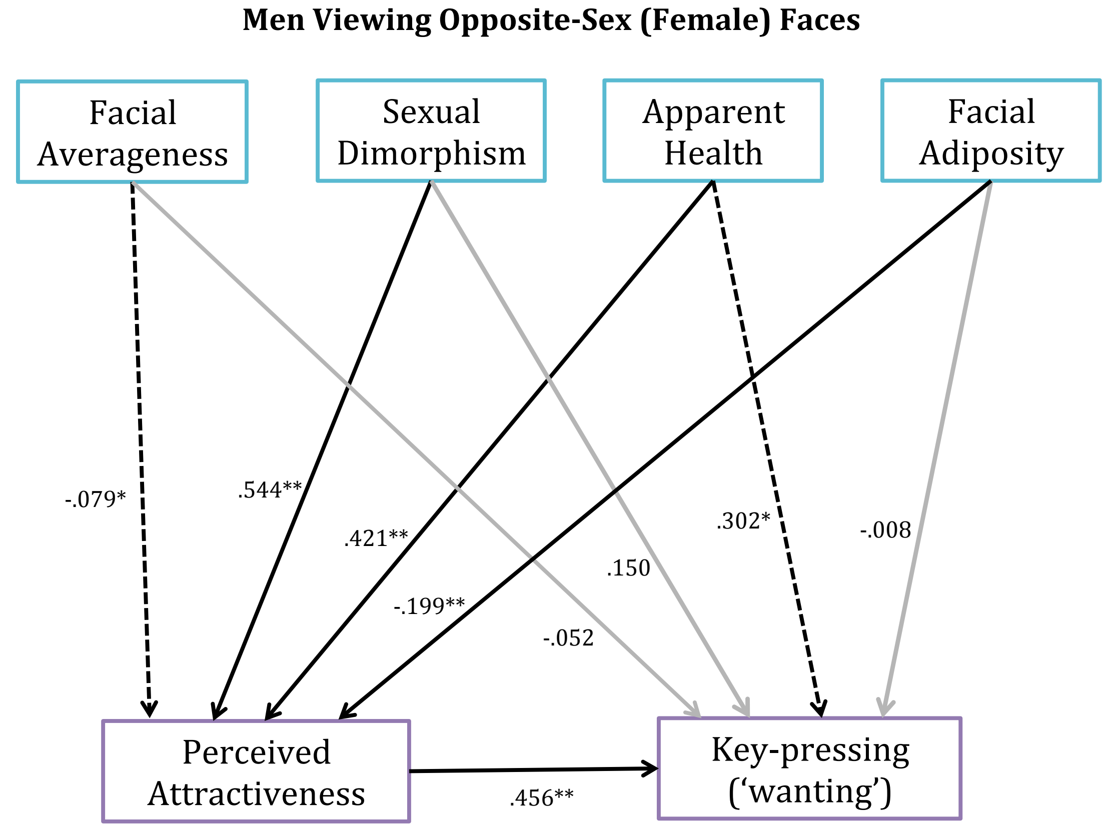

Figure 2.9 The path model and regression weights utilized to test the role of additional factors of facial appearance on liking and wanting for men viewing opposite-sex faces. Black bars represent significant direct effects, dashed bars represent effects that approached significance (p < .1), and grey bars represent non-significant effects.

It is possible that although some of the exogenous variables described above do not have a direct effect on motivation they may indirectly impact key-pressing through their relationship with perceived attractiveness. The impact of indirect effects of the exogenous variables on key-pressing was classified based on previously published criterion (Shrout & Bolger, 2002). In addition to the direct effect of apparent health on key-pressing, health also had a small indirect effect (β = .19). Sexual dimorphism had a moderate indirect effect on key-pressing (β = .25). Neither adiposity, nor facial averageness indirectly affected key-pressing. The observed direct and indirect effects are summarized in Table 2.1.

Table 2.1 Standardized regression weights of the direct and indirect effects of appearance factors on assessments of facial attractiveness ratings and motivation for heterosexual beauty among men.

	Direct Effects		**Indirect Effects**
Exogenous Variables	Attractiveness Rating (liking)	Key-pressing (wanting)	Key-pressing (wanting)
Facial Averageness	-.079*	-.052	-.036
Sexual Dimorphism	.544**	.150	.248^{++}
Apparent Health	.421**	.302*	.192^{+}
Facial Adiposity	-.199**	-.008	-.091
Endogenous Variables			
Attractiveness Rating (liking)	---	.456**	---

* .05 < p < .1, ** p<.05

$^{+}$ small effect, $^{++}$moderate effect, $^{+++}$large effect

2.3.3.2 Women Looking at Opposite-Sex Faces

Path analysis revealed a positive relationship between facial attractiveness and apparent health (β = .53, *p* < .001), as well as sexual dimorphism (β = .40, *p* < .001). Facial adiposity was negatively related to facial attractiveness (β = -.17, *p* = .006). There was no effect of facial averageness on perceived attractiveness. Again, facial attractiveness was a significant predictor of key-pressing (β = .83, *p* < .001). Interestingly, both apparent health (β = .26, *p* = .004) and sexual dimorphism (β = -.19, *p* = .022) independently impacted on motivation, although the directionality of these effects was different. Apparent health positively impacted key-pressing, suggesting increased motivation to view healthy individuals, while sexual dimorphism negatively impacted on key-pressing suggesting decreased motivation to view masculine men (or increased motivation to view feminine men) over and above the effect on key-pressing via the impact of sexual dimorphism on perceived attractiveness. The path model, including standardized regression weights, can be seen in Figure 2.10.

Women Viewing Opposite-Sex (Male) Faces

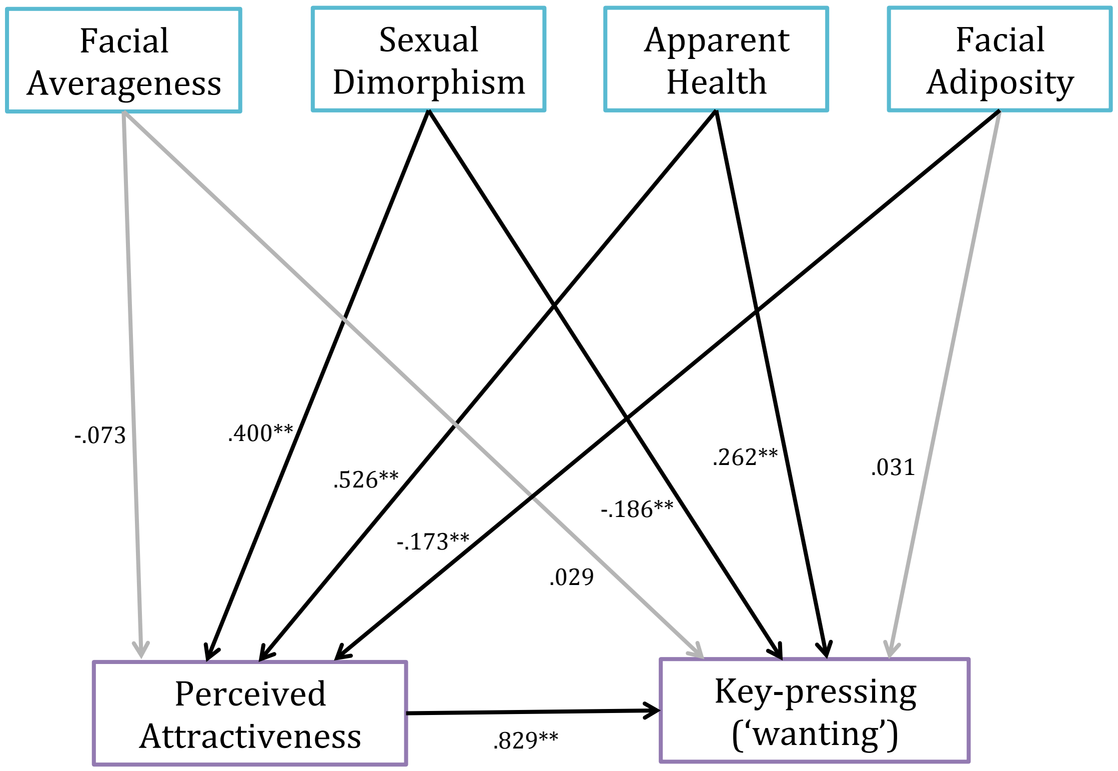

Figure 2.10 The path model and regression weights utilized to test the role of additional factors of facial appearance on liking and wanting for women viewing opposite-sex faces. Black bars represent significant direct effects, dashed bars represent effects that approached significance (p < .1), and grey bars represent non-significant effects.

Again, it is possible that although some of the exogenous variables described above do not have a direct effect on motivation they may indirectly impact key-pressing through their relationship with perceived attractiveness. Facial adiposity had a small, negative, indirect effect (β = -.14); while sexual dimorphism had a moderate indirect effect on key-pressing (β = .33) and apparent health had a large indirect effect on key-pressing (β = .44). Facial averageness did not indirectly affect key-pressing. The observed direct and indirect effects are summarized in Table 2.2.

Table 2.2 Standardized regression weights of the direct and indirect effects of appearance factors on assessments of facial attractiveness ratings and motivation for heterosexual beauty among women.

	Direct Effects		Indirect Effects
Exogenous Variables	Attractiveness Rating (liking)	Key-pressing (wanting)	Key-pressing (wanting)
Facial Averageness	-.073	-.029	-.061
Sexual Dimorphism	.400**	-.186**	.332^{++}
Apparent Health	.526**	.262**	.436^{+++}
Facial Adiposity	-.173**	.031	-.143^{+}
Endogenous Variables			
Attractiveness Rating (liking)	---	.829**	---

* .05 < p < .1, ** p<.05

$^{+}$ small effect, $^{++}$moderate effect, $^{+++}$large effect

2.3.3.3 Women Looking at Same-Sex Faces

Path analysis revealed a positive relationship between facial attractiveness and apparent health (β = .42, *p* < .001), as well as sexual dimorphism (β = .54, *p* < .001). Facial adiposity was again negatively related to facial attractiveness (β = -.20, *p* < .001), as was deviation from facial averageness although this relationship failed to reach significance (β = -.08, *p* = .085). As documented in the literature (Levy et al., 2008), as well as previously in this chapter, the attractiveness of same-sex face influenced women's key-pressing behavior (β = .34, *p* = .042). Again, health was also shown to have an independent effect on key-pressing (β = .56, *p* < .001). Notably, this effect was stronger than that of attractiveness. Facial adiposity, sexual dimorphism, and deviation from facial averageness did not independently impact key-pressing (all p > .48). The path model, including standardized regression weights, can be seen in Figure 2.11.

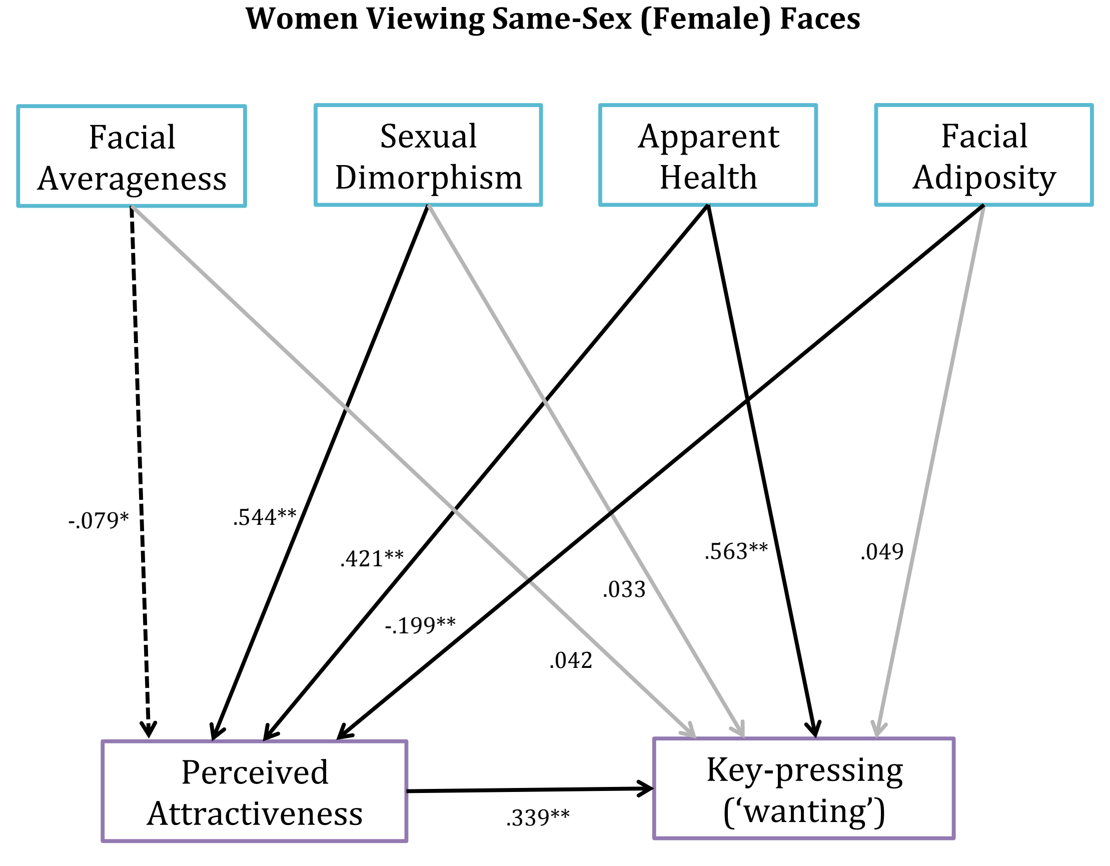

Figure 2.11 *The path model and regression weights utilized to test the role of additional factors of facial appearance on liking and wanting for women viewing same-sex faces. Black bars represent significant direct effects, dashed bars represent effects that approached significance (p < .1), and grey bars represent non-significant effects.*

Again, it is possible that although some of the exogenous variables described above do not have a direct effect on motivation they may indirectly impact key-pressing through their relationship with perceived attractiveness. Sexual dimorphism (β = .18) and health (β = .14) both had a small indirect effect on key-pressing. Neither adiposity nor deviation from facial averageness had indirect effects on key-pressing. The observed direct and indirect effects are summarized in Table 2.3.

Table 2.3 *Standardized regression weights of the direct and indirect effects of appearance factors on assessments of facial attractiveness ratings and motivation for same-sex beauty among women.*

	Direct Effects		**Indirect Effects**
Exogenous Variables	Attractiveness Rating (liking)	Key-pressing (wanting)	Key-pressing (wanting)
Facial Averageness	-.079*	.042	-.027
Sexual Dimorphism	.544**	.033	.184^{+}
Apparent Health	.421**	.563**	.143^{+}
Facial Adiposity	-.199**	.049	-.068
Endogenous Variables			
Attractiveness Rating (liking)	---	.339**	---

* .05 < p < .1, ** p<.05

$^{+}$ small effect, $^{++}$moderate effect, $^{+++}$large effect

2.3.4 Discussion

In this study, path analysis was used to determine the relationship between a number of factors known to influence perceptions of facial attractiveness and motivated behavior. In accordance with previous observations in the literature, our analyses indicate that sexual dimorphism, apparent health, deviation from facial averageness, and facial adiposity all influence the perceived attractiveness of faces. For both sexes, apparent health and sexual dimorphism were positively related to perceived attractiveness while facial adiposity and deviation from facial averageness were negatively linked to perceived attractiveness. In each of the analyses presented here, apparent health was shown to directly effect key-pressing (although in the case of men viewing opposite-sex faces, this effect failed to reach significance). The directionality of this relationship was positive in each instance, suggesting that faces which appear healthier hold greater incentive salience than those that appear unhealthy. This effect is over and above the effect apparent health may have through its impact on perceived attractiveness. Interestingly among women viewing same-sex faces, apparent health was a stronger predictor of key-pressing than perceived attractiveness. If same-sex faces hold incentive salience among women due to a "greater bisexual interest" as previously suggested (Levy et al., 2008), we might expect that attractiveness would be the strongest predictor of women's motivation to view other women. This finding suggests that the underlying causes of women's motivation to view same-sex individuals may be more complex than previously thought. The incentive salience of same-sex faces among women is further explored in Chapters 4 and 5.

In the case of male facial attractiveness, some previous studies have indicated that a high degree of sexual dimorphism may be considered attractive (e.g. Grammer & Thornhill, 1994), while others have found that low levels of sexual dimorphism (i.e. a more feminine appearance) are preferred (e.g. Perrett et al., 1998). Here I show that a more masculine appearance in male faces is linked to higher perceived attractiveness. Interestingly, the directionality of this relationship was reversed for sexual dimorphism and key-pressing. Women were more likely to key-press for faces with low levels of sexual dimorphism despite these faces being perceived as less attractive. When choosing a mate, women must consider the trade-offs between the negative aspects of masculinity, such as low paternal investment and negative personality traits (Gangestad & Simpson, 2000; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Mazur & Booth, 1998), and the positive aspects of masculinity, such as high immunocompetence and 'good genes' (Folstad & Karter, 1992; Rantala et al., 2013; Rhodes et al., 2003). It may be the case that, in spite of being considered less attractive, men with low sexual dimorphism appear friendlier and these prosocial aspects of their appearance drive women's key-pressing behavior. Motivation to seek out a less sexually dimorphic mate could provide a woman with more direct benefits (i.e. increased paternal investment, emotional support, etc.) although at the cost of reduced indirect benefits (i.e. less healthy offspring). In addition to its direct effect on women's motivation to view opposite-sex individuals, sexual dimorphism had positive indirect effects on key-pressing to view opposite-sex faces for men and women, as well as key-pressing behavior among women viewing same-sex faces. Further studies isolating this individual aspect of facial appearance may provide more insight into the role of sexual dimorphism on 'wanting' and liking responses.

In this study, I present novel findings regarding the influence of apparent health on motivation. Cues to health may hold incentive salience in that it would be beneficial to be drawn to healthy potential mates, while avoiding sick looking individuals who could have direct (i.e. transmission of infectious diseases) and/or indirect (i.e. produce less healthy offspring) negative impacts on health. As discussed in Section 1.1.4, the literature to date is equivocal with regard to the link between apparent health and actual health (Henderson & Anglin, 2003; Kalick et al., 1998; but see Singh & Young, 1995; Singh, 1993) . However, in light of the costs associated with social contact with unhealthy individuals, it may be that we have developed behaviors to avoid potential sources of contagions. This is known as the behavioral immune system – a collection of psychological mechanisms that function to detect cues of pathogens and trigger the relevant cognitive responses and avoidance behaviors (Schaller & Park, 2011; Schaller & Duncan, 2007). The costs associated with misidentifying an unhealthy individual as healthy far outstrip the costs of the reverse situation (i.e. identifying a healthy individual as unhealthy), and so apparent health may influence behavior regardless of the connection between apparent and actual health – the behavioral immune system sometimes misidentifies harmless physical features (such as an unhealthy facial appearance) as implicative of infectious disease or a physical threat.

According to the Compensatory Behavioral Prophylaxis Hypothesis (Fessler, Eng, & Navarrete, 2005; Fessler, 2001), humans avoid or remove cues of potential contagion through prophylactic behavior. This prophylactic behavior should be enhanced during periods of increased vulnerability such as pregnancy and the luteal phase of the menstrual cycle in women (characterized by high progesterone, an immunosuppressant), and during periods of immune deficiency (i.e. when we are ill) in both men and women. Consistent with this theory, Fleishman and Fessler (2011) found that progesterone levels in women correlate positively with self-reported behaviors, emotions and thoughts consistent with enhanced prophylaxis. Similarly, Jones et al. (2005) found that when women are particularly susceptible to infection (i.e. during periods of high progesterone, such as the luteal phase of the cycle or pregnancy) they demonstrate increased preferences for facial cues associated with health. This behavior may act in an adaptive fashion by impacting avoidance behavior of individuals with higher risk of contagion to compensate for the immunosuppressive effects of progesterone.

The observed aversion to unhealthy faces in the present study is congruent with the current literature on social avoidance behavior in response to perceived threats. Aversive responses or avoidance of conspecifics that appear unhealthy are evident across the animal kingdom, from lobsters to chimpanzees (Behringer, Butler, & Shields, 2006; Goodall, 1986; Kiesecker, Skelly, Beard, & Preisser, 1999). In humans, individuals who feel vulnerable to disease tend to have fewer social relationships with disabled individuals than those who do not feel vulnerable (Park, Faulkner, & Schaller, 2003), and after being primed with disease-relevant images, people rate themselves as less extroverted and less open to new experiences (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010). Similarly, disgust responses are triggered in humans when shown images of skin lesions, runny noses, and other symptoms of pathogenic infection (Curtis, Aunger, & Rabie, 2004). Viewing unattractive faces alone results in greater disgust responses (as measured by facial electromyography) than for attractive faces (Proverbio & Langlois, 2011), possibly due to the link between attractiveness and apparent health.

This study is the first to demonstrate that facial characteristics other than attractiveness or beauty may hold incentive salience. The reward value of a healthy appearance, or aversion to illness, needs to be studied further to determine the neural correlates of this health perception.

2.4 General Discussion

There were three main aims of the present set of studies. First, we endeavoured to set up the relatively novel key-press task to measure motivation and replicate previously observed gender differences in the incentive salience of beauty. In Experiment 1, we demonstrated that opposite-sex beauty holds high incentive salience among men while both same- and opposite-sex beauty holds moderate incentive salience among women. These findings are in accordance with previous work using male participants (Aharon et al., 2001; Dai, Brendl, & Ariely, 2010; Elman et al., 2005) and work using both male and female participants (Levy et al., 2008). Next, I aimed to extend the current knowledge of the incentive salience of beauty by looking at a wider range of attractiveness, rather than using categorical high- and low-attractiveness groups. In the follow up analysis of Experiment 1, I demonstrated that the relationship between attractiveness and incentive salience is linear; the more attractive a face, the more effort participants will exert to prolong viewing time for the face. For women, this pattern of results was apparent for both same- and opposite-sex faces. Beauty, regardless of the sex of the face, holds incentive salience among women. For men, face sex had a significant influence on motivation. Opposite-sex beauty holds high incentive salience, with men working extremely hard to prolong viewing duration of attractive female faces and exerting relatively little effort for average or unattractive female faces. For same-sex faces, men did not show much motivation to prolong viewing. Rather, they worked to remove unattractive faces from the screen, suggesting that men may be averse to viewing same-sex individuals – particularly unattractive same-sex individuals.

The final goal of this work was to explore beyond beauty to determine if other factors known to influence perceptions of facial attractiveness in potential mates can act to influence motivated behavior independently of their impact on attractiveness. To this end, I explored the impact of facial adiposity, apparent health, sexual dimorphism, and facial averageness on motivation to view opposite-sex faces. Of these factors, apparent health was the only aspect of appearance to influence motivation directly. Health may drive motivated behavior above and beyond its impact on attractiveness due to the evolutionary advantages of socially bonding with healthy individuals while avoiding sick individuals who could compromise one's own health. This study is the first to explore the incentive salience of facial appearance outside of attractiveness. Across cultures, there is wide agreement as to which faces are attractive

(Langlois et al., 2000), but we still do not fully understand what beauty *is*. By exploring the link between motivation and factors known to influence perceptions of facial attractiveness we may gain a better understanding of *how* and *why* beauty holds incentive salience. Does it lead us to select better quality mates? The key-press motivational task may yield interesting new findings when employed in studies of mate preferences versus mate choice. Similarly, use of this relatively inexpensive behavioral paradigm could help guide future neuroimaging studies exploring the reward value of beauty and neural responses to cues of health.

Chapter 3 Gender Differences in the Incentive Salience of Infants

The following chapter is based on work published in the Quarterly Journal of Experimental Psychology. The reference for this work is as follows:

Hahn, A.C., Xiao, D-K., Sprengelmeyer, R. & Perrett, D.I. (2013). Gender differences in the incentive salience of adult and infant faces. *Quarterly Journal of Experimental Psychology, 66*(1), 200-208*.*

Abstract

Facial appearance can motivate behavior and elicit activation of brain circuits putatively involved in reward. Gender differences have been observed for motivation to view beauty in adult faces—heterosexual women are motivated by beauty in general, while heterosexual men are motivated to view opposite-sex beauty alone. Although gender differences have been observed in sensitivity to infant cuteness, infant faces appear to hold equal incentive salience among men and women. In the present study, we investigated the incentive salience of attractiveness and cuteness in adult and infant faces, respectively. We predicted that, given alternative viewing options, gender differences would emerge for motivation to view infant faces. Heterosexual participants completed a “pay-per-view” key-press task, which allowed them to control stimulus duration. Gender differences were found such that infants held greater incentive salience among women, although both sexes differentiated infant faces based on cuteness. Among adult faces, men exerted more effort than women to view opposite-sex faces. These findings suggest that, contrary to previous reports, gender differences *do* exist in the incentive salience of infant faces as well as opposite-sex faces.

3.1 Introduction

In the much the same way that beauty in adult faces captures attention, infant facial appearance can also draw interest (Brosch, Sander, & Scherer, 2007). Adults have been shown to smile when presented with an image of an infant (Hildebrandt, 1978), suggesting infants may elicit positive affective responses. Darwin (1872) explained that this natural inclination towards infants might have evolved to increase individual fitness (by increasing reproductive success through increased offspring survival rates. Indeed, non-human studies have indicated that maternal responsiveness to infants impacts long-term cognitive development (Liu, Diorio, Day, Francis, & Meaney, 2000) and maternal behavior in adulthood (Champagne et al., 2006). Human infants are relatively helpless and dependent on parental care for survival. As such, there are strong evolutionary reasons why they would benefit from having high incentive salience.

Brain responses to infant faces have been observed in reward-related areas (specifically, the nucleus accumbens) in nulliparous women (Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009). When comparing neural responses of humans to the face of their own infant and unfamiliar infants, a number of studies have demonstrated stronger activation in reward-related brain regions such as the striatum and prefrontal cortex for own-infant as compared to unfamiliar infants (Nitschke et al., 2004; Ranote et al., 2004; Strathearn, Li, Fonagy, & Montague, 2008; Swain, Lorberbaum, Kose, & Strathearn, 2007). While responses may be strongest to own offspring, images of unfamiliar infants are also capable of eliciting neural responses in equivalent brain regions (specifically the orbitofrontal cortex), regardless of participant gender or parental status (Kringelbach et al., 2008). Using MEG techniques, Kringelbach et al. (2008) found an early (130ms) surge of activity in the orbitofrontal cortex in response to infant faces that was not observed for adult faces.

Cuteness in infant faces has been shown to be positively correlated with a number of behaviors such as: parental orientation towards the infant (Langlois, Ritter, Casey, & Sawin, 1995), the elicitation of caregiving responses (Alley, 1983), positivity of parent-infant interactions (Glocker et al., 2009a), and likelihood of being adopted (especially among women; Volk & Quinsey, 2002). Experimental work has suggested that infant facial morphology (i.e. the baby-schema, as described in Section 1.2) impacts perceptions of cuteness and can also affect resultant behavior. Glocker and colleagues (2009) experimentally manipulated infant faces to have high and low baby-schema. Using these faces, they tested perceptions of infant cuteness and motivation to care for the infants in a set of undergraduate students. They found that both men and women rated infant faces as cuter the more they conformed to the baby-schema. Baby-schema also influenced motivation to care for the infant such that low baby-schema resulted in reduced motivation to care for the infant in men and women. High baby-schema increased women's motivation to care for the infant (above the unmanipulated images), but did not impact men's motivation to care for the infant (although men did report greater motivation for the unmanipulated images as compared to the low baby-schema stimuli).

Additional gender differences have been shown in response to infant faces. Women tend to smile more at cute infants than men do (Hildebrandt, 1978), and women rate infants as more sociable and easier to care for than men do (Karraker & Stern, 1990). Using computer graphics to subtly manipulate facial appearance, a number of studies have shown gender differences in the ability to detect baby-schema (or cuteness). Sprengelmeyer et al. (Sprengelmeyer et al., 2009) used a 2 alternative forced choice paradigm in which they paired infant faces that had been manipulated in varying degrees of cuteness (using a shape only transform) to give difficulty levels of 25%, 50%, 75% and 100%. They found that pre-menopausal women were better at discriminating between the cute and less cute infant faces at every level of difficulty than were post-menopausal women or men (both young and old), suggesting there may be an underlying hormonal mechanism that is responsible for gender differences in cuteness sensitivity. Similarly, Lobmaier and colleagues found that women exhibit greater sensitivity to infant cuteness than men do, but both sexes are equally able to discern cues of infant age and emotional expression (Lobmaier et al., 2010). These gender differences in cuteness sensitivity may be due to underlying gender differences in infant face processing. EEG studies have shown that both men and women show an increased N1 response to infant faces over adult faces, but the baby-specific N1 response is much larger in women than men (across the left hemisphere). Women also exhibit dissociable anterior N2 responses to infants and children. LORETA analyses indicate that the limbic and orbitofrontal sources of this N2 response are much larger in women than men (Proverbio, Riva, Zani, & Martin, 2011). Women also exhibit a larger P1 response in than men to infant faces (Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006). These findings indicate that gender differences exist in the early visual processing of infant faces[12].

The importance of infant cuteness in adult-infant interactions suggests that infant facial appearance may hold incentive salience and thus motivate behavior. Indeed, cuter infants draw visual attention and tend to be looked at for longer periods of time than less cute infants (Hildebrandt, 1978). With apparent gender differences in terms of ability to discriminate infant cuteness (Lobmaier et al., 2010; Sprengelmeyer et al., 2009), it is plausible that cuteness may hold different incentive salience among men and women. However behavioral work, to date, has not revealed any such gender differences when considering normal healthy infants (Lewis, Hahn, Perrett, & Sprengelmeyer, in revision; Parsons, Young, Kumari, Stein, & Kringelbach, 2011a); however, these studies have utilized natural infant faces, which vary widely in appearance (i.e. age and expression, Lewis et al., *in revision*; and cuteness, Lewis et al., *in revision* & Parsons et al., 2011a) while discrimination studies employ image manipulation techniques to alter facial appearance much more subtly.

Notably, studies utilizing infant stimuli with the presence of facial deformities have yielded conflicting results with respect to gender differences. Yamamoto et al. showed men and women normal infants and infants with a range of facial abnormalities (including fetal alcohol syndrome, cleft palate, and strabismus). They found that women gave higher attractiveness ratings (i.e. liking responses) to normal infants than men did, while no gender differences were

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[12] Notably, Platek et al. (Platek, Keenan, & Mohamed, 2005) failed to show gender differences in general infant face processing using fMRI (specifically, fusiform gyrus activation) but did observe that women show greater responses in face processing areas than men do when self-resemblance is not modelled in infant faces whereas men showed greater responses than women to infants that resembled them.

apparent in the ratings of deformed infants. Gender differences were not observed for motivation to view normal infants, while women showed significantly greater aversive responses (i.e. negative key-presses) to deformed babies than did men (Yamamoto, Ariely, Chi, Langleben, & Elman, 2009). Parsons et al. repeated this study using only infant faces. Infant faces showing deformation were restricted to cleft palate only. Here, the authors found that women rated infant faces as more attractive than did men (regardless of the presence of a facial abnormality), but men and women showed equal patterns of motivation to view infants (both normal and deformed). This pattern of results extends cross-species as revealed by liking and wanting responses towards normal and deformed puppies (Parsons et al., 2011b).

While behavioral work utilizing natural infant images has yielded equivocal evidence with regard to the presence or absence of gender differences in the motivational salience of infant faces, the impact of subtle changes to infant facial morphology has yet to be explored. Perceptual studies utilizing subtle manipulation techniques have provided the bulk of the evidence for gender differences in cuteness sensitivity. As such, subtle changes to the cuteness of infant faces may reveal gender differences in motivated behavior, particularly when such faces are presented in the context of additional viewing options, such as attractive adult faces. Parsons et al. (2011a) presented infant and adult faces in the same context, but used adult faces of average attractiveness and observers showed low motivation to view any stimuli (as indexed by little change to the viewing duration). More attractive faces, or a higher range of facial attractiveness, could produce a different profile of motivated behavior across face categories.

In this study, the incentive salience of infant cuteness was explored in the context of adult beauty. Computer-graphic techniques were used to transform faces to appear more or less attractive (adult faces) or cute (infant faces). By presenting infant faces together with adult stimuli (same- and opposite-sex), we aimed to explore the relative incentive salience of different face classes. With the use of highly attractive adult faces, we anticipated that gender differences in motivation to view infant faces would emerge such that men would work less than women to view infant faces. Sensitivity to small variations in infant cuteness is modulated by hormone status (Sprengelmeyer et al., 2009). As women traditionally fill the role of primary care giver, their increased ability to detect these small changes may have evolved in order to help develop and maintain the mother-infant bond, which would act to increase infant survival rates. In light of this, we also anticipated that women would differentiate more than men (in terms of work/effort) between the cute and less-cute infant faces.

3.2 Pilot Study: Manipulating Attractiveness

In order to manipulate attractiveness or cuteness subtly within a given face identity, we first needed to develop prototypical "high-attractive/cute" and "low-attractive/cute" faces. Using these prototypes, it was possible to manipulate the appearance of individual face identities in order to make them appear more attractive (adult faces) or cute (infant faces). Lastly, to ensure that these transformed faces actually were perceived as cuter or more attractive, this pilot study was conducted to validate the transformation.

3.2.1 Prototype Creation

Adult Prototypes. A sub-set of the images described in section 2.2.1.1 was used for prototype creation. From that set, 92 adult faces (46 female, 46 male) with neutral facial expressions were selected. These images were full-face shots of Caucasian individuals, estimated age 18-35, with no visible body art/jewellery. Stimuli were masked with a black background to remove cues from hairstyles and clothing. Because attractiveness ratings can be subject to contextual effects, a new set of independent ratings of attractiveness were obtained whereby only these 92 faces were presented to raters. These attractiveness ratings were used in order to develop high- and low- attractiveness prototypes. Each face was rated for attractiveness on a 7-point Likert scale (where 1=Very Unattractive, 7=Very Attractive). Presentation order was randomized across participants.

Ratings were obtained from 70 independent evaluators (36 female) that ranged in age from 18 to 33 years (*mean*= 22.19, *SD* = 3.48). Overall, there was a high level of inter-rater agreement between individual evaluators (Cronbach's $\alpha = .97$). A one-way ANOVA of the average rating for each face revealed that female faces tended to be rated higher than male faces, ($F(1,90) = 3.81$, $p = .054$). Men and women's ratings of attractiveness correlated highly for both the female faces (Spearman's $\rho_{46} = .95$) and male faces (Spearman's $\rho_{46} = .94$), suggesting that men and women had similar opinions regarding adult attractiveness.

Based on these ratings, the top and bottom 10 faces for each sex were selected to create high- and low-attractiveness prototypes. Faces were mapped using established techniques for facial manipulation (Rowland & Perrett, 1995; Tiddeman et al., 2001). The shape of each face was delineated using 188 manually placed facial demarcation points. Composite images (i.e. average face shape and color across all 10 images) were created using Psychomorph (Burt & Perrett, 1995; Tiddeman et al., 2001). These composites contained the average face shape that was considered attractive and unattractive.

Infant Prototypes. Prototypical high-cute shape and low-cute shape infant faces were created in a previous study (Sprengelmeyer et al., 2009). It is possible that men and women attend differently to the neotenous and expressive characteristics of infant faces (Lobmaier et al., 2010). Prior research possibly conflated both face shape associated with neotenony (e.g. large forehead) and infant face expression (e.g. smile). Since smiling may confound the relationship between attractiveness and motivation, we sought to keep expression constant. The mouth shape was averaged across all four previously created prototypes (high- and low-cute male and female). This average mouth was then remapped onto each of the four infant prototypes. This process ensured that while vertical mouth position, relative to chin, within the facial configuration may change during shape transformation, the curvature of the mouth and smile would remain constant.

3.2.2 Image Manipulation

Adult Stimuli. Ten textured composites (base faces) were created of adult male and female faces (Tiddeman et al., 2001). Composites were used rather than originals in order to create new/unique face identities for use in the present study. Each base face was comprised of two individual faces from the original set of neutral adult faces (excluding those used to create the attractiveness prototypes). The prototype faces described above were used to alter the shape of each base face. The transformation process involved calculating the difference in face shape between the low-attractiveness and high-attractiveness prototypes and applying a proportion of that difference to a base face (see Figure 3.1a). Each base face (10 male, 10 female) was transformed by -50% in attractiveness (creating the low-attractive stimuli) and +50% in attractiveness (creating the high-attractive stimuli), resulting in 40 total adult stimuli.

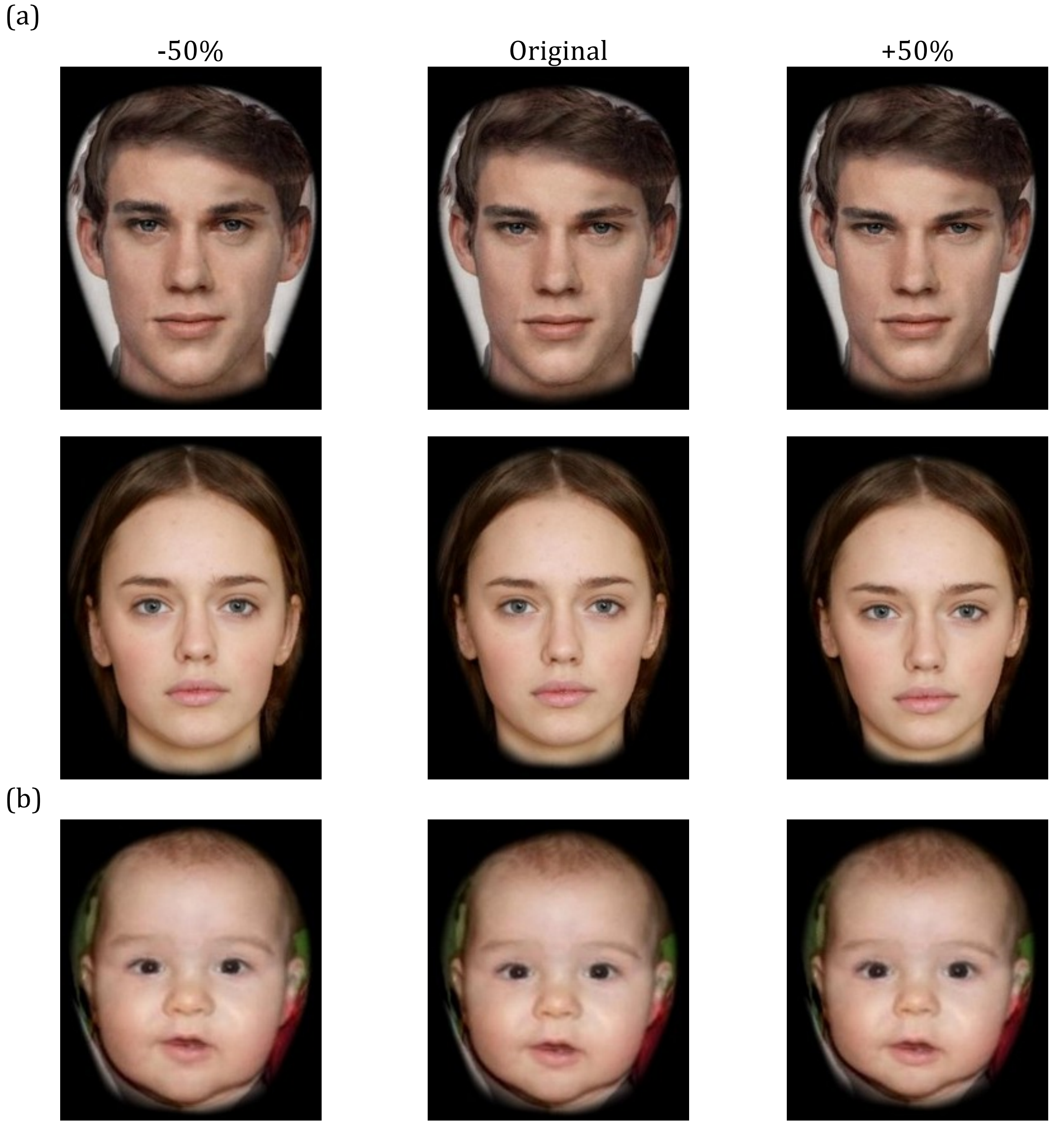

Figure 3.1 (a) Example base faces (middle) for adult male (top) and adult female (bottom) stimuli shape transformed by -50% (left) and +50% (right) in attractiveness. (b) Example base infant face (middle) shape transformed by -50% (left) and +50% (right) in cuteness. The full set of stimuli used can be seen in Appendix A.

Infant Stimuli. Ten infant base faces (5 male, 5 female) were created in the same fashion as the adult stimuli. Two-face composites were made from a set of 56 original faces (28 male, 28 female; 6-12 months of age with varying facial expressions) compiled from internet sources (Lewis et al., under review). Only those infants with neutral facial expressions (either open or closed mouth) were used to create the base faces, which were then transformed +/- 50% in cuteness (see Figure 3.1b).

3.2.3 Transform Validation Results

To ensure that the transforms actually affected perceived attractiveness or cuteness, the stimuli were evaluated by independent raters in an online test via the Perception Lab webpage. The age range for all raters was restricted to 18-35 years. Adult faces were rated for attractiveness on a 7-point Likert scale (1 = extremely unattractive, 4 = average looking, 7 = extremely attractive). Using a similar scale, the infant faces were rated for cuteness (1 = not at all cute, 4 = average looking, 7 = very cute). Within each rating test, the faces were presented individually and in random order. Participants in the online rating tasks all provided informed consent prior to beginning the experiment. They were not remunerated in any way for their participation.

Female Faces. One hundred and sixty-nine individuals (117 female, *mean age* = 24.1, *SD* = 4.9) rated the female faces. Overall, the high-attractive face versions (*mean* = 4.9, *SD* = 0.75) were rated as more attractive than the low-attractive face versions (*mean* = 4.4, *SD* = 0.73). T-tests confirmed that for 8 of the 10 female base faces, the high-attractive version was rated as significantly more attractive than the low-attractive version (all $t(168) > 2.92$, $p < .01$). For the two faces no rated as significantly different, the high-attractive version was rated as more attractive than the low-attractive version. No significant differences were found for attractiveness ratings based on rater gender in either the low-attractive ($F(1,168) = 0.49$, $p = 0.484$) or high-attractive ($F(1,168) = 2.58$, $p = 0.110$) female faces.

Male Faces. The male faces were rated by 172 individuals (121 female, *mean age* = 24.1, *SD* = 4.9). Overall, the high-attractive face versions (*mean* = 4.4, *SD* = 0.93) were rated as more attractive than the low-attractive face versions (*mean* = 3.6, *SD* = 0.89). For each of the 10 male base faces, the high-attractive version was rated as significantly more attractive than the low-attractive version (all $t(171) > 2.5$, $p < .05$). No significant differences were found for attractiveness ratings based on rater gender for the low-attractive ($F(1,171) = 0.13$, $p = 0.716$) male faces; however, women rated the high-attractive versions of male faces significantly higher than men did ($F(1,171) = 5.56$, $p = 0.019$; $mean_{women} = 4.52$, $SD_{women} = 0.90$; $mean_{men} = 4.16$, $SD_{men} = 0.97$).

Infant Faces. One hundred and one individuals (91 female, *mean age* = 23.2, *SD* = 4.5) rated the set of infant stimuli. Overall, the high-cute versions (*mean* = 4.4, *SD* = 0.96) were rated as cuter than the low-cute versions (*mean* = 3.6, *SD* = 0.97). T-tests confirmed that for each of the 10 infant base faces, the high-cute version was rated as significantly cuter than the low-cute version (each $t(100) > 3.0$, $p < .01$), thus validating the infant cuteness transform. No significant differences were found for cuteness ratings based on rater gender in either the low-cute ($F(1,100) = 1.83$, $p = 0.179$) or high-cute ($F(1,100) = 0.22$, $p = 0.638$) infant faces.

3.3 Main Experiment

3.3.1 Method

3.3.1.1 Participants

Eighty-two students from the University of St Andrews participated in the present study (35 men, 47 women; N.B. for clarity, the terms male/female are used when describing adult stimulus gender, while the terms men/women are used to describe participant sex). Participants were recruited from the psychology department participation pool (i.e. SONA), which includes age-, gender-, and ethnicity-screening questions at the time of sign-up. Participants ranged in age from 18-43 years (mean age: 20.4, SD = 3.9). Ethnicity was not restricted at the time of recruitment and the majority of participants (75%) were of Caucasian descent (the remaining 25% were of Asian descent). Participants first completed a questionnaire in which they reported their sexual orientation, parental status, and weekly contact with children. Sexual orientation was assessed using a 7-point Likert scale where 1 = completely homosexual, 4 = bisexual, 7 = completely heterosexual; those participants reporting non-heterosexual orientation (i.e. scores of 5 or lower) were excluded from the data analysis (N = 8). All participants were nulliparous (i.e. did not have children) and reported little to no contact with children[13]. Participants provided informed consent prior to participation, and were paid £5 per hour *pro rata* for their time.

3.3.1.2 Stimuli

The stimuli consisted of the 60 images (20 adult male, 20 adult female, 20 infant) tested in the pilot study. Each face identity was presented twice, once in the high-attractive/cute version and once in the low-attractive/cute version. Stimuli were presented in two separate blocks in counterbalanced order. Each block contained half high-attractive/cute face versions and half low-attractive/cute face versions, with each base face presented only once per block.

3.3.1.3 Procedure

Following completion of the training task (see Section 2.2.2.1), participants were given the key-press task described in section 2.2.3.2. Default viewing time for each image was set at 4 seconds. Participants who had an average number of total key-presses per face (regardless of increase versus decrease) that was less than 1.0 were excluded from the analysis (N = 1); the final analysis consisted of 72 participants (28 male).

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[13] Note: when contact with children was included as a covariate in the analysis reported here, the observed pattern of results did not change; there was no main effect of contact ($p = .11$) and no interaction between contact and any of the factors included in the analysis (all $p > .46$). Additionally, there were no significant gender differences reported for contact with children ($t(66.7) = 1.29$, $p = .20$).

3.3.2 Results

A 3x2x2 ANOVA was conducted with face type (3 levels: infant faces, female faces, male faces) and attractiveness (2 levels: ±50% transformed faces) as within-subject factors and participant sex as a between-subject factor. As expected, there was a main effect of attractiveness such that greater effort was exerted to prolong viewing time for high-attractive/cute faces ($F\ (1,70) = 31.4$, $MSE = 8.07$, $p < .001$, $\eta_p^2 = .309$). There was no interaction between participant gender and stimulus attractiveness level ($F\ (1,70) = 0.10$, $MSE = 0.75$, $p = .75$, $\eta_p^2 = .001$) suggesting that both genders were equally influenced by the attractiveness/cuteness transforms.

3.3.2.1 Gender Differences in Motivation to View Face Types

A main effect of face type existed (Greenhouse-Geisser correction used in all cases where assumptions of sphericity were not met, $F\ (1.6,109.4) = 17.7$, $MSE = 97.5$, $p < .001$, $\eta_p^2 = .202$). This effect was qualified by the interaction between face type and participant sex ($F\ (1.6,109.4) = 44.5$, $MSE = 97.5$, $p < .001$, $\eta_p^2 = .388$) suggesting that men and women performed differently across the three face classes. This interaction was explored with a one-way ANOVA comparing the average number of key-presses made by *men versus women for each face category* (regardless of attractiveness; see Figure 3.2). Men worked significantly harder than women to prolong viewing time for female faces ($F(1,71) = 20.0$, $p < .001$), while women worked harder than men to view both infant faces ($F(1,71) = 7.4$, $p = .01$) and male faces ($F(1,71) = 26.4$, $p < .001$).

Comparing the motivational salience of each face category *within participant sex*, we found that women exerted significantly more to view infant ($t(43) = 2.44$, $p = .02$) and opposite-sex faces ($t(43) = 2.95$, $p = .01$) than to view same-sex faces. Among men, significantly more effort was exerted to view opposite-sex faces than infant ($t(27) = 6.07$, $p < .001$) or same-sex faces ($t(27) = 5.97$, $p <.001$).

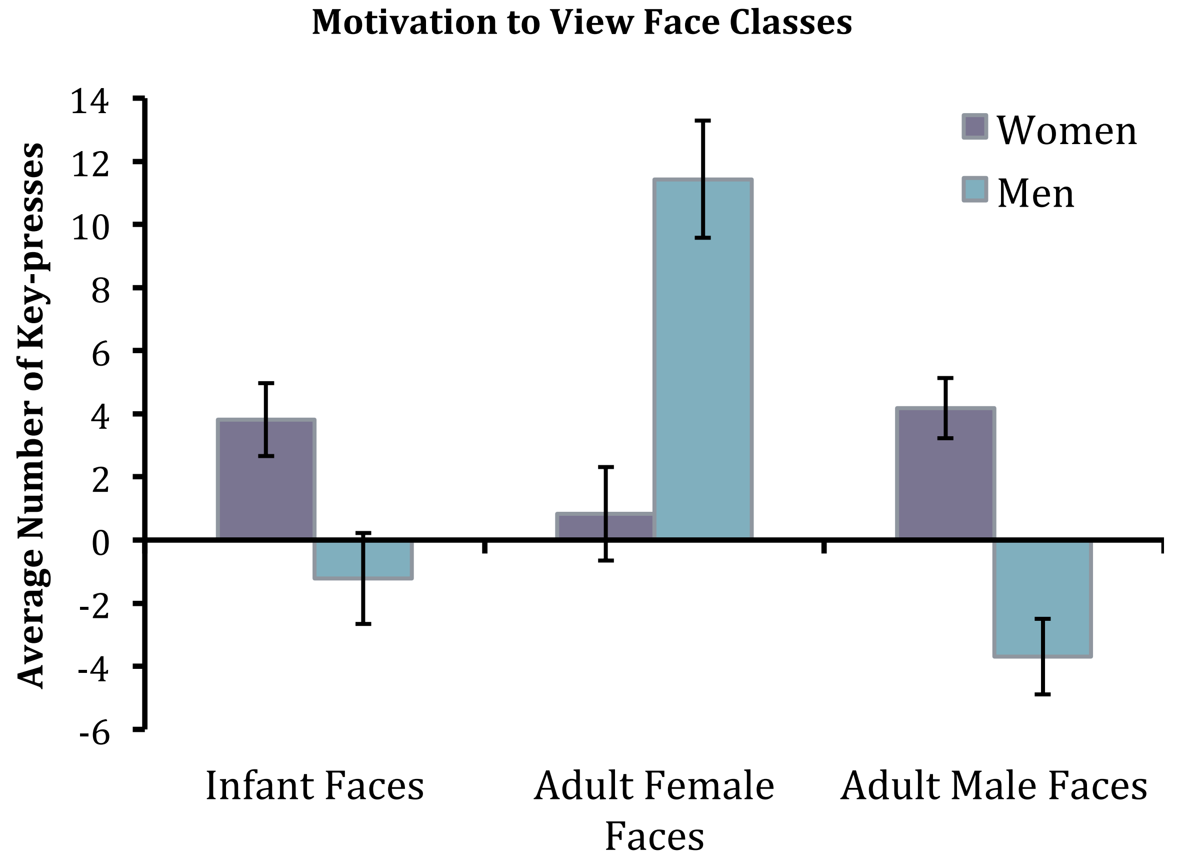
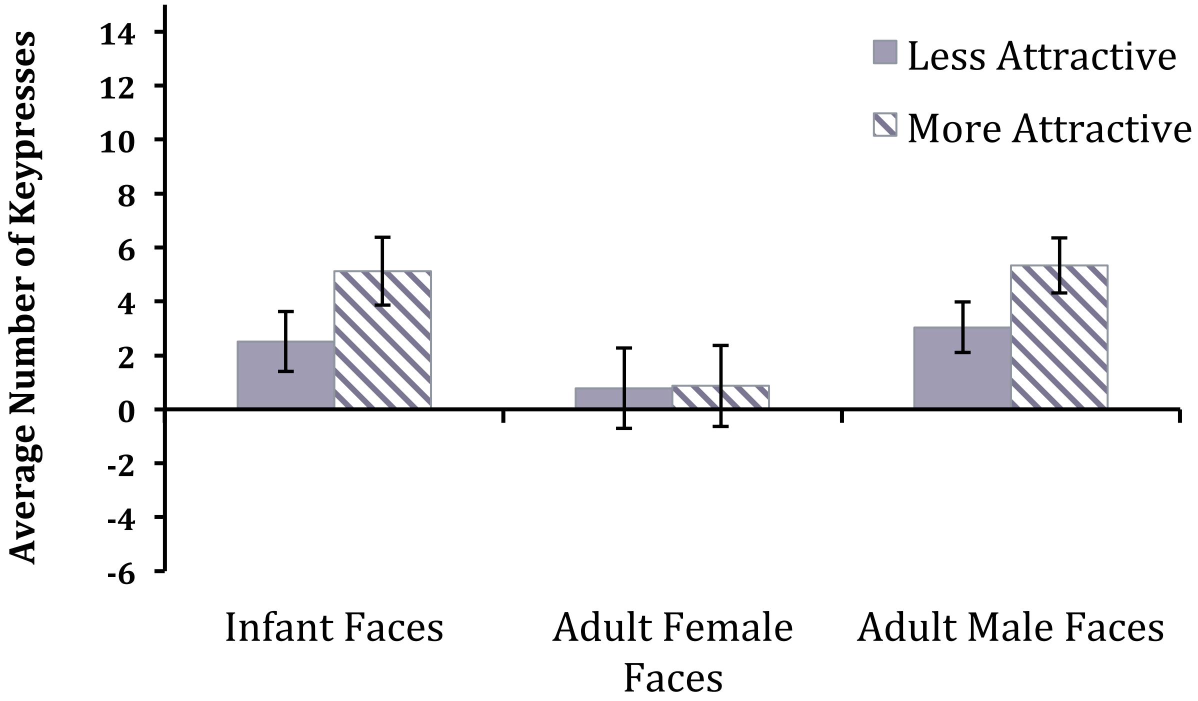


Figure 3.2 Average number of key-presses men and women exerted per face category. Women worked harder to view infant & adult male faces than men did, while men worked much harder to view adult female faces than women did. Error bars represent SEM.

3.3.2.2 Gender Differences for the Impact of Attractiveness/Cuteness

There was a significant 3-way interaction between face type, participant gender and stimulus attractiveness level (*F* (2.0,139.6) = 9.49, *p* < .001, *MSE* = 3.89, η_p^2 = .119). Figure 3.3a demonstrates that women exerted greater effort to view the more attractive/cute versions of infant faces (*t*(43) = 5.47, *p* < .001) and male faces (*t*(43) = 4.37, *p* < .001) than the less attractive/cute versions, while no difference in effort was apparent for the female faces (*t*(43) = 0.24, *p* = .81). As seen in Figure 3.3b, a different pattern occurred among men. Here, the attractiveness transforms affected the effort men exerted to look at female faces (*t*(27) = 2.65, *p* =.01) as well as infant faces (*t*(27) = 2.58, *p* = .02), but had no effect on work to view male faces (*t*(27) = 0.85, *p* = .40). The average number of key-presses men exerted for the high-cute infant faces did not differ significantly from zero (*t*(27) = 0.25, *p* = .80); for the low-cute infant faces,

(a) Women



(b) Men

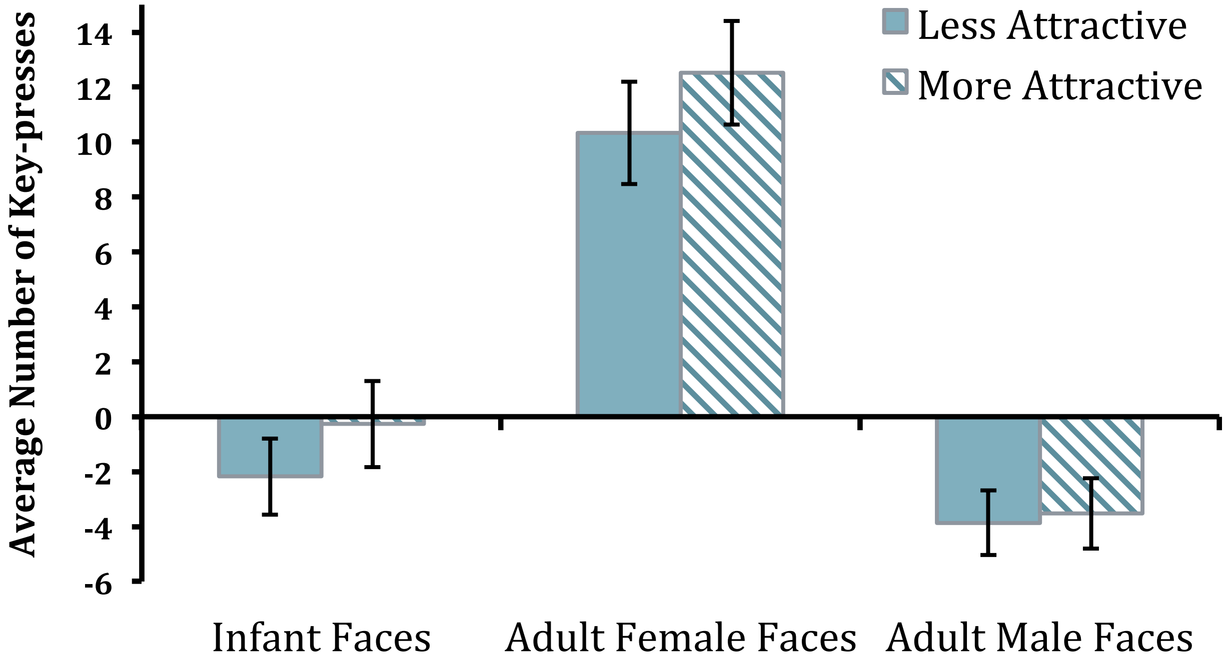


Figure 3.3 Average number of key-presses exerted by (a) Women and (b) Men for the more attractive/cute faces compared to the less attractive/cute faces across each face category. Women differentiated the more and less attractive/cute versions of infant and adult male faces, while men differentiated the more and less attractive/cute versions of infant and adult female faces. Error bars represent SEM.

the average number of key-presses was significantly different from zero ($t(27) = 2.35$, $p = .03$), suggesting that men sit passively viewing the high-cute infant faces but actively work to remove low-cute infant faces from the screen.

3.4 Discussion

3.4.1 Gender Differences in Motivation to View Opposite-Sex Faces

While both men and women worked to view opposite-sex adult faces in the present study, men exerted much more effort than women did. The marked difference in key-pressing between men and women for opposite-sex adult faces suggests that men have greater motivational drive to see opposite-sex individuals, and is in agreement with previous work on gender differences in the incentive salience of beauty (Levy et al., 2008), reward-related neural activation in response to opposite-sex stimuli (Hamann, Herman, Nolan, & Wallen, 2004; Kranz & Ishai, 2006; O'Doherty et al., 2003; Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004) and self-reports of arousal to erotic stimuli (Murnen & Stockton, 1997).

3.4.2 Gender Differences in Motivation to View Same-Sex Faces

As seen in the data presented in Chapter 2, we again found that women view same-sex faces for longer than men do. Further exploration of women's motivation to view same-sex faces are presented in Chapters 4 and 5.

3.4.3 Gender Differences in Motivation to View Infant Faces

This study is the first to demonstrate gender differences in the incentive salience of infant faces. We found that, in the context of other face classes, men find infants less motivating than do women. Men appear less able to discriminate small changes in cuteness between infant faces (Lobmaier et al., 2010; Sprengelmeyer et al., 2009), and here we find that men exert significantly less effort to view infant faces compared to women. Indeed men actively work to remove some infant faces from the screen when they have the opportunity to view attractive opposite-sex adult faces. Women, by contrast, show equal motivation to view infants and opposite-sex faces. Lewis et al. (in revision) conducted a similar study using natural images infants of varying cuteness. Both men and women viewed cuter babies for longer periods of time than less cute babies, but there were no gender differences in terms of overall viewing time for infant faces. Lewis et al. only presented participants with infant faces. It is possible that without the opportunity to view more desirable stimuli (i.e. attractive heterosexual adult faces), men will demonstrate greater effort to view infant faces. Parsons et al. (2011) found that the motivational salience of infant faces in the context of adult faces was similar for men and women, perhaps because the adult faces were only of average attractiveness. Participants in Parsons' study showed no overall tendency to alter viewing time from the default value for either the adult or infant face categories, suggesting that perhaps the stimuli employed were not particularly motivating.

Because the attractiveness or cuteness of the faces was experimentally manipulated, explicit liking responses were not collected from participants in the main study. Although liking responses were not assessed among the set of participants who completed the 'wanting' task, the aesthetic value of the stimuli can be inferred from the pilot data. In the pilot study each face (i.e. both the high-attractive/cute and low-attractive/cute version of each identity) was rated by both men and women. Gender differences were apparent in the set of attractive male faces, with women rating this group significantly higher than did men. For the set of female faces and infant faces, however, no gender differences were apparent. It is possible then to infer that men and women did not differ with regard to their liking of infant faces, while gender differences emerged with regard to 'wanting' responses. The lack of gender differences in the rating data is at odds with previous studies that have indicated that men are less sensitive to subtle changes in infant cuteness (Lobmaier et al., 2010; Sprengelmeyer et al., 2009); however, these previous works have used a forced choice discrimination task while individual ratings were collected here. Intuitively, it would seem that subtle differences would be *more* apparent when able to compare two faces side by side, resulting in greater discrimination ability in forced choice tasks as compared to rating tasks. Additional work comparing men's sensitivity to cues of facial cuteness across various task types could help clarify this discrepancy. Additionally, the infant faces were rated by a small number of men (N = 10) in the present work, which should be kept in mind when drawing conclusions about the larger group of men as a whole. Discrepancies in men's behavior across studies may suggest that we are incorrectly considering men as a single, unified group. Individual differences among men based on parental, experience with children, or other potentially influential factors have yet to be considered in either discrimination or motivational studies of infant cuteness.

To date, the findings regarding the motivational salience of infants among men and women have yielded conflicting results. When normal and deformed infants are considered, one study has indicated gender differences in liking but not wanting responses (Parsons et al., 2011b) while another has shown gender differences in both liking (normal babies only) and wanting (abnormal babies only) responses (Yamamoto et al., 2009). When only normal/healthy infants are concerned, again gender differences in liking but not wanting responses have been observed (Parsons et al., 2011a), and liking responses have been shown to correlate with wanting responses equally in men and women (Lewis et al., *in revision*). Interestingly, in both the latter studies (i.e. Parsons et al., 2011a & Lewis et al.) when the set of infant faces has been subdivided based on cuteness level into high-cute, medium-cute and low-cute groups the data seem to indicate the potential for gender differences to emerge when we consider very cute infants alone. In both cases, women show slightly higher levels of motivation to view the high-cute infant faces, however this pattern of results is not significant (this pattern of results only approached significance in the Lewis et al. study (p = .12) and is not reported in the Parsons et al. study due to a non-significant interaction between subject gender and cuteness group but can be seen in the graphical representation of the data). As such, the notion that gender differences may exist for highly cute infants alone is highly speculative and warrants further investigation. Perhaps the reason that gender differences have emerged in the present study is that the stimuli employed here were more attractive or cute than unmanipulated or natural images. Because the infant base faces were composites, they may be of high cuteness before the additional manipulation is applied. As such, even the low-cute versions of these faces may be cuter than average, real infants. If, in fact, gender differences are most apparent when dealing with high-cute infants, the present work may be particularly adept at picking up on these differences. Further exploration of the presence of absence of gender differences for highly cute infant faces is necessary to determine if such speculation is warranted.

The aesthetic appearance of an infant may influence the formation of the parent-infant bond. We explored subtle changes in infant cuteness on motivation while keeping other facial properties such as expression constant. We had predicted that men would show less motivational difference (as compared to women) for infant faces because men are less sensitive to subtle variations in infant cuteness (Lobmaier et al., 2010; Sprengelmeyer et al., 2009); yet, both men and women differentiated amongst the high- and low-cute infant faces. Interestingly, the manner in which infant facial cuteness affected motivation was markedly different between men and women. Women showed more motivation to view infant faces, in general, suggesting that infants have high incentive salience for women. Women also differentiated the amount of effort expended to increase viewing time based on how cute the infant face was - cuter infants elicited more effort. While men were also shown to differentiate based on infant cuteness, this behavior reflected passivity or avoidant behavior rather than positive motivation. Men passively viewed the high-cute infant faces and actively worked to remove the low-cute infant faces, suggesting these faces act as aversive stimuli compared to attractive adult female faces.

3.5 Conclusion and Future Directions

Men and women appear to be differentially motivated by same-sex, opposite-sex and infant faces. We found that male participants exerted much greater effort to view opposite-sex adult faces than any other face class, while female participants exerted moderate effort to view both opposite-sex and infant faces. Based on the present study, we suggest that reproductively relevant face classes hold the greatest incentive salience. High incentive salience for reproductively-relevant stimulus groups would be evolutionarily advantageous as increased motivation towards these groups could act to increase mating opportunities and reproductive success (through increased offspring survival rates).

Previous studies investigating gender differences in perception of infants have yielded conflicting results. A number of studies have demonstrated gender differences in early visual processing of infant faces (Proverbio et al., 2006), sensitivity to infant cuteness (Lobmaier et al., 2010; Sprengelmeyer et al., 2009), affective responses to cute infants (Hildebrandt, 1978) and aversive responses to infants with facial deformities (Yamamoto et al., 2009; but see Parsons et al. 2011b); however, gender differences have not been observed, to date, when investigating the incentive salience of infant faces (Lewis et al., *in revision*; Parsons et al., 2011a). The findings presented here are the first to suggest that gender differences *do* exist in the incentive salience of infant faces; however, these differences may only be apparent when evaluating subtle differences in cuteness, when highly cute infant faces are considered independently, or when infant faces are presented in the context of potentially more desirable options.

A limitation of the work done to date on incentive salience of infants is that men and women are considered as uniform groups. This type of analysis does not allow for individual differences in motivated behavior; however, it is feasible that individual differences may exist, particularly in the case of men. For example, 'baby longing' appears to be more strongly related to marital status and fertility intentions in men than in women suggesting that lifestyle factors may influence the incentive salience of infants in general (Rotkirch, Basten, Vaisanen, & Jokela, 2011). Additionally, the literature on mate preferences in women frequently describes the trade off involved when choosing a mate with high or low masculinity. On the one hand, highly masculine men show increased health or genetic fitness (Thornhill & Gangestad, 2006) which may be directly and indirectly beneficial to the female. However, these more masculine men are less likely to demonstrate prosocial behavior (Boothroyd, Jones, Burt, & Perrett, 2007), are less likely to invest in parental care as evidenced by their greater interest in short-term than long-term relationships (Kruger, 2006) and the fact that masculine men (as indexed by high testosterone levels) are less likely to marry than are feminine men (Booth & Dabbs, 2013). Particularly germane here, men with higher testosterone levels (i.e. masculine men) feel less of a need to respond when they hear infant cries than do men with lower testosterone (Fleming, Corter, Stallings, & Steiner, 2002). These individual differences in parental behavior may influence the incentive salience of infant stimuli. As testosterone is linked to masculinity there may also be hormonal influence on motivation to view infants.

Additionally, the literature has focused on healthy, nulliparous individuals (note: a small sample of parous individuals was included in Parsons et al. 2011b and Yamamoto et al., 2009) and has failed to consider individual differences among men and women. Although early brain responses (Kringelbach et al., 2008) and reward-related responses to infant facial cuteness (Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009) have been observed in nulliparous individuals, it is possible that having had a child or even just having experience with infants may influence the incentive salience of infant faces in general, as well as that of cuteness specifically. Neuroimaging work (utilizing EEG techniques) exploring the impact of gender and parental status when viewing unfamiliar infants has suggested that early and late brain responses to infant faces are stronger in women than men, overall, and this pattern is stronger in parents than in nulliparous individuals (Proverbio et al., 2006). Parents also show modulation of early brain responses to emotional expression, while nulliparous individuals do not.

Although it is necessary to first have a basic understanding of the motivational salience of infant stimuli before work can be done using clinical or at-risk populations, such as those suffering from postpartum depression and other bonding disorders, the key-press paradigm offers a unique and inexpensive way to study the reward value of infant stimuli. Elman et al. (2005) demonstrated that psychiatric disorders characterized by anhedonia can inhibit motivation as measured by the key-press paradigm. As such, it may be useful as a screening tool in clinical settings, especially among new parents to assess risk of postpartum depression.

Chapter 4 Individual Differences in the Incentive Salience of Beauty Among Women

The following chapter is based on work currently submitted for publication consideration. The reference for this work is as follows:

Hahn, A.C., & Perrett, D.I. (submitted). Own-attractiveness affects the incentive salience of beauty for women.

Abstract

Studies investigating the motivational value of beauty have shown that heterosexual men are motivated to view opposite-sex beauty alone, while heterosexual women are motivated to view beautiful faces of either sex. Here we investigate the role of own perceived attractiveness on women's motivation to view attractive and unattractive faces. Heterosexual women completed a key-press task whereby they were able to control stimulus presentation time of each image. Participants rated their own attractiveness prior to completing this key-press task. Our results suggest that the incentive salience of facial attractiveness may be condition-dependent. Own attractiveness was shown to predict motivation to view both same- and opposite-sex faces – women with higher self-perceived attractiveness work harder to prolong viewing of attractive faces than women with low self-perceived attractiveness. This effect tended to be larger for same-sex faces than opposite-sex faces. Individual differences in motivation to view attractive faces based on own attractiveness may relate to women's 'market value' – with more attractive women being able to obtain more attractive mates and compete with more attractive rivals. We argue that intrasexual competition may partially explain the incentive salience of same-sex faces for women.

4.1 Introduction

Previous work exploring the motivational value of faces in heterosexual individuals has demonstrated that beautiful women hold high incentive salience for men (Aharon et al., 2001; Elman et al., 2005), while both beautiful men and beautiful women hold incentive salience or reward value for women (Hahn, Xiao, Sprengelmeyer, & Perrett, 2013; Levy et al., 2008). This pattern of results in women is evident in behavioral tasks (Hahn et al., 2013; Levy et al., 2008; Lippa, Patterson, & Marelich, 2010), arousal responses (Chivers & Bailey, 2005), and neuroimaging studies (Kranz & Ishai, 2006). Little work has been done to assess reward and arousal within the homosexual or bisexual populations. However, work exploring neural and visual responses to face stimuli would suggest that an element of preference specificity exists. Visual attention to interocularly suppressed images is modulated by sexual preference – with heterosexual men and homosexual women preferentially attending to female nudes and heterosexual women and homosexual men preferentially attending to male nudes (Jiang, Costello, Fang, Huang, & He, 2006). Similarly, activation of brain regions associated with face processing as well as reward processing (specifically, the OFC) preferentially respond to female faces (as compared to male faces) in heterosexual women and homosexual men, while response biases are observed for male faces in heterosexual women and homosexual men (Ishai, 2007; Kranz & Ishai, 2006).

Interestingly, heterosexual women show the least differentiation between faces of the preferred and non-preferred sex (Kranz & Ishai, 2006). Lippa et al. (2010) demonstrated that heterosexual women rate photographs of attractive swimsuit models as sexually appealing regardless of model gender (whereas men only rated attractive female models as sexually appealing). Together, these data would suggest that women have a less category-specific arousal response than do me. While research has shown that heterosexual women generally find looking at other women rewarding (Kranz & Ishai, 2006; Levy et al., 2008) or arousing (Chivers & Bailey, 2005), to date there has been no investigation of individual differences in these responses to same-sex stimuli. In the present study, we explore the role of own attractiveness in motivation to view attractive faces.

Condition-dependent mating behaviors are observable in a number of species (Bakker, Künzler, & Mazzi, 1999; Eraly, Hendrickx, & Lens, 2009; Little, Burt, Penton-Voak, & Perrett, 2001; Vukovic et al., 2008). In the case of female condition-dependent mate choice, the female's own condition influences preferences for various attributes in the male that may be indicative of genetic fitness. For example, in wolf spiders food-stressed females (i.e. those with lower condition) show decreased size preferences (Eraly et al., 2009). Similarly, in three-spined stickelbacks (Bakker et al., 1999) and guppies (Lopez, 1999) female quality (as measured by body size and parasite load, respectively) influences their preferences for male coloration and display. More attractive females tend to show stronger preferences for traits that are indicative of high mate quality.

Similar effects of own condition are apparent in humans, particularly with respect to masculinity preferences in women. Women who consider themselves more attractive show stronger preferences for masculine facial appearance (Little et al., 2001) and masculine vocal features (Vukovic et al., 2008) than do women who consider themselves less attractive. Own attractiveness may influence actual mating behaviors in addition to preferences. Less attractive people have been found to be more receptive than highly attractive people to accepting date offers from unattractive individuals (Lee, Loewenstein, Ariely, Hong, & Young, 2008), suggesting that own condition may influence women's choosiness.

Own attractiveness has also been shown to influence sexual behavior, with women who consider themselves more attractive having higher sociosexuality (i.e. more likely to engage in short-term mating opportunities), suggesting that women's perceptions of their own mate value may be linked to their mating strategies (Clark, 2004). Women's perceptions of their own 'market value' (i.e. how attractive they think they are) influence their desire to date (Ha, Overbeek, & Engels, 2010), and self-rated attractiveness has been linked to women's amount of lifetime sexual experience (MacCorquodale & DeLamater, 1979), as well as their likelihood of being in a relationship, and their sexual esteem (Wiederman & Hurst, 1998).

Using a "pay-per-view" paradigm, we explored the impact of self-perceived attractiveness on the incentive salience of facial attractiveness among women. Because little work has been done on individual differences in motivation, this study was largely exploratory in nature. Nonetheless, given that women's perceptions of their 'market value' (Pawlowski & Dunbar, 1999) may influence their impression of the quality of mates they can obtain and the quality of rivals with whom they are able to compete, there is the potential for effects of own attractiveness on motivation to view both same- and opposite-sex beauty.

The literature suggests women may have condition-dependent motivation towards members of the opposite-sex. As more attractive women are able to be choosier in terms of their potential mates, it may be the case that women who consider themselves to be attractive invest greater effort in viewing attractive men. Similarly, if working to prolong viewing time of same-sex faces is a form of social comparison or intrasexual competition, own perceived attractiveness might impact positively on motivation to view same-sex beauty, since more attractive women are able to compete with highly attractive individuals of the same-sex. Conversely, if motivation to view same-sex beauty reflects a less stringent sexual preference or greater bisexual interest (Levy et al., 2008) rather than social comparison, all women should work to view attractive same-sex faces regardless of own perceived attractiveness. Therefore, we predicted that self-perceived attractiveness would enhance motivation to view attractive faces.

4.2 Methods

4.2.1 Participants

Ninety-two heterosexual women aged 18-30 years (*M* = 21.9, *SD* = 3.6) participated in the present study. As described in Chapter 2, only those women who had an absolute number of key-presses greater than or equal to 1 were included. Sexual orientation was assessed using a 7-point scale (where 1 = completely homosexual, 4 = bisexual, and 7 = completely heterosexual). Only those participants reporting a score of 5 or higher were included in the dataset. All data was collected online via the Perception Lab webpage. Previous research suggests that online and laboratory studies of individual differences in responses to facial cues produce very similar patterns of results (Conway, Jones, DeBruine, & Little, 2008; Jones et al., 2007). Ethnicity was not restricted, however Google statistics for the Perception Lab webpage indicate that the majority (>85%) of participant traffic originates from the USA and UK. Informed consent was obtained from all participants prior to beginning the experiment.

4.2.2 Stimuli

Thirty female faces and 30 male faces collected from various modeling/acting websites were utilized as stimuli. These faces were selected from the larger set of adult faces described in Section 2.2.1.1 and included 15 faces rated as attractive and 15 faces rated as unattractive for each gender. All images were emotionally neutral and depicted individuals aged 18-35 years. Presentation order was randomized, and both stimulus sexes were presented in a single intermixed block.

4.2.3 Procedure

Participants first rated their own attractiveness on a 7-point Likert scale (1 = not very attractive, 4 = average looking, 7 = very attractive). Due to low numbers in the extreme groups (i.e. 1 and 7), own attractiveness ratings were collapsed to 5 levels such that participants who rated themselves as a 1 (N=1) were included in the 2 group and those rating themselves as 7 (N=1) were included in the 6 group, giving 5 levels for the self-rated attractiveness factor (N_2 =

3, N_3 = 6, N_4 =25, N_5 = 35, N_6 = 23). Participants then completed a key-press task whereby they were able to control the viewing time of each image by pressing an alternating set of keys (e.g. pressing "N" & "M" alternately to increase viewing time, "Z" and "X" to decrease viewing time; see Aharon et al., 2001; Hahn et al., 2012). All participants were given a training task developed to familiarize online participants with the key-press paradigm prior to beginning the experiment. During this task, 6 slides were presented that described how the task functioned. The first three slides: (a) explained that image presentation time could be increased by pressing "N" and "M" alternately, (b) asked subjects to practice pressing these keys, and (c) drew their attention to the changes in the visual feedback timer bar that occurred with key-pressing. These three slides were then repeated with decreasing viewing time instructions. Default viewing time was set at 8 seconds. The measured number of key-presses per trial was calculated by subtracting the number of negative key-presses made from the number of positive key-presses made. This key-pressing task operationalizes motivation by measuring amount of effort/work exerted to view an image.

4.3 Results

A 2x2 repeated measures ANCOVA was run using self-rated attractiveness score as a covariate to explore the impact of own attractiveness on the incentive salience of beauty. Sex of the face (2 levels: male, female) and attractiveness (2 levels: high, low) acted as within-subject factors.

There was no overall effect of face sex ($F(1,90) = 2.19$, $p = .142$, $MSE = 28.0$, $\eta_p^2 = .024$), or interaction between face sex and attractiveness level ($F(1,90) = 2.61$, $p = .110$, $MSE = 16.9$, $\eta_p^2 = .028$) in the present dataset. Overall, women with higher self-rated attractiveness exerted slightly more effort to prolong viewing time for same-sex faces than did women with low self-rated attractiveness, although this effect of self-rated attractiveness failed to reach significance ($F(1,90) = 3.64$, $p = .060$, $\eta_p^2 = .039$). Surprisingly, the previously documented effect of face attractiveness (i.e. beauty, see Levy et al., 2008) on motivated behavior in women was non-significant[14] ($F(1,90) = 0.003$, $p = .955$, $MSE = 121.8$, $\eta_p^2 = .000$). Rather, an interaction occurred between face attractiveness and self-rated attractiveness ($F(1,90) = 4.15$, $p = .044$, $\eta_p^2 = .044$). As seen in Figure 4.1, self-rated attractiveness impacted motivation to view attractive faces, while motivation to view unattractive faces was relatively unaffected by own appearance.

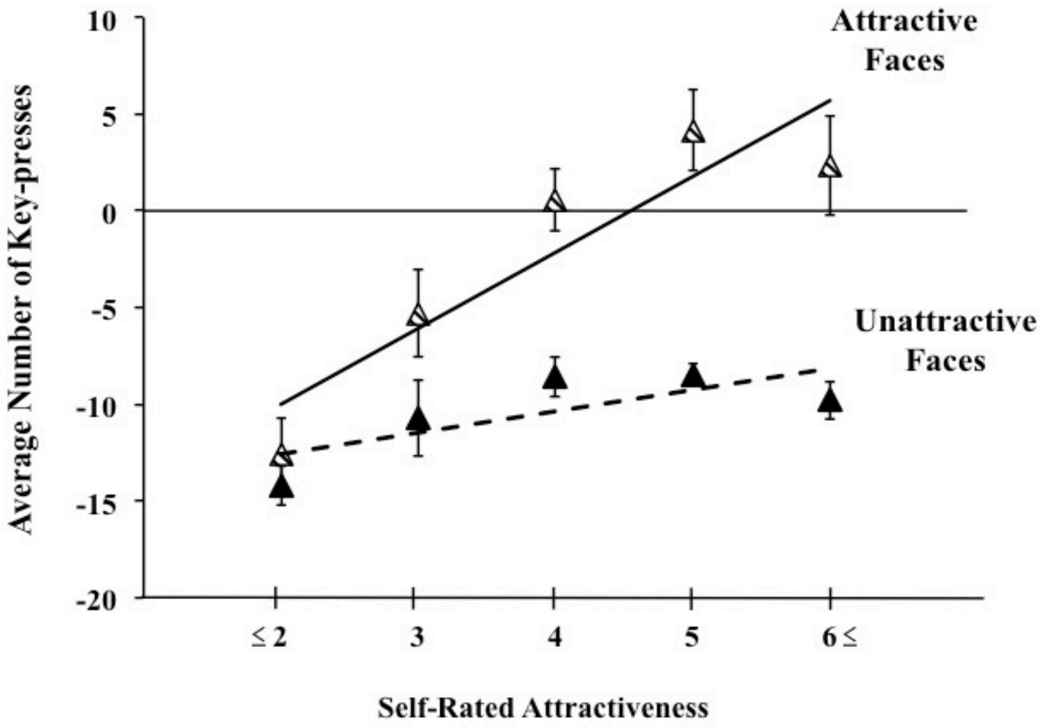

Impact of Own Attractiveness on Motivation to View Attractive and Unattractive Faces (independent of face sex)

Figure 4.1 *Average number of key-presses exerted to view attractive and unattractive faces by level of self-rated attractiveness. Self-rated attractiveness impacts motivation to view attractive faces, but not unattractive faces. Error bars represent SEM.*

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[14] It is important to note that this pattern of results does not reflect differences in behavior between online versus in-lab participants. When the analysis was conducted independently of self-rated attractiveness, the results were in line with previously observed findings (i.e. women show increased motivation to view attractive faces, but this is not sex-specific). A repeated measures ANOVA with face sex (2 levels: male, female) and attractiveness (2 levels: high-attractive, low-attractive) as within-subject factors revealed a significant main effect of attractiveness ($F(1,91) = 84.3$, $p < .001$, $MSE = 126.0$, $\eta_p^2 = 481$) such that greater effort was exerted to view attractive faces than unattractive faces. There was no interaction between attractiveness and face sex ($F(1,91) = 0.097$, $p = .757$, $MSE = 17.3$, $\eta_p^2 = .001$), suggesting that women are equally motivated to view attractive same-sex and opposite-sex faces as has previously been observed (Levy et al., 2008)

The 3-way interaction between self-rated attractiveness, sex of the face and face attractiveness approached significance ($F(1,90) = 2.95$, $p = .089$, $\eta_p^2 = .032$). Although this interaction failed to reach significance, separate ANCOVAS were conducted for male and female faces with face attractiveness as a within-subject factor (2 levels: high, low) and self-rated attractiveness as a covariate to better understand this potential interaction. For the male faces there was no interaction between face attractiveness and women's self-rated attractiveness ($F(1,90) = 1.81$, $p = .182$, $\eta_p^2 = .020$) suggesting that women's condition does not affect their motivation to view opposite-sex individuals. Conversely, for the female faces the interaction between face attractiveness and women's self-rated attractiveness was significant ($F(1,90) = 6.00$, $p = .016$, $\eta_p^2 = .062$), suggesting that individual differences exist in women's motivation to view other women based on own condition and the attractiveness of potential rivals (see Figure 4.2).

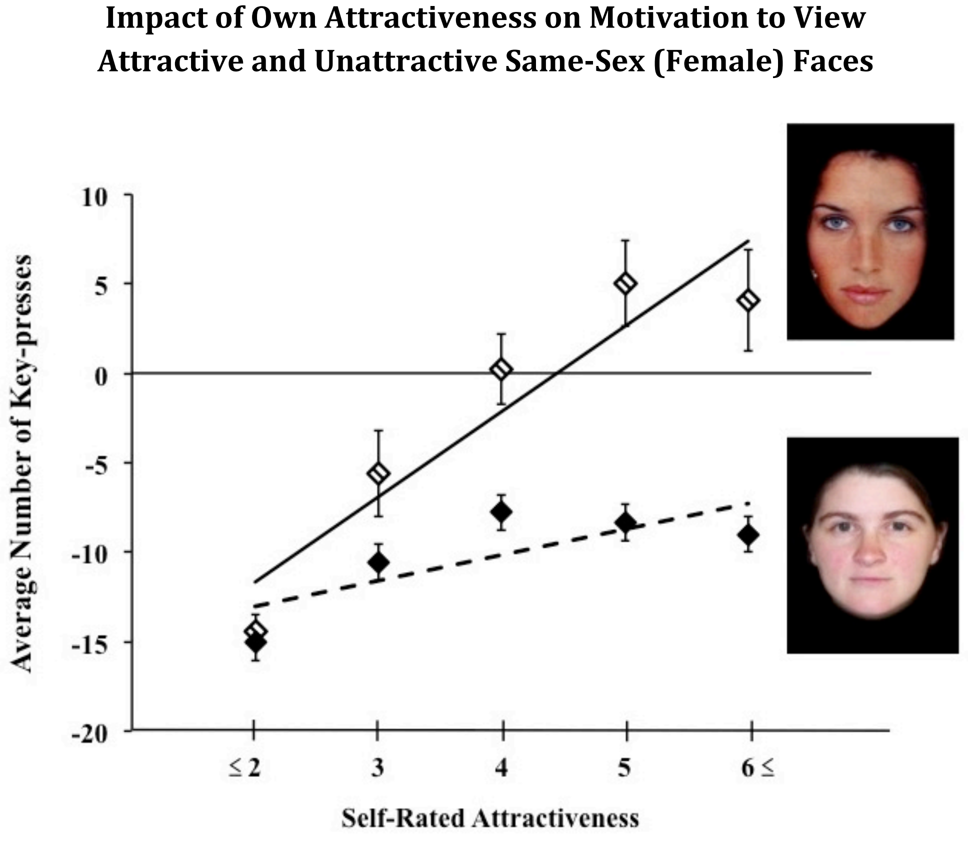
Impact of Own Attractiveness on Motivation to View Attractive and Unattractive Same-Sex (Female) Faces

Figure 4.2 *Average number of key-presses exerted for attractive and unattractive same-sex faces based on self-rated attractiveness. Women with higher self-rated attractiveness show increased motivation to view attractive same-sex faces as compared to women with low self-rated attractiveness. Error bars represent SEM.*

4.4 Discussion

Motivation to view attractive individuals (of either sex) was found to be contingent on self-rated attractiveness. Women with higher self-rated attractiveness worked harder to prolong viewing of attractive faces, overall. In fact, women with very low self-rated attractiveness actually worked to remove attractive faces (of either sex) from the screen (as seen in Figure 4.1). Our results suggest that women's self-rated attractiveness impacts the incentive salience of beauty, particularly for same-sex faces. Levy et al. (2008) argued that same-sex beauty holds incentive salience for women due to "greater bisexual interest among heterosexual women". Our findings indicate that same-sex beauty holds higher incentive salience among women who consider themselves attractive, suggesting social comparison rather than arousal may drive women to look at other women. These findings suggest that intrasexual competition (via social comparison) rather than, or in addition to, women's fluid sexual preference, may underlie motivation to view same-sex beauty. Previously, we have argued that face classes with high reproductive significance may hold the greatest incentive salience (Hahn et al., 2013). In line with this argument, it may be that women with low self-rated attractiveness do not consider themselves potential competitors because they are not high quality mates. As such, focusing attention on more attractive same-sex rivals may be futile, as they cannot compete with such women for access to genetically fit males. Indeed, intrasexual competition may even cause unattractive women to find the act of viewing attractive same-sex images damaging to their self-esteem, rendering such images aversive (Little & Mannion, 2006).

Social comparison among women could potentially act to increase mating success, in spite of the fact that attentional resources are being allocated to both same- and opposite-sex beauty. Gathering relevant information about competitors may aid women in determining when it is worthwhile to exert mating opportunities. Beautiful women pose a threat (with regard to mating attempts) and are, therefore, relevant social stimuli. Primate studies have shown that social stimuli may act as rewards or reinforcers; monkeys and apes will exert effort (e.g. lever-press, rope-pull) in order to view a conspecific (Andrews & Rosenblum, 1993; Fujita & Matsuzawa, 1986; Fujita, 1987; Swartz & Rosenblum, 1980). Macaque monkeys will even forego food rewards to view conspecifics (Andrews, Bhat, & Rosenblum, 1995; Deaner, Khera, & Platt, 2005). Additionally, status impacts the salience of social stimuli. Patas monkeys (*Erythrocebus patas*) show preferences in visual attention for dominant conspecifics. Individuals tend to focus visual attention on those that out-rank them in the dominance hierarchy, rather than lower-ranking individuals (McNelis & Boatright-Horowitz, 1998). Deaner et al. (2005) found that male rhesus macaques would sacrifice juice rewards to view high-status male faces and female genitalia, but not low-status male or female faces. In light of the evidence that status impacts motivation to view same-sex individuals, it is possible that women work to view other women as a form of intrasexual competition or social comparison.

Intrasexual competition is a multifaceted phenomenon and includes competition for mates as well as to establish same-sex dominance hierarchies, derogation of same-sex competitors, and sexual poaching tactics (Buss, 1988). Men place a high premium on physical appearance when assessing a potential partner (Buss & Barnes, 1986). Given that men prefer physically attractive women, and mate preferences are the underlying force driving intrasexual competition (see Darwin, 1871), it follows that women should compete with one another in terms of physical appearance (Campbell, 2004). Indeed, Buss (1988) found sex differences with respect to intrasexual competition tactics such that women compete by altering of their physical appearance while men compete through resource possession and display.

Women appear to be quite sensitive to the attractiveness of other women. Women report higher distress about mating rivalry for females rated as highly attractive (Buss, Schackelford, Choe, Buunk, & Dijkstra, 2000). Attractive women are often perceived as a greater threat to current relationships (Baenninger, Baenninger, & Houle, 1993; Brewer & Archer, 2007) and evoke stronger jealousy reactions (Dijkstra & Buunk, 1998; Massar & Buunk, 2010; Yarab & Allgeier, 1999). Women also discriminate against highly-attractive same-sex individuals in terms of hiring preferences (Agthe, Spörrle, & Maner, 2010). This pattern is particularly prevalent among moderately attractive women who consider highly attractive same-sex individuals to be salient social threats. Exposure to other attractive same-sex individuals can also influence self-perceptions. After viewing attractive same-sex individuals, women tend to rate themselves as less desirable partners (Gutierres, Kenrick, & Partch, 1999) and to be less satisfied with their own appearance (Richins, 1991). Exposure to attractive women can also increase body dissatisfaction and alter eating habits (Li, Smith, Griskevicius, Cason, & Bryan, 2010).

The current study is the first to explore individual differences in the incentive salience of same-sex beauty among women. Here, we demonstrate that own attractiveness impacts motivation to view attractive faces; women who consider themselves attractive show increased motivation to view attractive faces as compared to women who do not consider themselves attractive. This pattern was particularly true of viewing behavior for same-sex faces. Our finding is the first to suggest that individual differences may exist in women's motivation to view same-sex individuals. The evidence for a link between self-rated attractiveness and other-rated attractiveness is equivocal. Marcus and Miller (2003) found women's perceptions of their own attractiveness to be positively correlated with ratings given by both male and female observers. Similarly, Weeden and Sabini (2007) found that women's ratings of their own attractiveness were positively correlated with subjective ratings (based on facial photographs), and negatively correlated with objective measures of attractiveness (i.e. BMI and waist-to-hip ratio). Conversely, Brewer, Archer and Manning (2007) found no correlation between women's ratings of their own attractiveness and the attractiveness ratings given to these women by male observers or by more objective measures of female quality (i.e. BMI and waist-to-hip ratio). Future work exploring the impact of other-rated attractiveness or other objective measures of female attractiveness may provide illumination on the possible condition-dependent nature of motivation to view attractive individuals.

We argue that same-sex beauty may be motivationally salient due to its role in social comparison or intrasexual competition, above and beyond the previously assumed reward value of same-sex faces due to women's greater bisexual interest. Although this argument is somewhat speculative based on the current evidence, the effect of own-rated attractiveness on motivation to view same-sex faces has been replicated in ongoing research (Barr, Hahn, & Perrett, n.d.; Hahn, Fisher, & Jones, n.d.), as well as in a subsample of the women who participated in the infant study (Chapter 3). Across these preliminary datasets, the effect of own-attractiveness on women's motivated behavior appears to be more prevalent for same-sex than opposite-sex faces. If own-attractiveness influenced a general choosiness, we would anticipate that responses to both male and female faces, or male faces alone (i.e. mates) would be affected by own-attractiveness. Yet, we continue to pick up effects for same-sex faces. Future work exploring social comparison tendencies, or levels media exposure in relation to motivation to view same-sex individuals may help illuminate this interesting effect.

Future work exploring motivation in heterosexual, bisexual and homosexual individuals could further our understanding of women's motivation to view same-sex faces. Firstly, it remains unknown whether gender differences in motivation (i.e. men show a stronger response to faces of the preferred sex, women show general motivation) are apparent in the homosexual population. Although homosexual men and women have shown category-specific brain responses to facial attractiveness (Kranz & Ishai, 2006), genital arousal studies indicate that only homosexual men show category-specific arousal responses. Homosexual women on the other hand, show a more general arousal response, similar to that observed in heterosexual women (Chivers et al., 2004). In light of the equivocal evidence, it remains unclear if gender or sexual orientation differences in the incentive salience of beauty. Exploring the motivational salience of beauty in the heterosexual and homosexual populations together could help tease apart the respective roles of sexual fluidity and intrasexual competition among women. For example, providing cues to the sexual-status of a given stimulus as a potential mate or a potential competitor by simply labeling images of faces (both female and male) as "gay" or "straight" when they are shown to participants to determine if this type of knowledge impacts viewing behavior could provide further support for the sexual fluidity or intrasexual competition explanation of women's behavior towards same-sex faces. Alternatively, experimentally manipulating women's level of sexual arousal to determine if motivation to view same-sex beauty is affected could also provide new insight into the underlying incentive salience of same-sex faces.

Women compete with one another for access to mates using physical attractiveness (Campbell, 2004; Pawlowski & Dunbar, 1999). Although men may need to compete with one another in terms of physical attractiveness on some level, cues to dominance, status and resources may be more important than cues to attractiveness (Buss, 1988; Mazur & Booth, 1998) Data on men is not presented in the current study due to relatively small sample sizes; however, preliminarily exploration of these data suggests that own-attractiveness may not impact on men's behavior. If the intrasexual comparison argument holds true, this finding may not be all that surprising. Since physical attractiveness is a critical factor when women compete with one another to access mates, it is necessary to attend to the attractiveness of other same-sex individuals. The data presented here provide evidence for individual differences motivation. Highly attractive women are able to obtain high quality mates and compete with high quality rivals, while less attractive women must compete on a lower level. That motivation to view attractive faces may be contingent on the observer's own 'market value' suggests that individual differences in the incentive salience of beauty do exist.

Chapter 5 Variations in Motivation Across the Menstrual Cycle

This chapter is based on work currently under review at Evolution and Human Behavior. The reference for this work is as follows:

Hahn, A.C., & Perrett, D.I. (under review). Menstrual cycle phase moderates women's motivation to view faces. *Evolution and Human Behavior.*

Abstract

Studies investigating the incentive salience of facial attractiveness have shown that heterosexual women are motivated to view attractive same-sex faces in addition to attractive opposite-sex faces. Menstrual cycle phase moderates the incentive salience of monetary rewards, subjective reports of the hedonic quality of drug administration, and neuronal activation to male faces in the orbitofrontal cortex. However cyclical variations in the incentive salience of facial attractiveness have yet to be explored. Here we investigated the effects of menstrual cycle phase on motivation to view same- and opposite-sex faces varying in attractiveness. Heterosexual women completed a key-press task in which they controlled presentation time of each stimulus. Women showed greater motivation to view attractive *same-sex* faces during peak fertility than during periods of low fertility. No cycle effects were found on motivation to view attractive opposite-sex faces. During peak fertility, women may exert greater effort to monitor attractive women because this is the time during which they are most likely to compete for mates. Our results suggest that intrasexual competition may explain women's motivation to view attractive same-sex faces.

5.1 Introduction

Among humans, attractiveness has a premium and can influence social, personal and professional success (Eagly, Ashmore, Makhijani, & Longo, 1991; Hamermesh & Biddle, 1994; Hosoda, Stone-Romero, & Coats, 2003). Strong preferences for attractive faces are evident from very early in life (Langlois, Ritter, Roggman, & Vaughn, 1991; Slater et al., 2000), potentially because attractive faces have an intrinsic reward value. Indeed, neuroimaging studies indicating that attractive faces stimulate brain regions associated with 'reward' or motivated behavior to a greater extent than do unattractive faces suggest that facial attractiveness may be rewarding in much the same was as food and drugs (Aharon et al., 2001; Cloutier, Heatherton, Whalen, & Kelley, 2008; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). These 'reward-related' responses to attractiveness are stronger for faces of the preferred sex, suggesting that the 'rewarding' nature of attractiveness may serve an adaptive function by increasing motivation towards potential mates (Kranz & Ishai, 2006).

Robinson and Berridge's incentive salience hypothesis parses reward into distinct states of 'wanting' (the appetitive or incentive salience of a given stimulus) and 'liking' (the hedonic quality of the stimulus, Berridge & Robinson, 2003). In the case of attractiveness, 'liking' may refer to the aesthetic assessment given to a face while 'wanting' may refer to any behavioral changes elicited in the viewer by the face. Importantly, the aesthetic value of facial attractiveness can be dissociated from its reward value, or incentive salience; Aharon et al. (2001) found that men gave similar attractiveness ratings to attractive male and female faces (suggesting similar 'liking' for same- and opposite-sex attractiveness) while they only work to view attractive faces of the opposite-sex (suggesting differential 'wanting' for same- and opposite-sex attractiveness). It may be the case that attractiveness is rewarding due to its adaptive value; with facial attractiveness signaling higher mate quality (Thornhill & Gangestad, 1993, 1999), it would be evolutionarily advantageous for attractive individuals to be both liked and 'wanted'. This is particularly true in the case of opposite-sex attractiveness; a greater "wanting" of attractive opposite-sex individuals would increase motivation to seek out high-quality mates and could act to increase reproductive success.

Previous work exploring the motivational value of faces in *heterosexual* adults has demonstrated that attractive women hold high incentive salience for men (Aharon et al., 2001; Elman et al., 2005; Hahn, Xiao, Sprengelmeyer, & Perrett, 2013; Levy et al., 2008), while both attractive men and attractive women hold incentive salience for women (Levy et al., 2008). This difference in the sex-specificity of the motivational value of faces has been interpreted as evidence that sexual preference/orientation is a fluid concept for women (Bailey, 2009; Baumeister, 2000). This theory is supported by a large body of evidence demonstrating that the sex of individuals depicted in sexual stimuli is less important for women's than men's sexual arousal. For example, when viewing erotic images depicting male-female interactions, heterosexual women spend an equal amount of time looking at same-sex and opposite-sex individuals, whereas heterosexual men focus selectively on opposite-sex figures (Lykins, Meana, & Kambe, 2006; Lykins, Meana, & Strauss, 2008). Similarly, the stimuli that elicit a genital response (e.g. sex or species of stimuli) are much less specific for women than they are for men, suggesting that women have an arousal response to sexual stimuli that is not preference specific, whereas men's responses are specific to their sexual interests (Chivers & Bailey, 2005; Chivers, Rieger, Latty, & Bailey, 2004; Lippa, Patterson, & Marelich, 2010). As such, women's sexual desire has been suggested to be broadly directed towards attractive individuals in general, while men's is more specific to their preferred sex (Bailey, 2009; Welling, Jones, & DeBruine, 2008).

Women have been shown to exhibit a shift in mate preferences across the menstrual cycle, with increased preferences for femininity and apparent health during periods of low conception risk (i.e. high progesterone; preferences for femininity occur in both male and female faces, see Jones et al., 2005), and increased preferences for masculinity and symmetry during periods of high conception risk (i.e. high estrogen), particularly when evaluating men as short-term partners (Little, Jones, Burt, & Perrett, 2007; Penton-Voak et al., 1999). Although these shifts in preferences across the menstrual cycle have been extensively explored (see Jones et al., 2008 for a review), very little work has been done exploring the incentive salience of potential mates across the cycle. While it seems women change what they like across the cycle, do they also change what they want? A better understanding of how these factors influence motivated behavior among women could help bridge the gap in the current literature regarding mate preference versus mate choice.

Women's sexual interests fluctuate across the cycle – arousability and frequency of female-initiated sex both peak mid-cycle (Hendricks, Piccinino, Udry, & Chimbira, 1987; Slob, Bax, Hop, Rowland, & van der Werff ten Bosch, 1996). The tendency to show intrasexually competitive behaviors also peaks mid-cycle, with heightened derogatory responses to other women (Fisher, 2004) and altered consumer behavior to enhance appearance and outdo attractive rivals (Durante, Li, & Haselton, 2008). Gangestad and colleagues recently found that women show an increased emphasis on the importance of physical attractiveness when considering a potential partner, as well as increased arousal at the thought of attractive men and greater interest in having sex with attractive men during peak fertility (Gangestad, Thornhill, & Garver-Apgar, 2010). Taken together, these studies suggest that women may show cyclic shifts in their motivation to view high quality mates (i.e. attractive men) across the menstrual cycle.

Using a key-press paradigm (Aharon et al., 2001), we explored the incentive salience of facial attractiveness across the menstrual cycle. Previous work exploring the incentive salience ('wanting') of attractiveness among men has indicated liking (i.e. attractiveness ratings) and 'wanting' (i.e. motivation) are dissociable aspects of reward and can yield differential patterns of face preferences (Aharon et al., 2001; Elman et al., 2005). Specifically, men have been shown to give equally high aesthetic ratings to attractive male and female faces, whereas they only work to view attractive female faces. These findings suggest that the motivational key-press paradigm may yield new insight into face preferences and mating behaviors. Menstrual cycle phase has been shown to modulate reward-related brain responses to monetary and food rewards (Dreher et al., 2007; Frank, Kim, Krzemien, & Van Vugt, 2010), male faces evaluated as potential sexual partners (Rupp et al., 2009), and subjective reports of pleasure following drug administration (Evans, Haney, & Foltin, 2002). In accordance with these previously observed effects of cycle phase on the hedonic quality of drug use, it may be that women experience a general increase in positive appraisal of stimuli during the follicular phase (i.e. mid-cycle), which exaggerates the incentive salience of rewarding stimuli. If this were the case, we would expect a general increase in motivation to view attractive faces across the cycle (regardless of stimulus sex).

Alternatively, as preferences (or liking) for aspects of male appearance that indicate high genetic quality have been shown to increase during the follicular phase of the menstrual cycle, it may be the case that these features hold greater incentive salience and are also 'wanted' more during periods of high conception risk. Rupp and colleagues (2009) found that when assessing male faces as potential sexual partners, women show increased activation in the orbitofrontal cortex during the follicular phase of the menstrual cycle (as compared to the luteal phase). Rupp et al. did not report on female faces, but based on available evidence, it is possible that women will show increased motivation to view opposite-sex attractiveness, rather than attractive faces in general, during the follicular phase of the menstrual cycle. Indeed, this prediction follows from studies of other primates: female macaque monkeys and chimpanzees display increased preference for viewing conspecific male faces during the receptive part of estrus/menstrual cycle, but show no comparable change in preference for viewing conspecific female faces – in fact, they show increased agonistic responses towards other females (Lacreuse, Martin-Malivel, Lange, & Herndon, 2007; Martin-Malivel, Lange, & Lacreuse, 2006).

In light of the evidence, three possible predictions can be made about women's motivation to view attractive faces across the menstrual cycle. First, because women show a non-specific arousal response and heightened reward-related responses mid-cycle it may be that motivation to view attractive faces of either sex increases during peak fertility. Secondly, because intrasexually competitive behaviors increase mid-cycle, it may be the women show heightened motivation to view attractive female faces (i.e. potential rivals). Third, because women have greater interest in sexual partners during peak fertility women may show cyclic shifts in their motivation to view high quality mates (i.e. attractive men).

5.2 Methods

5.2.1 Participants

Twenty-seven Caucasian women aged 18-25 years (*M* = 21.0, *SD* = 1.9) were recruited to participate three times during the menstrual cycle: menstrual phase, late follicular phase (i.e. peak fertility, ovulation), and luteal phase. Ethnicity was initially assessed in the tracking phase and confirmed at the time of participation. All participants were students at the University of St Andrews and were native English speakers. Participants were paid £5 per hour at each testing session for their time. All participants provided informed consent prior to participation and were debriefed at the end of the final testing session.

Menstrual cycle work is inherently difficult to conduct due difficulties in accurately assessing and scheduling test dates. In the present work, participants were asked to complete a monthly online report of the onset of menstruation for three months prior to testing. This process served dual functions; firstly, as menstrual cycle studies are characterized by high drop out rates, three months of survey completion prior to actual testing acted as an initial screening to help eliminate participants who were unlikely to complete all three test sessions. The second, and most important, function of the prescreening survey was to establish cycle length, which aids in the *accurate* scheduling of testing sessions. The menstrual session, characterized by low levels of both estrogen and progesterone (see Figure 5.1 for estimated hormone levels across the menstrual cycle), was scheduled during the time of menstrual bleeding (day 2-6, *Mean* = 3.8, *SD* = 1.3). Timing of the late follicular phase (i.e. ovulation, high estrogen relative to progesterone and a spike in testosterone, approx. day 12-16, *Mean* = 14.9, *SD* = 2.6) was confirmed using at-home LH surge testing (BabyMad Ltd), which has been shown to be 97% concordant with ovulation detection using ultrasonography (Guermandi et al., 2001). All women were tested within 48 hours after a positive test result. The luteal session, characterized by high progesterone relative to estrogen, was scheduled during days 19-28 of the cycle (assessed using the count forward method; *Mean* = 24.2, *SD* = 2.9).

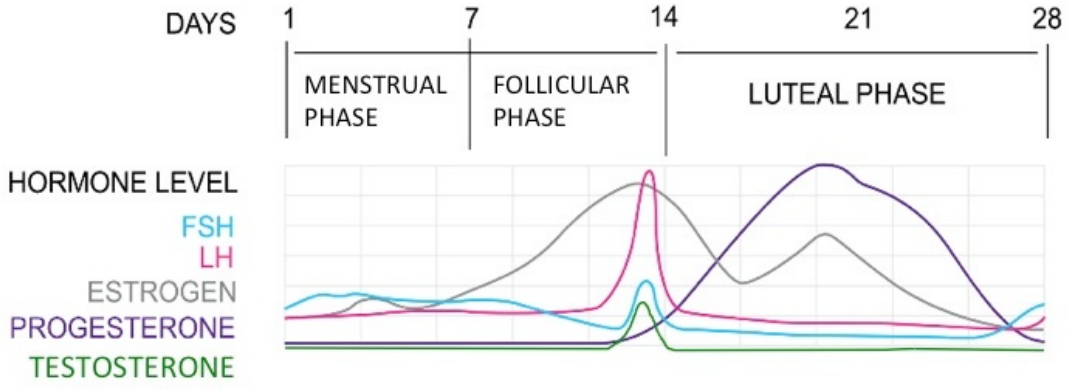

Figure 5.1 Estimated relative levels of estrogen, progesterone, testosterone as well as follicle stimulating hormone (FSH) and luteinizing hormone (LH) across a normal 28-day menstrual cycle.

Order of cycle phase at first testing was varied across participants (10 menstrual, 4 follicular, 12 luteal). Data from one woman was excluded due to contraceptive use within the past 90 days; none of the remaining women had used hormonal contraceptives or hormone-containing medications in the past 90 days, nor were they pregnant or breastfeeding. Thirteen women did not complete all three testing sessions and were not included in the analysis. Sexual orientation was assessed using a 7-point scale where 1 = completely homosexual, 4 = bisexual, and 7 = completely heterosexual. Only heterosexual participants (i.e. those reporting a score of 5 or higher) were included in the analysis presented here; two women were excluded on the basis that one identified as homosexual and the other as bisexual. The final analysis consisted of

11 women. Although this is a relatively small sample size, within subject studies[15] of cyclical effects often utilize samples smaller than 20 (Dreher et al., 2007; Evans et al., 2002; Jones, Perrett, et al., 2005; Krug, Plihal, Fehm, & Born, 2000; Little, Jones, & Burriss, 2007; Miller, Tybur, & Jordan, 2007; Rupp et al., 2009; Wallen & Rupp, 2010) and cyclical shifts have been observed in samples as small as N=7 (Laeng & Falkenberg, 2007). Average cycle length was 28.7 days (SD = 2.7). Of these 11 women, 8 were currently single while 3 had partners.

5.2.2 Stimuli

Twenty attractive and unattractive adult faces of each sex were presented in random order to participants (with 46 filler faces of average attractiveness; Hahn et al., 2012). The male and female attractive and unattractive stimulus groups were matched for attractiveness based on independent ratings obtained from 76 raters (36 female) that ranged in age from 16-42 (*M* = 22.16, *SD* = 4.402; see Table 5.1 for stimulus group statistics). All images were head-on facial shots of individuals (approximated age 18-35 years). Images were aligned (based on interpupillary distance) and masked with a black background to remove clothing/background information prior to presentation.

Table 5.1. *Attractiveness ratings for the "attractive" and "unattractive" male and female face groups.*

Stimulus Group	*Mean*	*SD*	Chronbach's α
Attractive Female	4.7	0.28	.906
Unattractive Female	2.8	0.46	.926
Attractive Male	4.5	0.42	.943
Unattractive Male	2.6	0.34	.942

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[15] A number of these studies report multiple experiments with a large between subject sample and a small within subject sample.

5.2.3 Procedure

Participants first completed a demographics questionnaire that assessed their relationship status, sexual orientation (7-point Likert scale), pregnancy (past and current), and contraceptive use (past and current). They then completed a key-press training task (as described in Section 2.2.2.1) and the experimental key-press task whereby they were able to control the viewing time of each image by pressing an alternating set of keys. Default presentation time was set at 4 seconds. However, participants could increase this duration by pressing "N" & "M" alternately or decrease this time by pressing "Z" and "X" alternately (following Aharon et al., 2001). Participants were told that the length of the task was set (although in actuality the total task duration was dependent on their key-pressing behavior). Participants were informed of this deception during the experiment debriefing. The measured number of key-presses per trial was calculated by subtracting the number of negative key-presses (i.e. to decrease viewing time) from the number of positive key-presses (i.e. to increase viewing time). This key-pressing task operationalizes motivation by measuring amount of effort/work exerted to view an image, and its previous use in conjunction with neuroimaging has indicated that it is an accurate behavioral measure of incentive salience (Aharon et al., 2001). Following the key-press task, participants were asked to rate the attractiveness of each face using a 7-point Likert scale (where 1 = very unattractive, 7 = very attractive).

5.3 Results

5.3.1 Analyses

Separate 2x2x3 repeated-measures ANOVAs were run on the rating and key-press data. For both analyses *stimulus sex* (2 levels: female, male), *attractiveness* group (2 levels: attractive, unattractive) and *cycle phase* (3 levels: menstrual, follicular, luteal) served as within-subject factors. Although some studies have shown stronger cyclical shifts in partnered as compared to single women (Havlicek, Roberts, & Flegr, 2005; Pillsworth, Haselton, & Buss, 2004), due to very small sample sizes in the relationship groups, particularly the partnered women ($N_{single} = 8$, $N_{partnered} = 3$), relationship status was not included in the analyses presented here[16].

5.3.2 Rating Task

A main effect of *attractiveness* was the only significant finding among the rating data. Unsurprisingly, attractive faces were rated higher than the unattractive faces ($F(1,10) = 102.8$, $p < .001$, $MSE = 1.54$, $\eta_p^2 = .911$). No other effects or interactions were observed for the within-subject factors in the rating data ($.097 < p < .984$). These data suggest that women's "liking" of facial attractiveness does not change across the menstrual cycle. See Figure 5.2 for graphical representation of the liking data.

5.3.3 Key-press Task

There was a main effect of *attractiveness* ($F(1,10) = 25.7$, $p < .001$, $MSE = 73.3$, $\eta_p^2 = .720$) such that more effort was exerted to view attractive faces than unattractive faces. All other main effects and two-way interactions were non-significant ($.091 < p < .579$). There was a significant 3-way interaction between *stimulus sex, attractiveness* group and *cycle phase* ($F(2,20) = 4.42$, $p = .026$, $MSE = 2.97$, $\eta_p^2 = .307$, see Figure 5.3). To better understand this interaction, individual analyses were conducted for male and female faces (repeating the 2x3 ANOVA as described above separately by stimulus sex). For the male faces, only a significant effect of *attractiveness* was observed ($F(1,10) = 28.7$, $p < .001$, $MSE = 39.1$, $\eta_p^2 = .741$). There was no effect of *cycle phase* ($p = .285$), and the *attractiveness* by *cycle phase* interaction was non-significant ($p = .401$). For female faces, there was a significant effect of attractiveness ($F(1,10) = 19.4$, $p = .001$, $MSE =$

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[16] When *relationship status* was included as a between-subject factor (2 levels: single, partnered), there was no between-group difference in the rating task (i.e. liking) based on relationship status ($p = .752$), and relationship status did not interact with any of the within-subject factors ($.104 < p < .708$). For the for the key-press task (i.e. wanting), a significant interaction occurred between *stimulus sex* and *relationship status* ($F(1,9) = 9.26$, $p = .014 \eta_p^2 = .507$). Although post-hoc paired comparison t-tests indicated that single women exerted greater effort to view male faces than female faces ($t(7) = 3.78$, $p = .007$) while partnered women worked equally hard for faces of both sex ($t(2) = 1.24$, $p = .341$), there were no group differences in effort expended to view same-sex faces, overall, between single and partnered women ($t(9) = 1.04$, $p = .324$). The small sample size for partnered women makes any interpretation of these data *extremely* speculative, however it may be that partnered women split their effort between mate search and mate guarding behavior while single women focus more effort on mate search. There were no interactions between *relationship status* and *cycle phase* or *attractiveness* (all $p > ..61$). Additionally, the *stimulus sex by attractiveness by cycle phase* interaction persisted when *relationship status* was included in the model ($p = .03$).

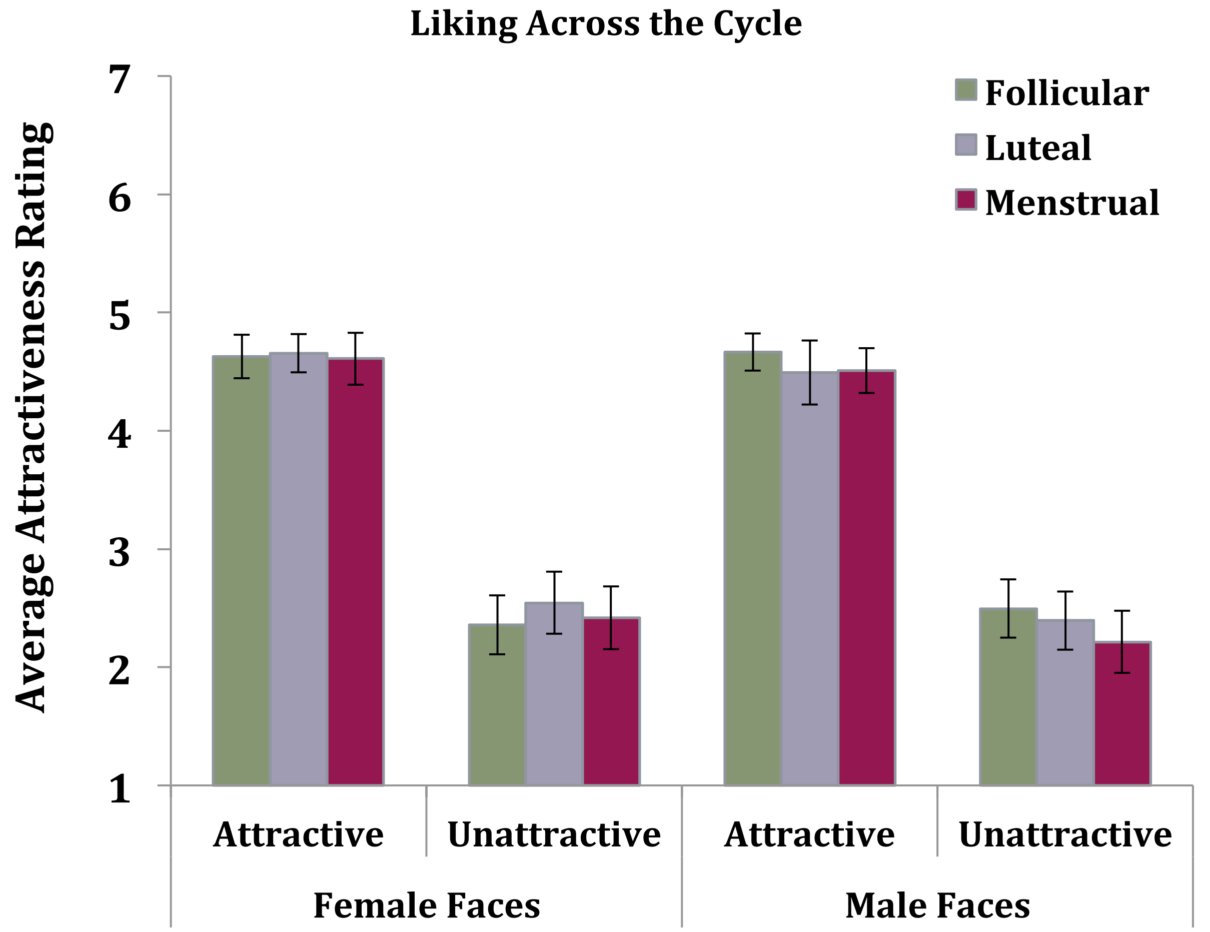

Figure 5.2 Average attractiveness rating for same-sex and opposite-sex faces at different cycle phases (error bars represent SEM). No cyclical changes in liking responses were observed.

39.9, $\eta_p^2 = .660$), but no effect of *cycle phase*, overall ($p = .103$). The *attractiveness* by *cycle phase* interaction was marginally significant ($F(2,20) = 3.29$, $p = .058$, $MSE = 3.61$, $\eta_p^2 = .248$), suggesting that cyclical shifts in motivation to view same-sex faces were driving the previously reported 3-way interaction. Paired comparison t-tests indicate that women show more motivation to view attractive same-sex faces during the follicular phase than during the menstrual phase ($t(10) = 2.31$, $p = .043$). A similar pattern was seen when comparing the follicular phase and luteal phase, although this difference was not significant ($t(10) = 1.75$, $p = .110$). No difference in motivation to view attractive same-sex faces was seen between the luteal and menstrual phases ($t(10) = 1.24$, $p = .244$). No differences were observed between cycle phases for the unattractive female faces ($.372 < p < .797$).

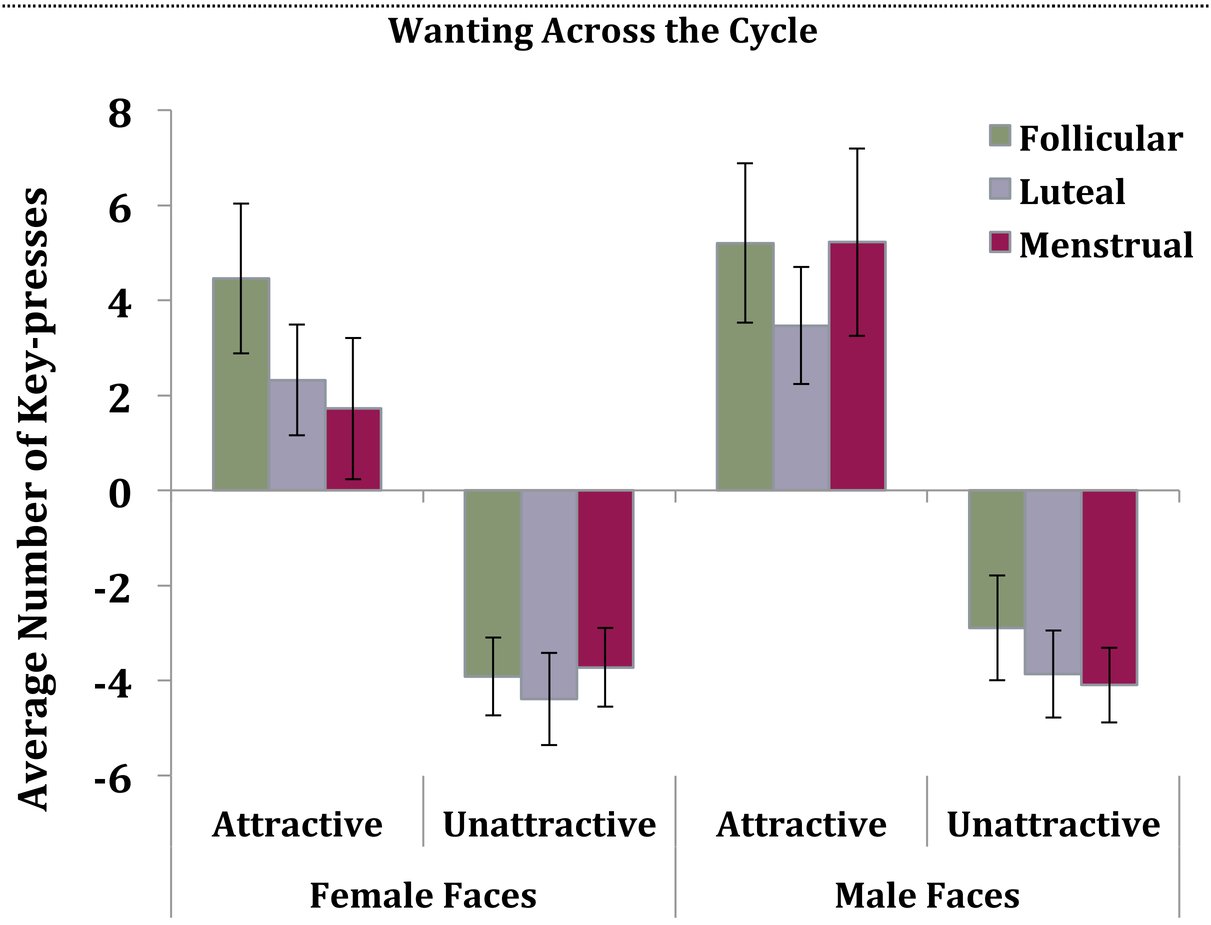

Figure 5.3 Average number of key-presses for same-sex and opposite-sex faces at different cycle phases (error bars represent SEM). Women exert greatest effort to prolong viewing time of same-sex faces during the follicular phase of the menstrual cycle.

5.4 Discussion

The present study demonstrated cyclical shifts in the motivational salience of facial attractiveness among same-sex faces in a small within-subject sample of heterosexual women. This work is the first to demonstrate that the motivational salience of beauty may be variable *within* an individual. Notably, within-subject menstrual cycle data is among the more difficult types of data to collect. Due to high demands on participants (i.e. multiple test sessions, cycle tracking, at-home ovulation testing, etc.), a high attrition rate is very common in these types of studies (e.g. Havlíček, Dvořáková, Bartoš, Flegr, & Dvor, 2006). In spite of these difficulties, it is critical that researchers in the field endeavor to ensure accurate scheduling so that reliable inferences can be made with respect to the hormonal mechanisms that may underlie observed behavioral and preference shifts across the menstrual cycle. To that end, in the present work we chose to utilize LH-surge tests to aid in the scheduling of the follicular test session rather than relying on diary data alone. Participants need to return to the lab within 48-hours of attaining a positive result on the LH-surge test. This constrain proves particularly difficult as participant schedules are not always easy to negotiate and constant contact must be maintained with participants to allow for testing within the required window. We also elected to test women at three points across the menstrual cycle, rather than two, because very different hormonal profiles are exhibited at each phase with respect to relative levels of estrogen and progesterone (see Section 5.2.1). Due to the difficulties associated with scheduling for menstrual cycle studies, even the relatively small sample collected in this study required 6 months (including pre-testing tracking). In light of this, researchers intending to collect menstrual cycle data in the future should bear in mind the time constraints and high attrition rates associated with this type of work.

Although we had predicted that women's motivation to view attractive faces of the *opposite-sex* would vary across the menstrual cycle, we found that it was actually motivation to view attractive *same-sex* individuals that shifted across the cycle. That women did not show increased motivation to view attractive faces, in general, suggests that our finding is not simply due to a general increase in the hedonic quality of stimuli or elevated sexual arousal during the follicular phase of the menstrual cycle. If women's increased motivation to view other women were due to a general increase in the hedonic quality of the stimuli during the follicular phase, we should have seen increased motivation to view attractive male faces in addition to attractive female faces. While the argument that women have a "fluid" sexual preference might account for women's motivation to view attractive same-sex faces *in* general, it does not explain cyclical variations in this behavior. If mid-cycle increases in sex-drive were responsible for increased motivation to view attractive same-sex individuals, we would expect to see a similar cyclical shift in motivation to view attractive opposite-sex faces. However, no such cyclical changes in motivation to view men existed in the present dataset. Cyclical changes in motivation to view same-sex faces may reflect increased motivation to view potential rivals; as such, we posit that increased motivation to view attractive females may reflect intrasexual competition in addition to sexual attraction/interest.

Women may exert effort to view attractive peers to "check out the competition" during peak fertility – the time when it would be most likely for women to compete for high quality mates. This behavior could potentially act to increase mating success. Gathering relevant information about competitors may aid women in determining when it is worthwhile to invest effort in potential mating opportunities; when there is high competition (i.e. attractive rivals), women may waste energy pursuing high quality potential mates who might choose another female. Additionally, the most attractive peer faces can be a source of aspiration and fashion tips. By attending to attractive peers, women can realize their own-mate value and be informed in decisions about competition for a mate (see Little & Mannion, 2006).

Intrasexual competition is a multifaceted phenomenon and includes competition for mates through the establishment of same-sex dominance hierarchies, derogation of same-sex competitors, and sexual poaching tactics (Buss, 1988; Schmitt & Buss, 1996). Men place a high premium on physical appearance when assessing a potential partner (Buss & Barnes, 1986; Buss, 1988); it follows that women must compete with one another in terms of appearance (Campbell, 2004). Women appear to be quite sensitive to the attractiveness of other women. The lack of cyclical shift in women's liking responses to attractive peers (i.e. attractiveness ratings given in the rating task) suggests that women's sensitivity to rival attractiveness may not be shifting. Rather it is the motivation to view these rivals that changes across the cycle.

Attractive women evoke stronger jealousy reactions than unattractive women (Dijkstra & Buunk, 1998; Massar & Buunk, 2010; Yarab & Allgeier, 1999), and women discriminate against highly attractive same-sex individuals in terms of hiring preferences (Agthe, Spörrle, & Maner, 2010). This jealousy response may be related to estrogen levels, as women using highdose estrogen contraceptives show stronger jealousy reactions than those using low-dose contraceptives (Cobey, Pollet, Roberts, & Buunk, 2011; Welling, Puts, Roberts, Little, & Burriss, 2012), and jealousy within an individual woman has been shown to be highest during the fertile phase of the cycle (K. D. Cobey et al., 2012). Additional evidence that estrogen may play a role in jealousy comes from work on post-menopausal women. Post-menopausal women show decreased dislike for attractive (feminine) same-sex rivals (Vukovic et al., 2009). That motivation to view attractive same-sex individuals in the follicular phase (characterized by high estrogen) was significantly higher than during the menstrual phase (a period of low estrogen) but not significantly higher than the luteal phase (characterized by low estrogen relative to progesterone, but not necessarily low levels of estrogen overall) may be explained by the relationship between estrogen and jealousy. Women showed decreased motivation to view attractive same-sex individuals during the luteal phase as compared to the follicular phase, but this difference was not significant. This may be because estrogen levels can remain quite high during the luteal phase.

Alternatively, testosterone may be influencing motivation to view attractive same-sex individuals if this motivated behavior is impacted by intrasexual competition. Studies exploring intrasexual competition in men have consistently demonstrated a link to testosterone (Kivlighan, Granger, & Booth, 2005; Mazur & Lamb, 1980; Mazur, Susman, & Edelbrock, 1997; Suay et al., 1999); however comparatively less work has been done exploring intrasexual competition among women. Recent work has demonstrated that when starting hormonal contraceptives, which suppress testosterone production, women show decreased levels of intrasexual competition – although this effect was only apparent in partnered women (Cobey, Buunk, & Roberts, *in press*). Interestingly, no differences in intrasexual competition were detected when comparing women at the fertile versus non-fertile phase of the menstrual cycle. Because we did not measure hormone levels directly, however, it is not possible to draw any definitive conclusions about the mechanisms underpinning the observed behavioral shifts in motivation.

The observed relationships in the literature between estrogen, testosterone and jealousy or intrasexual competition in women have yet to be confirmed using measured hormone levels. It is possible that trait levels of estrogen between women may account for variation in the general tendency to be jealous or intrasexually competitive while variation within a given menstrual cycle may account for state differences in these behaviors. The speculation presented here, that estrogen and/or testosterone may be linked to motivation to view attractive same-sex faces, would be further supported by assessing the relationship between the incentive salience of same-sex beauty and hormonal variations across the menstrual cycle. Unfortunately, due to the high cost of hormonal assays, it was not possible to conduct this analysis in the present study (although saliva samples were collected at the time of testing with the hope of being able to conduct hormonal analysis). Future work more directly testing the proposed link between sex hormone levels and motivation (as well as intrasexual behaviors such as competition and jealousy) would increase our understanding of the proximate mechanisms of these behaviors.

Women have been shown to increase intrasexually competitive behaviors during peak fertility in other behavioral domains. For example, Fisher (2004) found that women are more likely to derogate competitors during peak fertility. In the present dataset, there was a slight decrease seen in the attractiveness ratings given to female faces during the follicular phase (although this pattern was observed for all female faces, not just attractive faces). Although this was non-significant, this pattern of behavior is similar to that observed by Fisher (2004), and may add to the argument that intrasexual competition influences motivation to view same-sex individuals. Similarly, Durante et al. (2011) found that women alter consumer behavior across the menstrual cycle to enhance own appearance and “outdo attractive rivals” during peak fertility; specifically, in the follicular phase of the menstrual cycle women are more likely to purchase sexy clothes and accessories, particularly when primed to consider local same-sex peers (i.e. rivals). At peak fertility, women’s clothing plans reveal more of their body and hence may be more competitive in gaining male attention (Durante, Li, & Haselton, 2008).

The current study demonstrates that motivation to view attractive same-sex individuals increases during peak fertility and provide new insight into women's motivation to view same-sex faces. Previous research has indicated that attractive faces of both same-sex and opposite-sex individuals hold incentive salience among women (Levy et al., 2008). Here, we replicated this finding; women worked to increase the viewing time of attractive faces, regardless of the sex of the face. Levy (2008) emphasized that attractive same-sex faces hold incentive salience for women due to a "greater bisexual interest among heterosexual women." However, based on the present findings, we argue that intrasexual competition may also play a key role in women's motivation to view attractive same-sex individuals.

Chapter 6 General Discussion

For the past 30 years, evolutionary psychologists have worked to determine what beauty is. Key aspects of facial appearance, such as symmetry, apparent health, facial adiposity, and sexual dimorphism have been shown to influence perceptions of facial attractiveness, and are apparent in mate preferences. But how do these aspects of appearance influence the motivational salience of faces? In this dissertation, I utilize the novel key-press paradigm designed by Aharon et al. (2001) to explore mate preferences and mate choice behavior, as well as individual differences and cyclical changes in motivated behavior among women.

In Chapter 1, I discuss the decades of research that have suggested beauty can be decomposed into a number of quantifiable aspects of facial appearance. In Chapter 2, I explore the role of each of these factors with respect to the incentive salience of opposite-sex faces (i.e. potential mates). Cues to health may hold incentive salience in that it would be beneficial to be drawn to healthy potential mates, while avoiding sick looking individuals who could have direct (i.e. transmission of infectious diseases) and/or indirect (i.e. produce less healthy offspring) negative impacts on an individual's own health. The behavioral immune system (Schaller & Park, 2011) is sensitive to perceptual cues of pathogens and can trigger behavioral avoidance when such cues are detected. In light of the costs associated with social contact with unhealthy individuals, it would be evolutionarily advantageous to avoid unhealthy individuals, as they are potential sources of contagions. That other factors which have been shown to influence mate preferences (i.e. liking responses) such as facial averageness, sexual dimorphism, and facial adiposity did not have consistent direct effects on motivation (i.e. wanting responses) suggests that what we like and what we want in a mate may not be the same. Interestingly, a number of these factors had small indirect effects on motivation, suggesting that they may influence the incentive salience of faces through their effect on facial attractiveness. Studies utilizing rating or forced-choice paradigms should be cautious when interpreting results in regards to mate choice. Although some studies have indicated that mate preferences and mate choice are highly correlated (DeBruine et al., n.d.), others have indicated that preferences are differentiable from choice (Todd et al., 2007). Future work utilizing the key-press paradigm may yield a better understanding of how the underlying aspects of physical appearance impact the incentive salience of faces, and facial beauty.

In Chapters 2 and 3, I provide evidence of gender differences in the incentive salience of adult and infant faces, and suggest that reproductively relevant cues may hold incentive salience – the more relevant the cues, the higher incentive salience it should hold. High incentive salience for reproductively-relevant stimulus groups would be evolutionarily advantageous as increased motivation towards these groups could act to increase mating opportunities and reproductive success through increased offspring survival rates. Opposite-sex beauty appears to hold incentive salience among both men and women, although the incentive salience of this kind of beauty is stronger among men. Men benefit more from short-term relationships/encounters whereby they can maximize their reproductive success by impregnating many different women (males from polygamous societies have greater rates of reproductive success than those from monogamous societies, although serial monogamists have highly variable rates of reproductive success; see Brown et al., 2009). As such, men should seek out a greater number of partners than women. This may be reflected in the substantial effort men exert to view attractive opposite-sex individuals. Motivation to seek out multiple mates would act to increase men's reproductive success. In the case of same-sex faces, women are motivated to view both same- and opposite-sex beauty equally whereas men are only motivated by opposite-sex beauty. Because women compete with one another in terms of attractiveness (whereas men compete in terms of status and resources), same-sex beauty may be a more reproductively relevant cue for women than it is for men. This would explain the observed gender difference for motivation to view same-sex faces based on attractiveness.

In the case of infant faces, women show stronger motivation to view infant faces than do men. Because women typically invest more heavily in offspring than do men (Bjorklund &

Shackelford, 1999), it may be that infants hold higher incentive salience among women than men because they are more reproductively-relevant for women. Parental care is associated with lower offspring mortality (Clutton-Brock, 1991). In the case of *paternal* care, paternal investment may improve offspring survival rates; as such, the reproductive benefits of seeking out additional mates may not necessarily outweigh the benefits of parental investment. As such, human males typically show a mixed reproductive strategy with individual males varying in their emphasis on mating and parenting (Geary, 2005). In light of this evidence, as discussed in Section 3.4.3, lumping all men together may occlude individual differences in the incentive salience of infants among men. Further work exploring individual differences among men may provide a better understanding of the motivational salience of infants, particularly in the case of nulliparous versus parous individuals.

Interestingly although men showed lower motivation to view infant faces than women did overall, men were able to differentiate between more-cute and less-cute infant faces. This finding brings to light the importance of context for motivational studies. The incentive salience of a given feature, such as beauty or age, may be contingent upon the alternative choices. Indeed, previous research has demonstrated that reward processing is context-dependent (Holroyd, Larsen, & Cohen, 2004; Nieuwenhuis et al., 2005). Using fMRI, Holroyd et al. demonstrated that reward-sensitive areas throughout the brain, including the striatum and prefrontal cortex, exhibit context sensitivity and the value of a given option/outcome is determined based on the range of possible outcomes/options available. As such, it is possible that a stimulus that holds incentive salience in once instance may lose its salience in the context of ‘better options’, as may be the case for men viewing infant faces in the context of attractive female faces. This context dependency is particularly interesting with regard to evolutionary psychology due to the high presence of media influence in the modern age. Human mate choice is a ‘frequency dependent market’, in which attractive individuals (i.e. those with a high mate value) are in demand and can choose among potential mates (Buston & Emlen, 2003; Pawlowski & Dunbar, 1999). Exposure to media ideals has shifted perceptions of what is ‘normal’ or average over the past few decades and this may affect mate preferences and mate choice (Hargreaves & Tiggemann, 2003; Kenrick & Gutierres, 1980; Spillman & Everington, 1989). The incentive salience of 'normal' beauty may become lost in the context of supermodel beauty as seen on the media.

These potential media effects seem particularly salient for women. In Chapters 4 and 5, I report individual differences and cyclical shifts in the incentive salience of same-sex beauty among women. Although this phenomenon was previously explained as the result of a less stringent sexual preference among women, I argue that social comparison or intrasexual competition may partly explain this finding. Social comparison among women could potentially act to increase mating success, in spite of the fact that attentional resources are being allocated to both same- and opposite-sex beauty. Gathering relevant information about competitors may aid women in determining when it is worthwhile to invest effort in potential mating opportunities; when there is high competition (i.e. attractive rivals), women may waste energy pursuing high quality potential mates who might choose another female. Additionally, the most attractive peer faces can be a source of aspiration and fashion tips. By attending to attractive peers, women can realize their own-mate value and be informed in decisions about competition for a mate.

6.1 Methodological Notes

6.1.1 Considering Sexual Orientation

In all studies presented in this thesis, data analysis was restricted to heterosexual participants. Sexual orientation was assessed using a self-report scale that functions similarly to the Kinsey Scale (Kinsey, 1948). Participants are able to identify their sexual orientation on continuum that ranges from exclusively homosexual to exclusively heterosexual. It is possible that participants do not accurately report their sexual orientation, however this type of inaccuracy is a limitation of any self-report construct. Research in the field of Evolutionary Psychology typically relies on self-reported sexual orientation data collected using either dichotomous response options or continua (for a review of the benefits and limitations of each method, see Sell, 1997). In general, self-reports of sexual orientation have been shown to correspond to other measures of arousal or attraction such as pupil dilation (Rieger & Savin-Williams, 2012) and genital arousal (see Chivers, Seto, Lalumière, Laan, & Grimbos, 2010 for meta-analysis). Additionally, self-reported sexual orientation appears to be consistently reported across multiple test sessions. For example, in a set of 1300 male drug users, less than 5% demonstrated any inconsistency in self-reported sexual orientation across a 5-year span with an average number of 8 reports per participant during that time (Washington et al., 2006). Similarly in a normal, healthy population of 2560 participants heterosexuality was found to be more consistently and stably reported in both men and women than was bisexuality or homosexuality (Mock & Eibach, 2012).

6.1.2 Online versus In Laboratory Testing

The studies presented here consist of data collected both in the laboratory (Chapters 2, 3, and 5) as well as data collected online (Chapters 2 *(ratings)* and 4). An issue to consider when collecting data online is that of data quality. Because participants do not attend test sessions in the laboratory, it is not possible to confirm their gender, ethnicity, age, or additional demographic factors. However, by testing online we are able to reach a broader test population than the traditional young, relatively economically stable, University student population. It is possible that online participants have different motivation for participating than the Undergraduate students who receive course credit or payment because online participants are not remunerated in any way. Interestingly, in a sample of 380 online participants, 40% reported curiosity as their reason for participating, while 25% expresses a desire to help research or liking of taking part in surveys, and only 4% expressed boredom as their reason for having taken part (Buchanan, 2000).

Testing online versus in the laboratory therefore represents a trade off between sample diversity and data quality. Notably, a number of studies have suggested that participants from online and in lab studies behave similarly on questionnaire tasks (e.g. Buchanan & Smith, 1999; Pasveer & Ellard, 1998; Riva, Teruzzi, & Anolli, 2003) and provide similar perceptual judgments of faces (e.g. Buchanan, 2000; Conway et al., 2008; Feinberg et al., 2005; Jones et al., 2005; Krantz, Ballard, & Scher, 1997). For example, men tested online and in the lab both show preferences for facial composites of women with higher-pitched voices as compared to facial composites of women with lower-pitched female voices (Feinberg et al., 2005).

Similarly, in a large between-subject sample of women, cycle phase was shown to predict preferences for apparent health in male faces – with stronger preferences for health during the luteal phase of the cycle, when progesterone levels are high. This pattern of results was again demonstrated in a smaller within-subject sample collected in the laboratory (Jones et al., 2005). Indeed, a number of menstrual cycle studies have utilized small within-subject samples collected in the laboratory and larger between-subject samples collected online and have found comparable results in both test groups (e.g. Little, Apicella, et al., 2007; Little, Jones, & Burriss, 2007). In a series of studies on the interaction between gaze preference and emotion, Conway and colleagues (2008) found that participants tested online and participants tested in the laboratory both demonstrated stronger impact for direct gaze when rating facial attractiveness for faces which displayed a happy expression as compared to a disgust expression. This pattern of results was stronger in opposite-sex faces as compared to same-sex faces in both online and in lab samples.

Of particular relevance to the online work presented here (i.e. own-attractiveness effects), similar patterns of individual differences with respect to perceptual judgments of faces have been observed in online and in-lab samples. Men's interest in high-sensation activities (which reflects high-risk taking) has been found to be positively correlated with femininity preferences in female faces across two online and one in-lab samples (Jones et al., 2007). In women, individual differences in own-dominance has been shown to relate to perceptions of dominance in same-sex faces (Watkins, Quist, Smith, DeBruine, & Jones, 2012).

With the overwhelming evidence that perceptual judgments of faces (i.e. liking responses) are comparable for online and in-lab populations, it is reasonable to infer that the 'wanting' responses observed in the studies presented in this body of work may also be comparable between the two types of samples. Although we may be able to anticipate similar patterns of behavior across these samples, the feasibility of using the key-press task online warrants consideration. Because the key-press experiment will run through to completion with or without active participation, it was essential that we eliminate participants who failed to complete the key-press task (i.e. those who did not average at least 1 key-press per trial); as such, we are able to potentially control for participants who may have navigated away from the experiment while letting it run. Even with this step, it is not possible to confirm active participation from all participants (although the same could be said for those who participate in the laboratory).

An additional concern is that of task understanding. When participants attended test sessions in the laboratory, the experimenter was able to guide them through a training task designed to familiarize them with the key-press paradigm, as it is not necessarily intuitive to understand. Although we developed a similar training task for the online participants, these participants were not able to ask questions or express concern if they did not fully understand the task. By randomizing trial or block orders, we hoped to control for differences in learning rates. That a similar pattern of results for the incentive salience of beauty, as well as the impact of own-attractiveness has been observed in the online and in-lab samples described here indicates that the key-press task is a viable paradigm for online use. Future work validating the use of this task online, as well as optimization of the training task and experimental parameters (e.g. automatic running versus individual trial start) could enhance the attractiveness of this paradigm to researchers in other fields of Psychology.

6.1.3 Default Settings of the Key-Press Paradigm

The work presented here reflects motivated behavior when default viewing time was set at 4 seconds (Chapters 2, 3, and 5) or 8 seconds (Chapter 4). Including this work, there are a total of 11 studies that have used the key-press methodology[17] to explore the incentive salience of facial stimuli; default setting across these studies range from 4 seconds to 8 seconds (see Table 6.1 for a summary of the experimental parameters and findings). That attractive faces have typically yielded positive key-presses (i.e. to increase viewing duration) while unattractive faces have typically yielded negative key-presses (i.e. to decrease viewing time) would suggest that beauty is rewarding while unattractiveness is aversive. However, this aversive or avoidant response (i.e. negative key-pressing) could be a function of the default presentation time rather than the stimulus presented. It may be the case that any stimuli presented for an extremely long default duration would warrant negative or aversive key-pressing responses. The differential motivation between attractive and unattractive faces (i.e. the difference in time spent looking at each class of images) may be a more accurate variable to assess than absolute levels of key-pressing or viewing time.

Interestingly, studies that have looked at the incentive salience of same- and opposite-sex beauty among men have consistently demonstrated positive key-press behavior to attractive female faces and negative key-press behavior to attractive male faces and unattractive faces of either sex (see Table 6.1). This pattern of results holds when the default presentation time was 4 seconds (Dai et al., 2010; Elman et al., 2005; Hahn, Chapter 2; Levy et al., 2008) as well as 8 seconds (Aharon et al., 2001). Similarly, in women attractive faces of either sex have been found to elicit positive key-press behavior while unattractive faces elicit negative key-press behavior across studies with default presentation times of 4 seconds (Dai et al., 2010; Hahn, Chapter 2 & Chapter 5; Levy et al., 2008) and 8 seconds (Hahn, Chapter 4). Based on this evidence, it would seem that motivation to increase viewing for stimuli with high incentive

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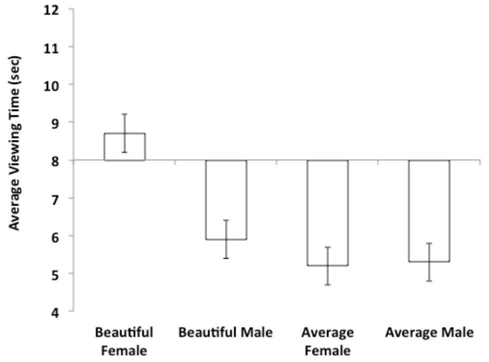
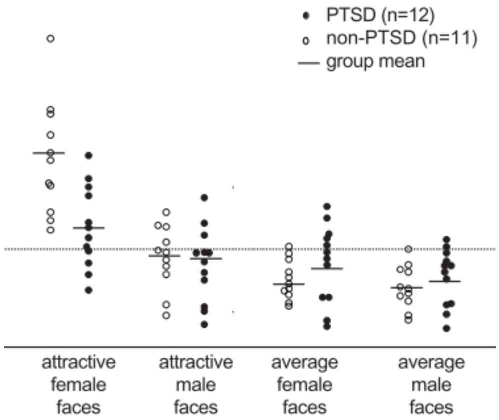
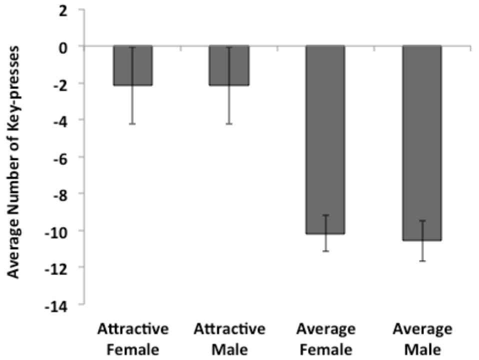
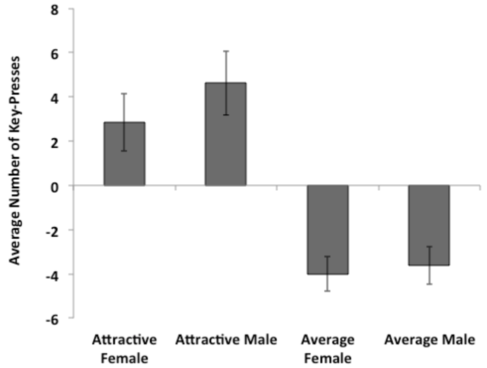
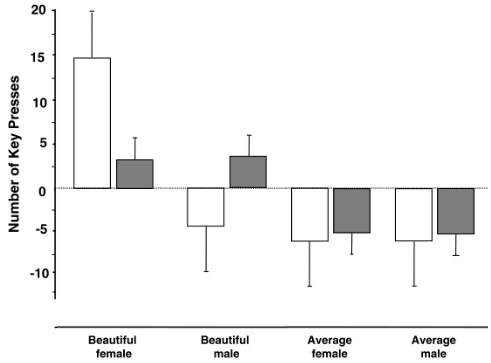
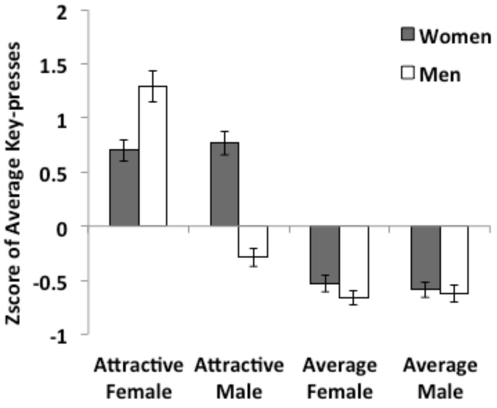
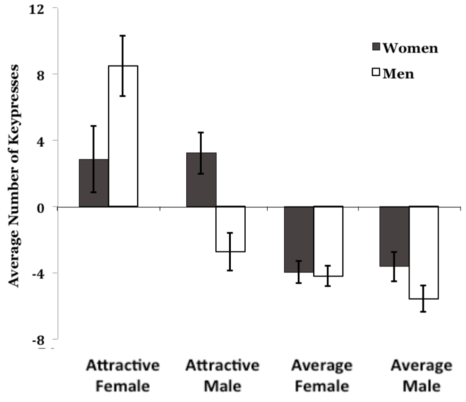
[17] Note: other studies have utilized effort-based tasks similar to the key-press task to measure motivation (e.g. Ferrey, Frischen, & Fenske, 2012; Lappalainen & Epstein, 1990; Treadway, Buckholtz, Schwartzman, Lambert, & Zald, 2009).

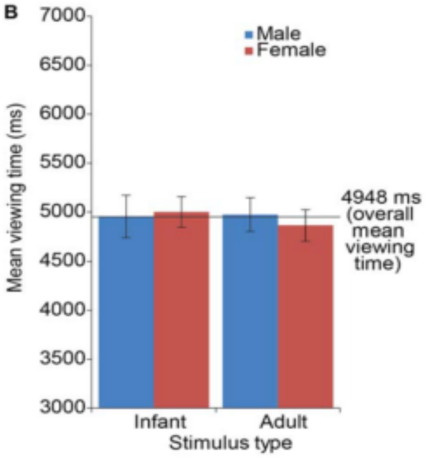
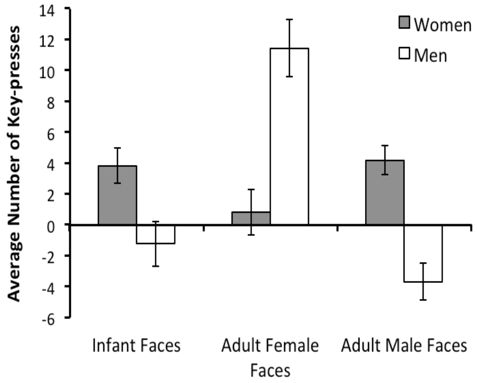
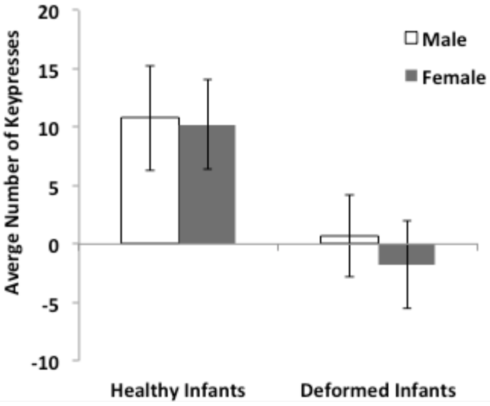
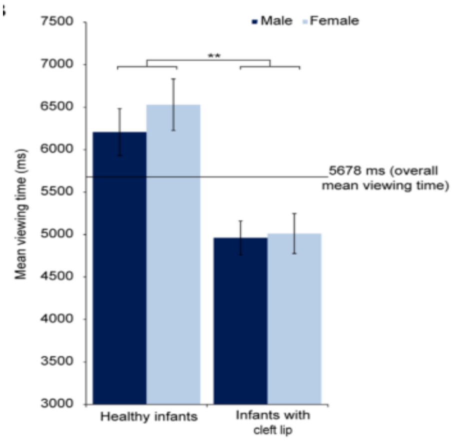
salience and decrease viewing for 'aversive' stimuli is a pattern of results that is quite robust to variations in experimental parameters. Similar follow up work I am currently conducting indicates that this pattern of responses in both men and women will hold true across default presentation times ranging from 1 second to 8 seconds (tested at each 1 second increment), however data collection is ongoing.

Studies utilizing infant faces as stimuli have varied default presentation time from 4 seconds (Hahn et al., 2013; Yamamoto et al., 2009) to 5 seconds (Parsons et al., 2011a) to 6 seconds (Parsons et al., 2011b). Interestingly, these studies are the ones that have failed to demonstrate a consistent pattern of results. Whether this is a factor of differences in default presentation time (or other experimental parameters), differences in the stimuli, or a combination of these factors remains to be determined. Both studies that compared responses to healthy and deformed infants demonstrated positive key-pressing to normal, healthy babies and negative key-pressing to deformed or abnormal babies when default presentation time was 4 seconds (Yamamoto et al., 2009) and 6 seconds (Parsons et al., 2011b). However, when normal infants were presented in the context of adult faces, Hahn et al. (2013) using a 4 second default viewing duration found that men and women behaved similar to previous studies with respect to adult beauty and demonstrated gender differences in motivation to view infants, with women demonstrating positive key-pressing overall to infant faces, and men showing neither positive nor negative key-pressing for the infant stimuli. Conversely, using a 5 second viewing duration, Parsons et al. (2011a) did not detect any gender differences in response to either adult or infant faces. Looking at the graph in Table 6.1 however, it appears that little key-pressing was exerted for any of the stimulus classes. These studies differ with respect to both default experimental settings and stimuli (Hahn: high versus low attractive for both adult and infant faces, Parsons: range of infant cuteness, average adult faces); as such, it is not possible to determine if the experimental parameters or the stimuli are responsible for the conflicting results.

Table 6.1 Summary of the experimental studies to date that have used the key-press methodology. Default presentation times range from 4 seconds to 8 seconds. Those studies that have explored the incentive salience of adult beauty have found similar patterns of positive and negative key-pressing across various default settings. Studies are arranged by stimulus type, then participant gender, then chronologically.

Authors	Date	Default Time	Participants	Stimuli	Result
Aharon et al.	2001	8 sec	Men Only	Female & Male Faces	
Elman et al.	2005	4sec	Men Only (PTSD vs control)	Female & Male Faces	
Hahn et al.	Chapter 4	8 sec	Women Only (Ignoring own-attractiveness ratings)	Female & Male Faces	
Hahn et al.	Chapter 5	4 sec	Women Only (Ignoring cycle phase)	Female & Male Faces	

<table>
<tr><th>Authors</th><th>Date</th><th>Default Time</th><th>Participants</th><th>Stimuli</th><th>Result</th></tr>
<tr><td>Levy et al.</td><td>2008</td><td>4sec</td><td>Men & Women</td><td>Female & Male Faces</td><td>
</td></tr>
<tr><td>Dai et al.</td><td>2010</td><td>4 sec</td><td>Men & Women</td><td>Male & Female Faces</td><td>
</td></tr>
<tr><td>Hahn et al.</td><td>Chapter 2</td><td>4 sec</td><td>Men & Women</td><td>Female & Male Faces</td><td>
</td></tr>
</table>

Authors	Date	Default Time	Participants	Stimuli	Result
Parsons et al.	2011a	5 sec	Men & Women	Adult & Infant Faces	
Hahn et al.	2013 Chapter 3	4 sec	Men & Women	Adult & Infant Faces	
Yamamoto et al.	2009	4 sec	Men & Women	Infant Faces (deformed vs healthy)	
Parsons et al.	2011b	6 sec	Men & Women	Infant & Animal Faces (deformed vs healthy)	

An additional parameter to be considered is that of the payoff participants receive per unit of effort (i.e. the change to presentation time elicited by each key-press). If participants receive high payout for their effort, they may not feel the need to exert much effort to prolong viewing time and receive sufficient 'reward'. Conversely, if participants receive very little payoff for their effort they may become frustrated and determine that the 'reward' they receive is not worth the effort. Additional validation studies on the key-press paradigm are necessary to optimize the experimental parameters for use in a broad range of psychological studies.

6.2 Limitations & Future Directions

There are some limitations to these studies that could be addressed with future work. Although apparent health was found to hold incentive salience independently of attractiveness, the link between apparent health and actual health remains unclear. Similarly, apparent health has been shown to be influenced by a number of factors including skin color (Stephen, Smith, et al., 2009) and skin quality (Fink et al., 2001; Jones et al., 2004). Further exploration of the motivational salience of these individual factors known to influence perceptions of health could provide a better understanding of how apparent health influences behavior.

An additional limitation of the present work is the restricted test population; all of the studies presented here were conducted using Caucasian, heterosexual individuals aged 18-35[18]. This sample is relatively limited in scope and additional work utilizing older populations or a cross-cultural sample could provide a more broad understanding of the motivational salience of faces. Cross-cultural work on the perception of beauty has suggested that high agreement is seen across a broad range of rater ages (Udry, 1965) and ethnicities (Cunningham et al., 1995; Fan, Dai, Liu, & Wu, 2005; Jones & Hill, 1993; Perrett et al., 1994; Swami & Tovée, 2005). The aspects of a potential mate considered to be most important are also consistent cross-culturally (Buss, 1989). Similarly, manipulating skin color in Caucasian, Asian, and African faces has been shown to have comparable effects on perceptions of health and attractiveness (Stephen,

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[18] With the exception of a single participant aged 43 in the infant study. When this participant was excluded from the analysis, the reported pattern of results did not change. As such, they were included in the analysis presented here.

Coetzee, et al., 2009; Stephen, Coetzee, & Perrett, 2011). In light of these findings, it is likely that the liking responded to beauty would be similar across cultures and age groups. However, this may not be the case for 'wanting' – if facial attractiveness accurately signals health and quality, it may be that the incentive salience of beauty and additional factors, such as health and infant cuteness vary across cultures based on variation in pathogen prevalence. Recent work has suggested that although both Western, industrialized and rural populations agree that symmetrical faces are more attractive, symmetry preferences are much stronger in individuals from rural populations where mortality rates and health threats are higher (Little, Apicella, et al., 2007). Similarly, masculinity preferences among women have been shown to vary with pathogen prevalence. Across a set of 30 different countries, the national health index was found to predict masculinity preferences, with increased preferences for masculine men as national health levels decreased (DeBruine, Jones, Crawford, Welling, & Little, 2010). Because masculinity signals health and genetic quality, it may be more important to seek out a healthy mate in regions where contagion threats are more prevalent. Future cross-cultural work may benefit from the key-press paradigm, which can act as an implicit assessment of approach/avoidance behavior.

Although evolutionary psychologists are typically interested in behaviors among heterosexual individuals, exploring motivation in a homosexual population could provide interesting insight into the incentive salience of facial beauty. As discussed in Section 4.4, it remains unknown whether gender differences in motivation are apparent in the homosexual population. Some neuroimaging studies have indicated that reward-related activation to faces is specific to faces of the preferred-sex, with heterosexual men and homosexual women showing strongest activation in response to female faces and heterosexual women[19] and homosexual men showing stronger activation in response to male faces (Kranz & Ishai, 2006). Although homosexual men and women have shown category-specific brain responses to facial

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[19] Note: heterosexual women are a unique group in that they show activation in reward-related brain areas to both male and female faces.

attractiveness, genital arousal studies indicate that only homosexual men show category-specific arousal responses. Homosexual women on the other hand, show a more general arousal response, similar to that observed in heterosexual women (Chivers et al., 2004). In light of the equivocal evidence, it remains unclear if the incentive salience of beauty is subject to sexual orientation effects within gender, or if gender and sexual orientation interact. Outside of beauty, it is also unknown how additional factors of facial appearance, such as health and sexual dimorphism, influence the behavior of homosexual individuals. Do these factors affect motivation among homosexual or bisexual individuals in the same way they influence the behavior of heterosexual individuals? And do homosexual individuals show a similar pattern of responses to infant faces? If evolution has in fact 'programmed' us to seek out healthy mates and invest in healthier offspring, we might expect that factors that influence motivated behavior will influence everyone, with only the sex of the face (i.e. preferred versus non-preferred sex) determining difference in incentive salience.

6.3 Conclusions

This work has only just begun to scratch the surface; future work may illuminate further individual differences in motivation and provide a better understanding of mate preferences, mate choice, parental behaviors, and intrasexual competition. Future work determining whether key-pressing is a pertinent measure of actual mate choice behavior may allow for a better understanding of the link between mate preferences and mate choice. The key-pressing paradigm has provides a novel approach to studying inter- and intra-sexual behaviors, and has a myriad of future applications in the field of evolutionary psychology. This paradigm also has applications in other fields. By understanding motivated behavior in normal, healthy populations we may further our understanding of the hedonic deficits that occur in many psychiatric disorders. Elman et al. (2005) have already demonstrated that the key-press paradigm can accurately detect behavioral changes in a clinical population of PTSD sufferers. It is likely that similar behavioral deficits can be observed in those suffering from depression. This may be particularly useful in the case of postpartum depression – do behavioral deficits exist for beauty in general? Or are the deficits specific to infant faces? Extending this paradigm may even allow for the development of training tasks which can aid new parents suffering from postpartum depression in learning to attend to infant-related cues and improve parent-infant bond formation. In summary, the work presented here demonstrates that the motivational salience of faces is influenced by inherent and external factors – from aspects of the faces themselves, such as health, to qualities of the observers, such as gender, hormonal status, and own appearance.

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Appendix A: Additional Stimuli

A.1 Infant Stimuli

<table>
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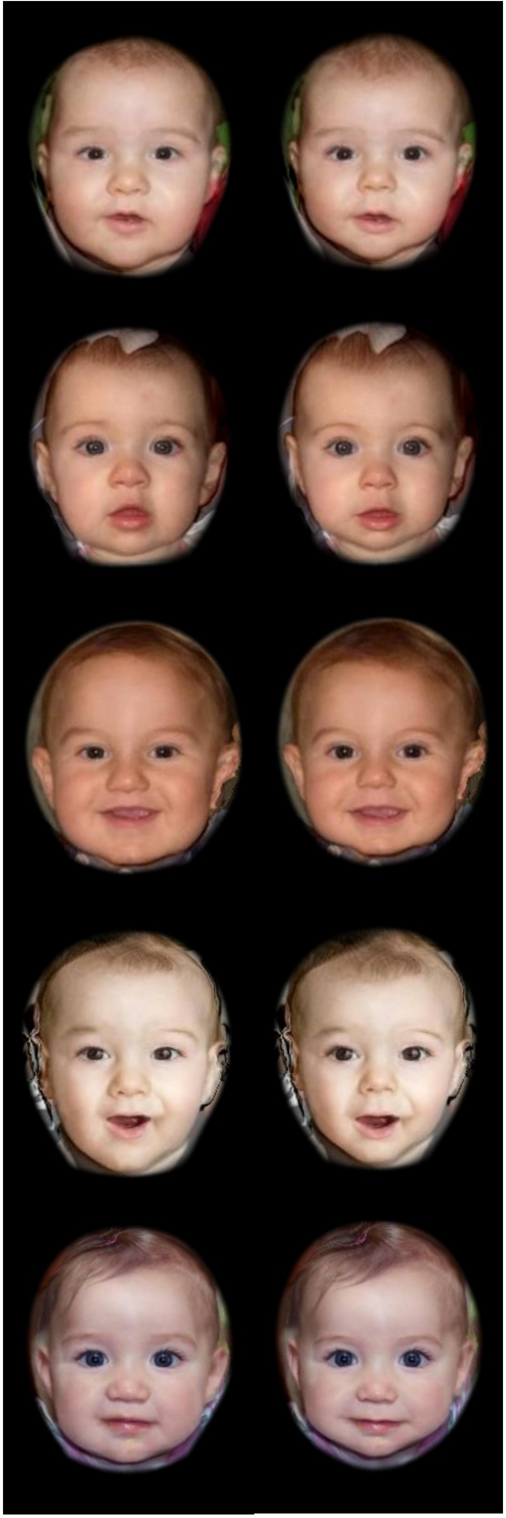
<tr><td colspan="2"></td><td colspan="2"></td></tr>
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A.2 Adult Female Stimuli

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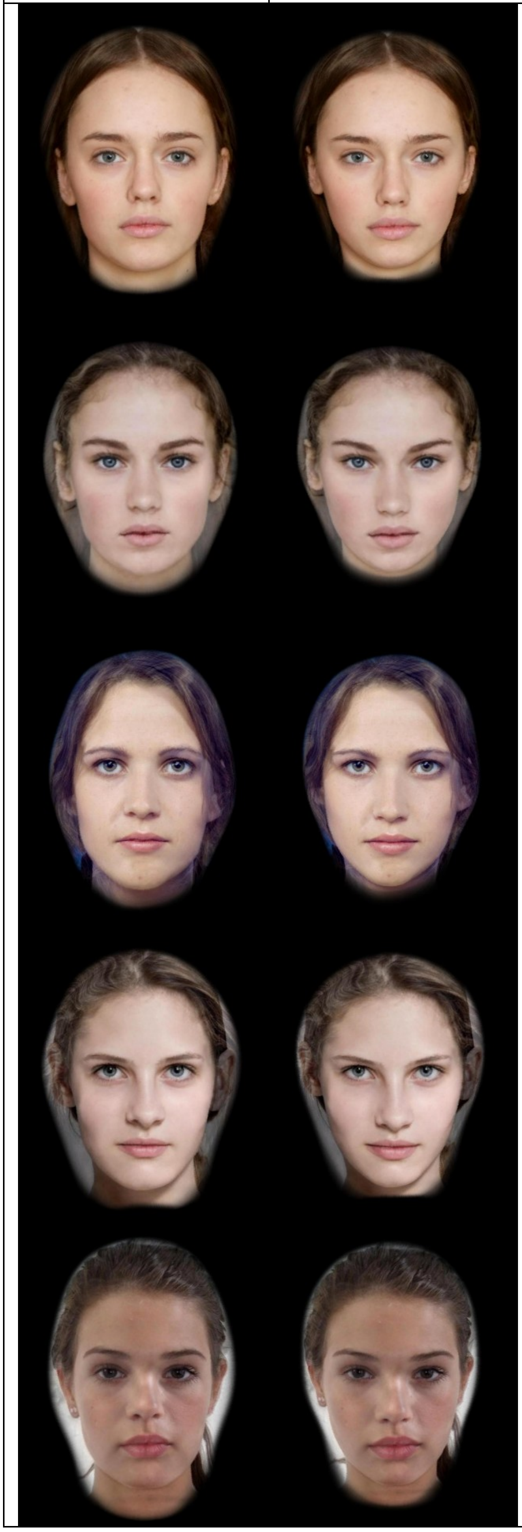
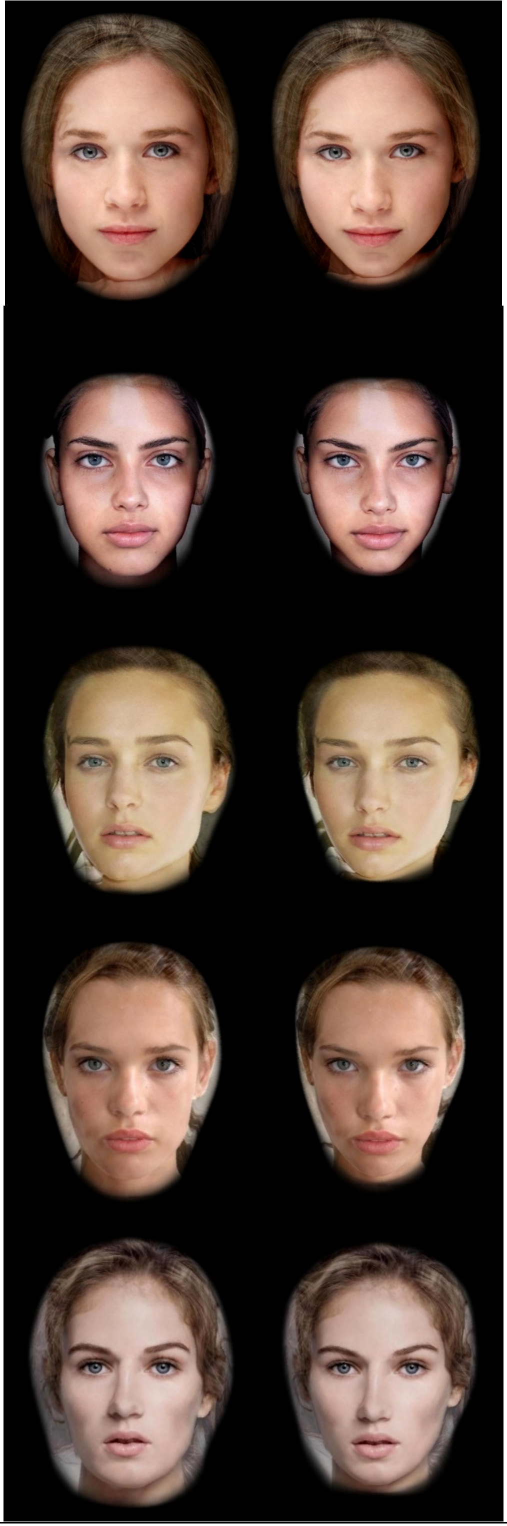
<tr><td colspan="2"></td><td colspan="2"></td></tr>
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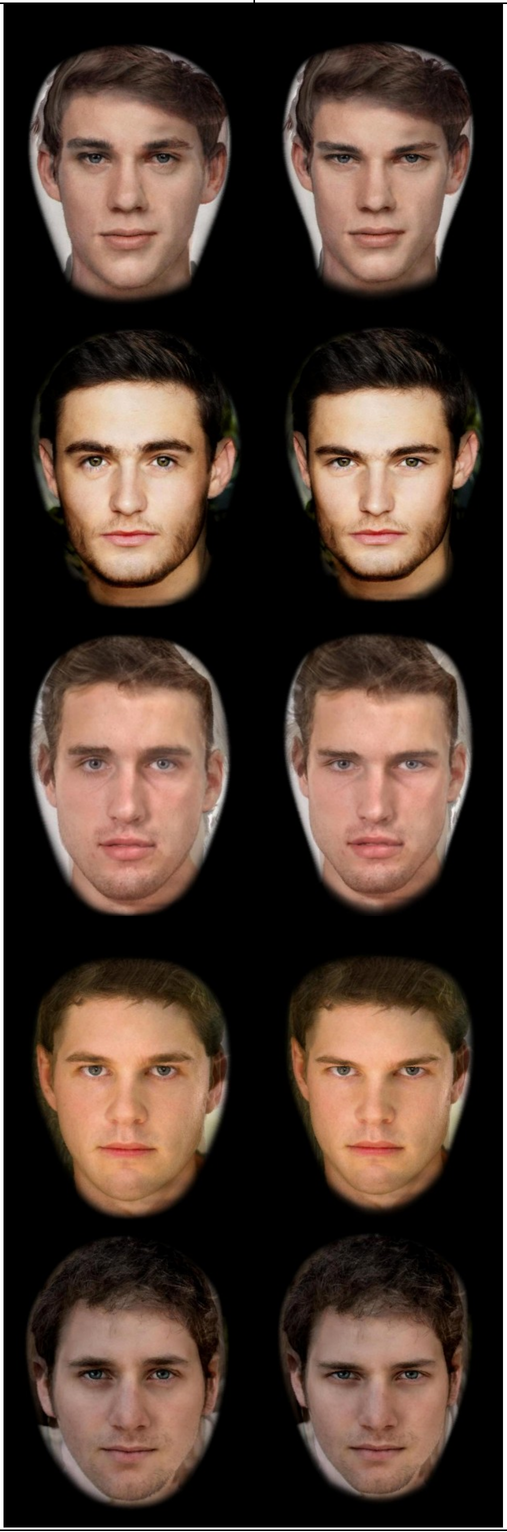
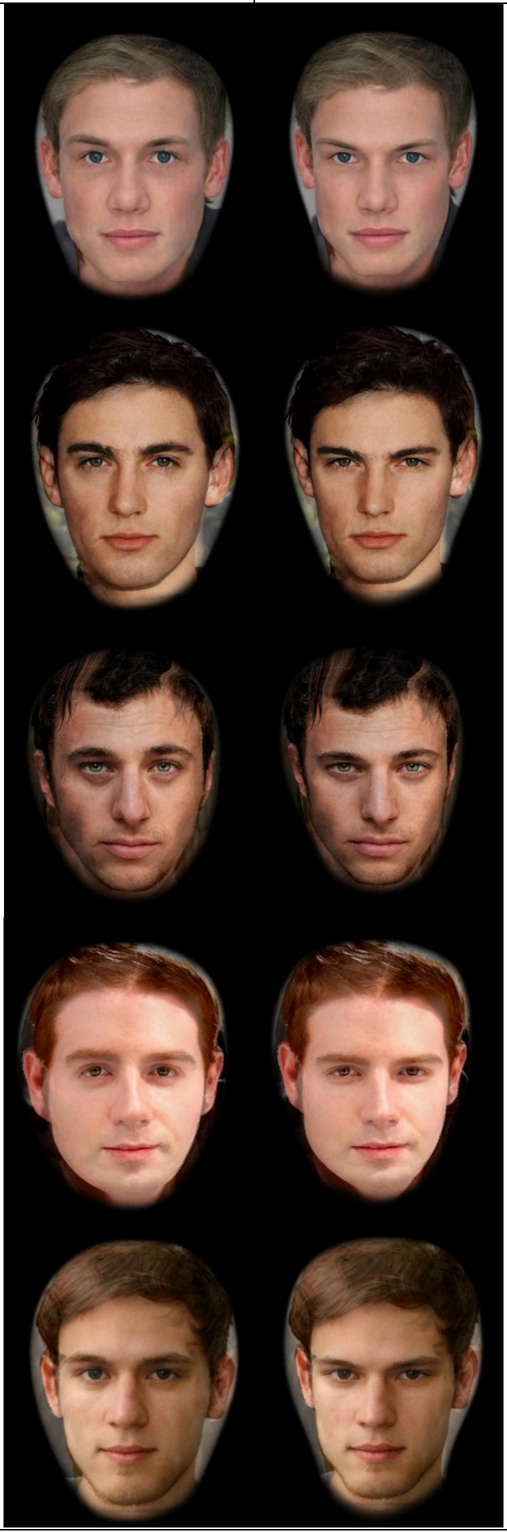
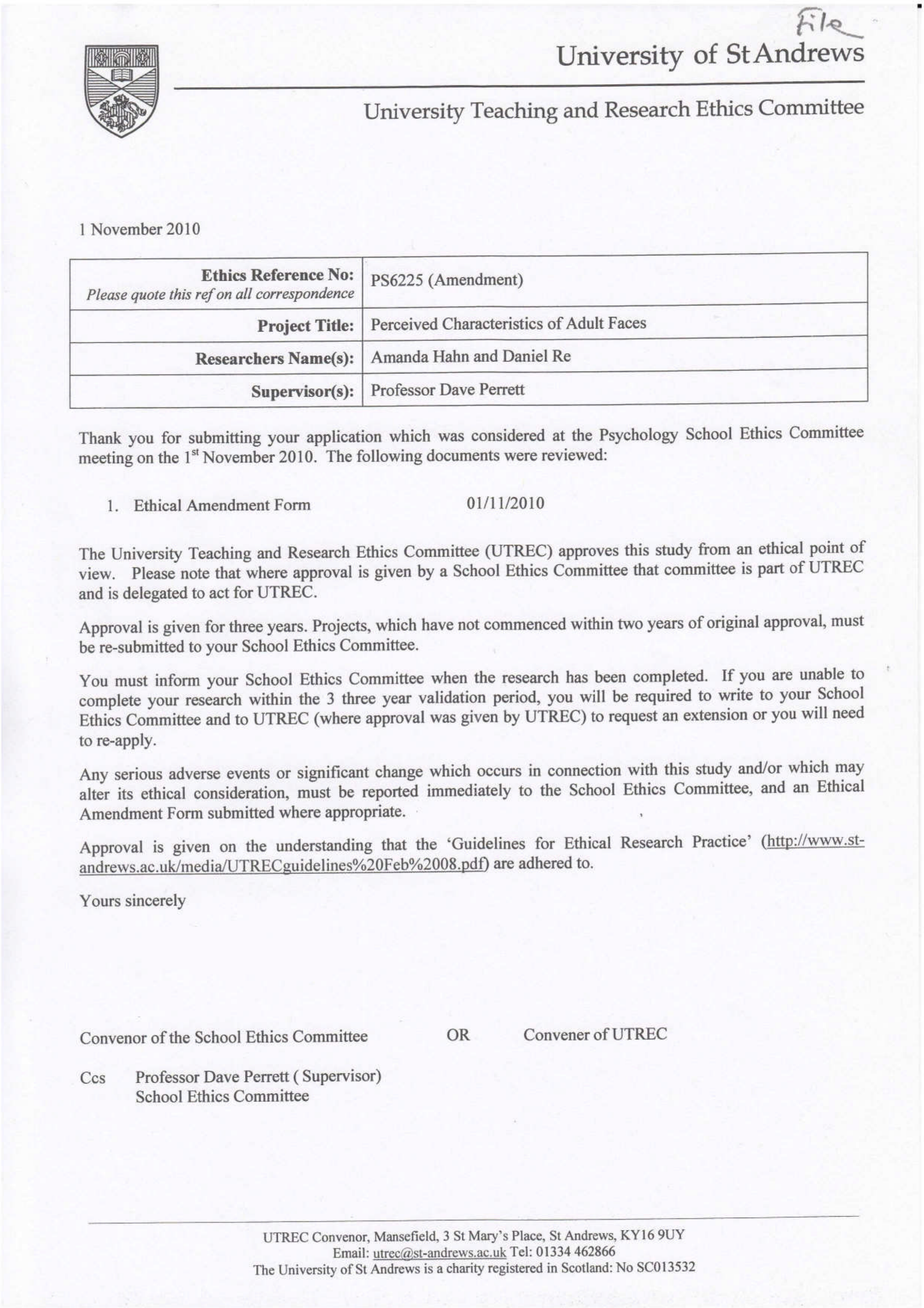
A.3 Adult Male Stimuli

Low-Attractive Version	High-Attractive Version	Low-Attractive Version	High-Attractive Version
			

Appendix B: Ethical Approval Forms

B.1 Ethical Approval: Face Ratings



File

University of St Andrews

University Teaching and Research Ethics Committee

1 November 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS6225 (Amendment)
Project Title:	Perceived Characteristics of Adult Faces
Researchers Name(s):	Amanda Hahn and Daniel Re
Supervisor(s):	Professor Dave Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 1st November 2010. The following documents were reviewed:

1. Ethical Amendment Form 01/11/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

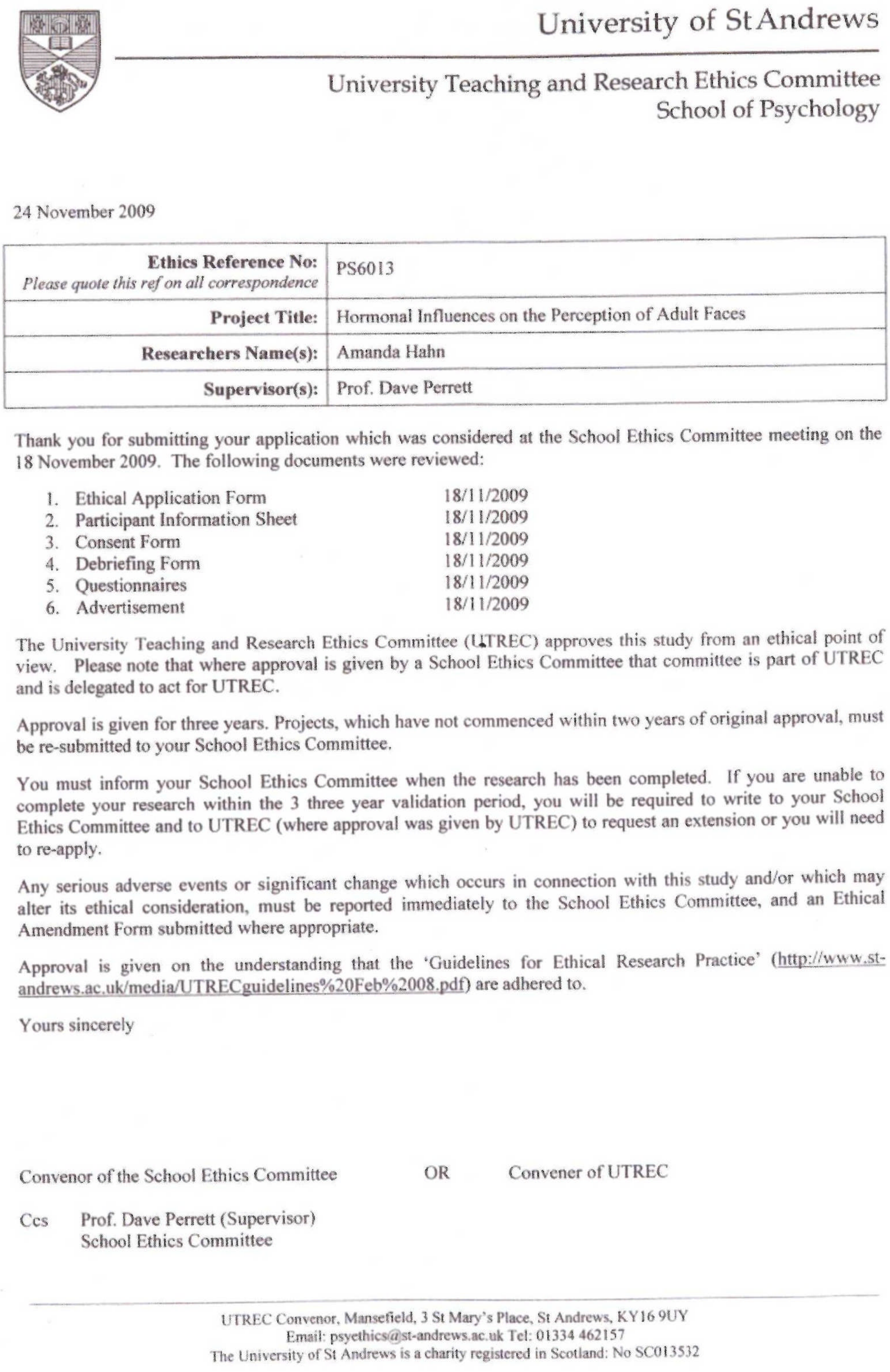
Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Professor Dave Perrett (Supervisor)
School Ethics Committee

B.2 Ethical Approval: Adult Faces & Variation Across the Menstrual Cycle



University of St Andrews

University Teaching and Research Ethics Committee
School of Psychology

24 November 2009

Ethics Reference No: *Please quote this ref on all correspondence*	PS6013
Project Title:	Hormonal Influences on the Perception of Adult Faces
Researchers Name(s):	Amanda Hahn
Supervisor(s):	Prof. Dave Perrett

Thank you for submitting your application which was considered at the School Ethics Committee meeting on the 18 November 2009. The following documents were reviewed:

1. Ethical Application Form	18/11/2009
2. Participant Information Sheet	18/11/2009
3. Consent Form	18/11/2009
4. Debriefing Form	18/11/2009
5. Questionnaires	18/11/2009
6. Advertisement	18/11/2009

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

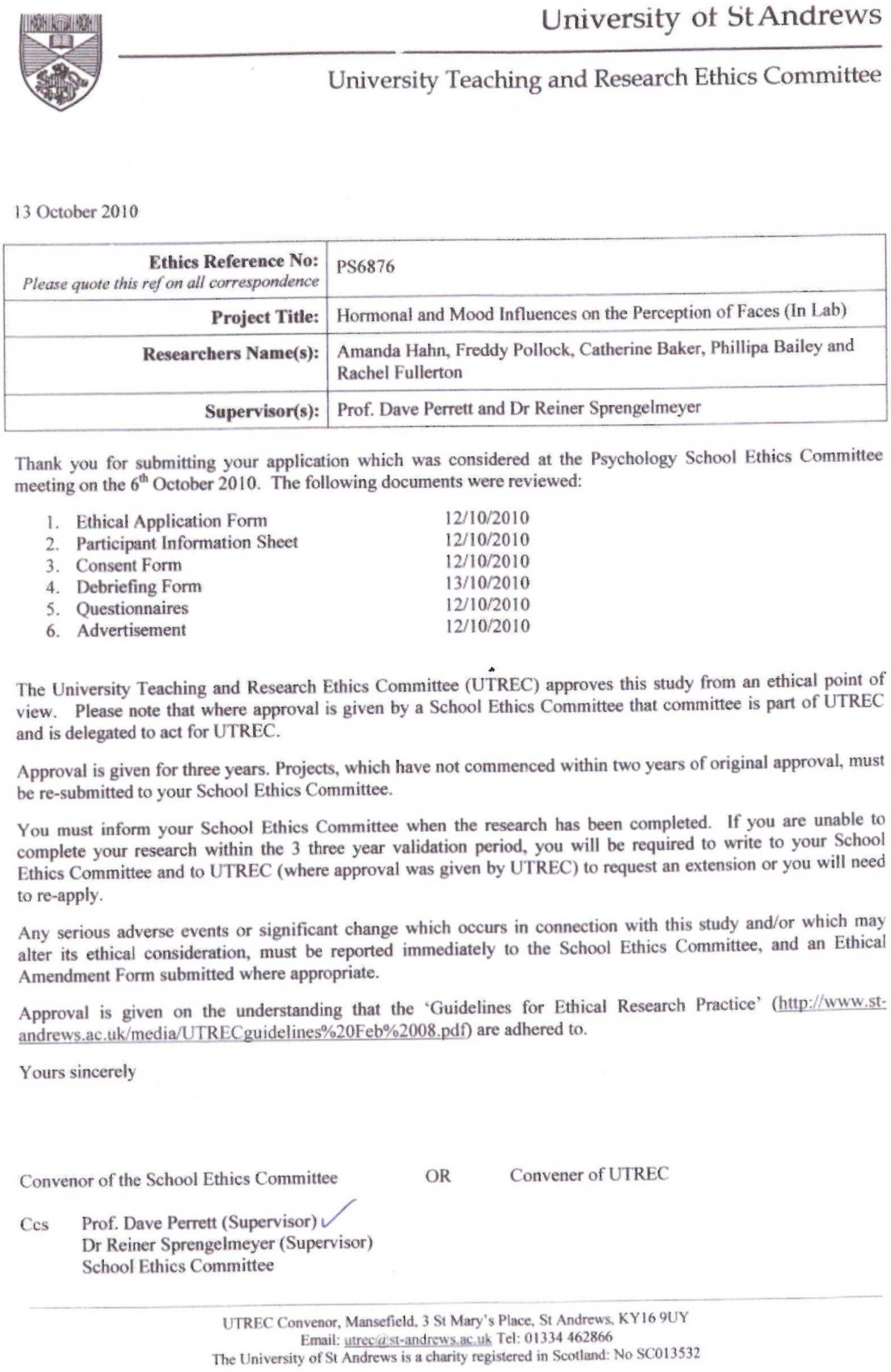
Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Prof. Dave Perrett (Supervisor)
School Ethics Committee

UTREC Convenor, Mansefield, 3 St Mary's Place, St Andrews, KY16 9UY
Email: psyethics@st-andrews.ac.uk Tel: 01334 462157
The University of St Andrews is a charity registered in Scotland: No SC013532

B.3 Ethical Approval: Infant Faces



University of St Andrews

University Teaching and Research Ethics Committee

13 October 2010

Ethics Reference No: *Please quote this ref on all correspondence*	PS6876
Project Title:	Hormonal and Mood Influences on the Perception of Faces (In Lab)
Researchers Name(s):	Amanda Hahn, Freddy Pollock, Catherine Baker, Phillipa Bailey and Rachel Fullerton
Supervisor(s):	Prof. Dave Perrett and Dr Reiner Sprengelmeyer

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 6th October 2010. The following documents were reviewed:

1.	Ethical Application Form	12/10/2010
2.	Participant Information Sheet	12/10/2010
3.	Consent Form	12/10/2010
4.	Debriefing Form	13/10/2010
5.	Questionnaires	12/10/2010
6.	Advertisement	12/10/2010

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

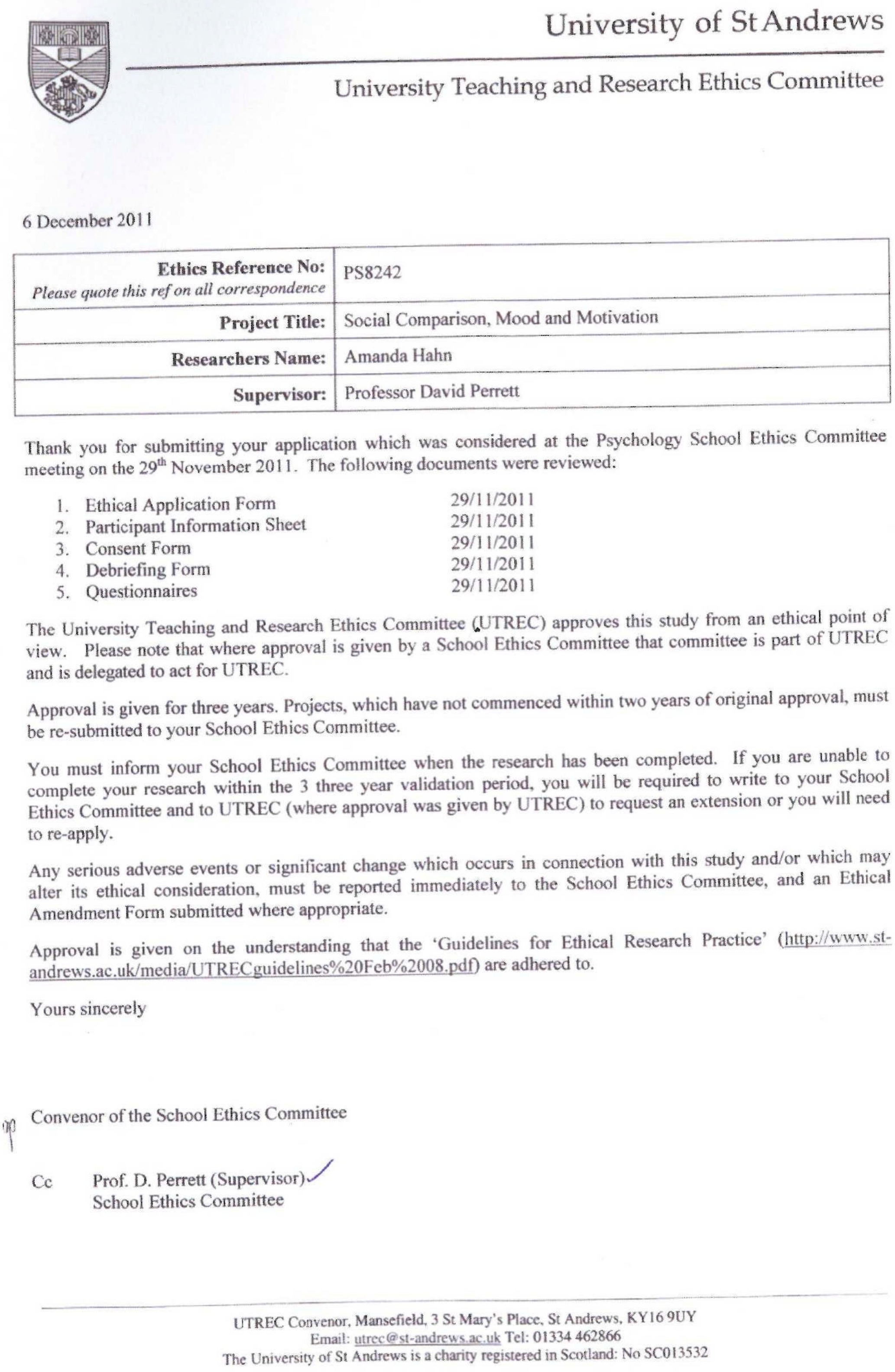
Yours sincerely

Convenor of the School Ethics Committee OR Convener of UTREC

Ccs Prof. Dave Perrett (Supervisor)
Dr Reiner Sprengelmeyer (Supervisor)
School Ethics Committee

UTREC Convenor, Mansefield, 3 St Mary's Place, St Andrews, KY16 9UY
Email: utrec@st-andrews.ac.uk Tel: 01334 462866
The University of St Andrews is a charity registered in Scotland: No SC013532

B.4 Ethical Approval: Individual Differences



University of St Andrews

University Teaching and Research Ethics Committee

6 December 2011

Ethics Reference No: *Please quote this ref on all correspondence*	PS8242
Project Title:	Social Comparison, Mood and Motivation
Researchers Name:	Amanda Hahn
Supervisor:	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 29th November 2011. The following documents were reviewed:

1. Ethical Application Form	29/11/2011
2. Participant Information Sheet	29/11/2011
3. Consent Form	29/11/2011
4. Debriefing Form	29/11/2011
5. Questionnaires	29/11/2011

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Cc Prof. D. Perrett (Supervisor)
School Ethics Committee

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