

Processes of Pair-bonding

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Abstract

This thesis expands our understanding of the role of several different mating behaviours in the process of forming and maintaining human mating pair-bonds. Chapter 2 investigated within-sex mating strategies and found that their distribution reflects the presence of two phenotypes, one favouring the pursuit of short-term mating and one the establishment of mating pair-bonds, each driven by prenatal testosterone exposure. Chapter 3 investigated the possible functional role of kissing in mating relationships, and found that it was utilised divergently by individuals pursuing different mating strategies, with those interested in short-term mating utilising it to assess the suitability of potential mates at initial relationship stages, and those interested in long-term mating using it to mediate pair-bond attachments. Chapter 4 examined female attitudes towards kissing across the menstrual cycle and found that attitudes varied with cycle phase, mediated by fluctuations in the hormone progesterone. This chapter also investigated the effects of kissing-related information on mate assessment and found that such information influenced mate desirability, even in the presence of typically dominant visual cues. Lastly, Chapter 5 investigated the cognitive effects of established pair-bonds, finding that individuals ‘in love’ with a mating partner show improved empathising abilities, particularly males when it comes to assessing negative emotional states in others.

Using an evolutionary framework, each chapter of this thesis contributes novel insights to our understanding of these diverse behaviours. These results suggest that that future research must take into account within-sex phenotypic differences in order to truly understand human mating strategy decisions, and that different mating strategy phenotypes might adaptively utilise the same courtship behaviours in divergent ways. Furthermore, these results also suggest that pair-bonding in humans may be a relatively recent phenomenon, and that the formation of such pair-bonds can have adaptive cognitive effects for males within such bonded relationships.

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List of Abbreviations

2D:4D	2nd Digit : 4th Digit
ANOVA	Analysis of Variance
BMI	Body Mass Index
BOLD	Blood-Oxygen-Level Dependent
EPC	Extra-Pair Copulation
ESS	Evolutionarily Stable Strategies
FA	Fluctuating Asymmetry
fMRI	Functional Magnetic Resonance Imaging
MHC	Major Histocompatibility Complex
MLE	Maximum Likelihood Estimation
MLM	Mixed Linear Modelling
OIS	Other In Self Scale
PAG	Periaqueductal Grey matter
PCA	Principal Components Analysis
PLS	Passionate Love Scale
RAS	Relationship Assessment Scale
ROI	Region of Interest
RTM	Reading the Mind in the Eyes Task
SOI	Sociosexual Orientation Inventory
VNO	Vomeronasal Organ
VTA	Ventral Tegmental Area
WHR	Waist-to-Hip Ratio

Chapter I – Mating Behaviours contributing to the Processes of Pair-bonding

I.1 Introduction

Mating and reproduction play a fundamental role in the process of evolution. While natural selection guides all animal behaviour towards the ultimate goal of maximising the genetic endowment passed on to succeeding generations, it is mating behaviours that are most directly associated with achieving these aims (Miller, 2001). In humans, as in most sexually reproducing species, the search tactics used to find potential mates, the assessment of a potential mate's suitability, mating, and the successful rearing of resulting offspring would have been of vital importance during our evolutionary past. As the rearing of human infants to maturity requires uniquely high levels of parental investment, mechanisms of pair-bonding (which aid in the coordination of bi-parental care) additionally play a prominent role in the human mating process (Clutton-Brock, 1989; Kleiman, 1977). The importance of these behaviours to the survival of our species means that selection pressures for adaptations that assist individuals in finding, selecting, and maintaining relationships with suitable mates are likely to have been extremely salient throughout our evolutionary past.

Evolutionary approaches to studying human behaviour have proven to be a useful framework for understanding the basis of various human activities across diverse populations (Barrett, Dunbar, & Lycett, 2001; Buss, 2005). Since the 1970s, a considerable body of research has been dedicated to examining mating behaviours across the full spectrum of human reproduction, with particular focus falling on their functional contribution towards reproductive fitness (M. Andersson & Simmons, 2006; Little, Jones, & DeBruine, 2011). Such behaviours have been examined across all stages of the mating process leading up to the establishment of pair-bonded attachments, including during the formation of mating strategies, the assessment of potential

mates and preferential choice of some mates over others, and finally the creation and maintenance of mating pair-bonds and attachments with suitable mates. Pair-bonding in humans, while not arising from all mating encounters, is nonetheless dependent on each of the mating stages that precede it. Behaviours that occur across each of these earlier stages of mating are deeply interconnected, and therefore must be examined not only in terms of their immediate functions and mechanisms, but must also be viewed in terms of their contribution to the processes of pair-bonding.

Long before a pair-bonded relationship can potentially be established, various mating problems must first be solved, the first of which involves finding a mate. The earliest phase of this process involves the establishment of a 'mating strategy', whereby a search for potential mates is initiated, directing and guiding an individual's mating efforts and energies (Buss, 1994). The search might entail looking for an exclusive mating partner with whom to pair-bond and make long-term investments in resulting offspring, or might alternatively involve forgoing pair-bonding with any one individual altogether, and instead seeking out short-term, low-investment mating interactions with multiple partners. The establishment of this mating strategy will in turn affect how potential mating partners are assessed and selected. During this second phase, when mate assessment and mate choice takes place, mate preferences are established and discernable qualities of potential mating partners are appraised in relation to these preferences. Various senses are utilised at this stage to make such mate assessments, with attraction preferentially felt towards some individuals more than others (usually those most closely matching established preference criteria). Only once a mating partner has been selected can the creation of pair-bonded relationships finally take place, triggering intense feelings of attachment and commitment to one partner, at the exclusion of others, and helping maintain the dyadic relationship long enough to rear offspring under the auspices of bi-parental care. Such pair-bonds between mating partners are not developed by every individual, and not at every mating opportunity – the likelihood of pair-bond formation depends

on the mating strategy being pursued. Individuals following long-term mating strategies, and searching for mates who are both willing and able to make long-term parental investments, are much more likely to pursue and form mating pair-bonds than individuals following short-term mating strategies.

Although evolutionary theory has contributed greatly to our understanding of many mating behaviours found across the whole spectrum of the mating process leading up to pair-bonding, many puzzles remain unanswered. What exactly, if any, are the functional benefits of some commonly observed mating human behaviours? How do some of these apparently disparate behaviours contribute to the process of pair-bonding? Do distinct biological substrates underpin all mating behaviours, shaped and driven by evolutionary pressures? What is the mediating role of environmental variables on these mating-related biological imperatives?

Pair-bonding, and the foundational mating processes which contribute to its establishment, is used in this thesis as an overarching evolutionary framework for examining in greater detail several diverse mating behaviours found among humans. When the various mating behaviours examined in this body of work are placed within this framework, it is possible to see the potential role that these behaviours play in the establishment of pair-bonds, and the relationships between one behaviour and the next become apparent. The goal of this thesis, therefore, is to examine in detail some functional roles and biological mechanisms behind three distinct human mating behaviours that contribute to the extended process of pair-bonding. Specifically, this thesis will examine the within-sex distribution of preferences for short- versus long-term mating during the initial search for mates and establishment of mating strategies, the possible functions of a common courtship custom (romantic kissing) in mate assessment and mate retention, and the cognitive effects of 'romantic love' as they relate to the formation and mediation of long-term attachments.

This body of work does not attempt to explain the functions and biological foundations of all the human mating behaviours that contribute to pair-bonding, nor to explain all the mysteries that remain when it comes to the formation and mediation of human pair-bond attachments. Rather, several distinct behavioural aspects which comprise the process of pair-bonding, which have thus far been little explored, have been selected so that their function in relation to reproductive fitness and their relationship to potential underlying biological substrates can be examined in some detail. By addressing gaps in our understanding of the functional and biological underpinnings of these behaviours and the relationships between them, we can gain a better understanding of the overall human mating process and the evolutionary forces that have shaped it. In addressing the gaps in our understanding, a broad array of techniques available to psychological researchers has been utilised in this thesis. These techniques include statistical modelling, analyses of original data gathered using questionnaire-based surveys, and analysis of data gathered using more traditional behavioural experimental methods in a controlled laboratory setting.

This first chapter provides an outline of the literature relevant to three mating processes that contribute to eventual pair-bond formation, briefly examining the current literature as it relates to mating strategies, mate selection, and pair-bonded attachments. As each of these three processes are examined in more detail, a unique question which remains unanswered by the current literature is identified, and is then further examined experimentally throughout the following four chapters of this thesis. The answers to these questions will allow us to gain a clearer understanding of not only the functions and drivers of several diverse mating behaviours, but will also enable us to see their greater role in the process of forming pair-bonded attachments.

1.2 Literature Review

A Brief History of Evolutionary Approaches to Human Mating Behaviour

One of the first people to recognise the central role of sexual reproduction in the process of evolution was Charles Darwin, building on the work of his grandfather Erasmus Darwin (C. U. Smith, 2009). In Charles Darwin's initial works on sexual selection, he outlined processes of adaptation arising from intrasexual competition and selective mate preference (Darwin, 1859, 1871). Darwin suggested that many features evolved in animals not just to aid the direct survival of that animal, but also to help maximise their chances of successful reproduction. He proposed that these chances could be improved in two ways. Firstly, by competing for mating opportunities with same-sex rivals (intersexual selection) and, secondly, by intimidating or subjugating rival suitors (intrasexual selection).

The first method by which chances of successful reproduction can be improved is through intersexual selection, where certain opposite-sex mate qualities are preferred over others by the choosing sex (females, according to Darwin). This preference in turn leads to greater mating opportunities for individuals possessing those qualities, and if those qualities are heritable leads to the prevalence of those qualities in the population over time (Darwin, 1871). Such theories explained the evolution of certain physical and behavioural traits, such as ornamentation or complex courtship rituals found among some mammals. During the latter process, members of one sex engage in various forms of competition with same-sex rivals in a process of intrasexual selection – which can take the form of direct combat, non-physical competition for status or position in a dominance hierarchy or access to territory. The victors of these competitions gain preferential access to mating opportunities with the opposite sex, while the losers may fail to mate. Any physical or behavioural characteristics that help to succeed in such competitions (and are heritable) are thereby passed down to future generations at a greater rate than characteristics

that were possessed by the losers. Over time, this differential in reproduction rates leads to the dominance of these 'winning' traits in a population (Darwin, 1871).

While these theories on biological approaches to human mating did not garner much scientific attention over the century that followed their introduction, in the 1970s interest in such biological approaches to mating and sexual selection was re-kindled. Trivers (1972) proposed that differing levels of parental investment acted as primary drivers of sex-differentiated behaviours (see also 'Sex Differences in Mating Strategy' below, p. 10). Meanwhile, the American psychologist Symons was one of the first to propose a coherent argument for the idea that human mating behaviours might arise from sexually dimorphic adaptations based on underlying psychological mechanisms shaped by evolutionary pressures (Symons, 1979). Symons argued that in order to examine behaviour from an adaptationist viewpoint, it was necessary first to identify the existence of very specific phenotypic adaptations, to examine these adaptations in light of the past environment in which they were likely to have been shaped, to look at the design of the adaptation and how this design affects differential reproduction, and finally to establish that genes are the primary driver of these adaptations (Symons, 1990).

These early insights into animal and human mating behaviour provided the theoretical foundations for a body of research that has since expanded to examine all aspects of human mating behaviour, including mate search strategies, mate choice, and pair-bonding, through the lens of an adaptive framework.

Human Mating Strategies

The study of human mating strategies, which direct mating effort towards either short- or long-term mating opportunities and thus influence whether eventual pair-bonding is likely to take place, has until now focused on either aggregate differences between the sexes, or on conditional strategies that vary in response to environmental variables (e.g. Gangestad & Simpson, 2000;

Schmitt, 2005b). Chapter 2 of this thesis takes a different approach to this subject by examining the interesting possibility that within-sex variation in mating strategy might actually be driven by two underlying polymorphisms, each in turn potentially driven by similar polymorphisms in an underlying biological driver, such as prenatal testosterone exposure. The section of this literature review which follows examines in brief the body of knowledge that exists about human mating systems and mating strategies, before introducing the idea of distinct within-sex polymorphisms as drivers of mating strategy, an idea which will then be further explored in more detail, and tested empirically, in Chapter 2 of this thesis.

Mating Systems

Mating systems refer to how sexual behaviour patterns, driven by mating strategies, are codified within a particular socio-cultural context (Buss, 1994). Considerable debate exists when it comes to establishing which mating system ‘typifies’ human mating, with evidence suggesting that human populations variously show signs of monogamy, polygyny, and promiscuity (Mealey, 2000). It is important to note that a difference exists between sexual mating pair-bonds, which are powerful physiological and behavioural attachments between two individuals arising from biologically mediated sexual attraction, and social pair-bonds, which may also involve intense attraction but originate from socially prescribed norms such as marriage arrangements (H. E. Fisher, 1992). While in many modern societies these two types of bonds are conflated (with marriage decisions often based on sexual attraction), this is a relatively recent phenomenon (Coontz, 2005). The pair-bonds referred to throughout this thesis are exclusively concerned with sexually mediated mating pair-bonds.

It has been argued that humans have evolved to be primarily monogamous over their lifetime, with monogamy in the human sense taking the form of either life-long (perennial) monogamy, or serial monogamy, whereby pair-bonds are exclusive during their tenure but do not last the

lifetime of the individual (H. E. Fisher, 1989). Evidence in support of the notion that humans are inherently inclined to be monogamous includes the observation that most pre-industrial marriages are actually monogamous, even within the context of notionally polygynous marriage systems (White et al., 1988), and the fact that humans show neurobiological adaptations to forming long-term attachments and pair-bonds (H. E. Fisher, 1989; Insel & Young, 2001). Other evidence used to support the notion that monogamous mating in humans forms the instinctive mating system includes the fact that bi-parental care is extremely important for human offspring survival (Geary, 2000), with monogamous attachment typically also arising in other species where offspring survival also depends on bi-parental care (Kleiman, 1977).

If monogamy was the primary system of mating in humans, however, then humans would be quite unique among mammals in this regard – monogamy only occurs in around 3% of all mammal species, with only 10% of mammal species making any form of significant ‘investment’ in their offspring (Clutton-Brock, 2009; Kleiman, 1977). Monogamy is more commonly seen in non-human primates, with around 30% of primate species utilising monogamous mating strategies (Opie, Atkinson, Dunbar, & Shultz, 2013). Evidence exists to support the notion that humans are primarily a polygynous species, with 85% of marital systems in preindustrial cultures allowing for polygynous mating (Murdock, 1967), evidence showing that polygyny reliably emerges in humans under certain environmental conditions (Marlowe, 2003), and signs that humans share behavioural and physical characteristics with other polygynous primates, such as sexual dimorphism and direct mate competition (Clutton-Brock, 1989; Harcourt, Harvey, Larson, & Short, 1981). It must be noted that although polygynous mating systems allow for concurrent multi-partner mating, this system does not preclude the formation of mating sexual pair-bonds between any mating partners.

Finally, data have also been brought to bear on the argument that humans are a primarily promiscuous species, which involves less discriminate, non-exclusive mating with multiple

mating partners. Firstly, research finds that extra-marital sex and mate poaching is prevalent in many cultures with ostensibly monogamous and polygynous mating systems at rates of up to 30% (for males and females) (Thompson, 1983; Wiederman, 1997). Furthermore, evidence also suggests human males display both morphological and behavioural adaptations for dealing with the kind of sperm competition which is prevalent in the promiscuous mating systems of other mammals (e.g. relatively large testes size) (Baker & Bellis, 1994; Gallup et al., 2003; Goetz et al., 2005; Mealey, 2000).

Firm conclusions regarding which is the predominant human mating system are not easily drawn (Mealey, 2000). The conflicting data suggests that humans display considerable variety and flexibility when it comes to choice of mating system, with the evidence pointing to the existence of varying mating systems across different cultures, ecological niches, and time periods. Because of the observed flexibility in the spectrum of mate search behaviours pursued by different individuals across cultures, it appears that humans have the option of following a wide variety of mating strategies, which range all the way from monogamous long-term commitments to short-term opportunistic copulations (Buss, 2006; Gangestad & Simpson, 2000).

Mating Strategies – Parental Investment versus Continued Mating Effort

The predominant mating system of any one culture most often reflects the most common ‘mating strategy’ being preferentially pursued by the sexes within any one particular ecological niche (Buss, 1994). These mating strategies are what organise and guide an individual’s reproductive effort, and involve preferentially favouring certain mating behaviours and tactics in the search for potential mates with the aim of maximising overall fitness outcomes for any one individual (Gangestad & Simpson, 2000). These strategies can, for example, affect the amount of mating effort expended in the search for a mate, the criteria by which potential mates are evaluated, or the amount of investment made in any one mate and the resulting offspring. Because time and

energy are finite resources, the choice of one particular strategy may sometimes preclude the pursuit of alternative strategies. The greatest trade-off to be made when it comes to choosing a mating strategy is typically related to the decision to invest energy either in parenting effort, or in multiple alternate mating opportunities (Buss & Schmitt, 1993). Parenting effort involves some kind of direct investment in one offspring which improves the chances of that offspring's survival (Trivers, 1972). However, as the time and energy involved in making such an investment reduces the time and energy available for other mating efforts and investments in other offspring, a trade-off between these two strategies must often necessarily be made. This need for compromise means that mating strategies fall on a continuum of 'parental investment' versus 'mating effort', with strategies at one end of the spectrum referred to as long-term strategies (with greater focus on longer-term commitment to one mating partner, the creation of pair-bond attachments, and investments in resulting offspring), and strategies at the other end of the spectrum referred to as short-term strategies (focusing on multiple mating opportunities, with lower investment in each mate and offspring) (Buss & Schmitt, 1993). The length of any one mating encounter will, in turn, vary with the strategy being pursued and may last anywhere from a few minutes to many years.

Sex Differences in Mating Strategy

The choice to pursue a long- versus short-term strategy will depend on the long-term fitness benefits afforded to the individual by a given strategy. In mammal species it is typically the female that makes the more costly minimum parental investment, in the form of internal fertilization, gestation, bearing and an extended period of lactation (M. B. Andersson, 1994; Trivers, 1972). Because of this, females, unlike males, cannot always increase their fitness outcomes by mating with multiple partners (ibid.). This imbalance in fitness outcomes afforded by multiple matings means that human females are on average more likely than males to pursue long-term mating strategies (Low, 1978), showing greater commitment to pair-bond relationships and intimacy,

pursuing them more vigorously than males, and finding romance and relationship themes generally more desirable and arousing than males (Baumeister & Bratslavsky, 1999; Ellis & Symons, 1990). Since the *minimal* parental investment levels for males are so much lower, on the other hand, males can sometimes increase their overall fitness by pursuing mating opportunities with multiple partners and siring many offspring in the same time period that a female is limited to birthing and raising one offspring. In this scenario, however, the amount of parental investment made by a male in each offspring must necessarily be reduced, in turn reducing the survival chances of each additional offspring sired (Geary, 2000; Trivers, 1972).

Variation within the Sexes

Although theories on the asymmetrical nature of parental investment between the sexes predict that males on the whole will be more likely to pursue short-term strategies than females, and thus less likely to pursue pair-bond formation, this does not preclude variations in strategy *within* each sex. Within each sex, either strategy may potentially lead to desirable fitness outcomes, with a strategy's fitness payoffs dependent on factors such as the physical and socio-cultural environment the individual finds themselves in, the type and number of mating partners available, and the individual's own physical attributes (Gangestad & Simpson, 2000). This more nuanced interplay between mating decisions and local environmental conditions among humans has only recently been explored in any detail, and has proved to be very useful in explaining some of the incredible flexibility displayed by humans across diverse cultures and situations (e.g. Lippa, 2009; Schmitt, 2005b).

The type of mating strategy chosen will also have an effect on the type of mate that will be preferentially pursued. Females pursuing a short-term strategy, for example, have been found to place greater importance on good gene and fitness indicators, whereas those pursuing long-term strategies are more likely to stress the value of resource acquisition potential and matching levels

of parental investment or long-term relationship interest (Buss & Schmitt, 1993; Gangestad & Scheyd, 2005; Gangestad & Simpson, 2000). However, previous research suggests that an inverse relationship might exist between a potential male mate's willingness to make parental investments, and their levels of underlying genetic fitness, as variously signalled by symmetry, sexual dimorphism, averageness, skin colour/texture and personality cues. For example, genetic fitness and social dominance in men has been linked to testosterone, with higher testosterone levels in utero responsible for the development of masculine features, adult fluctuating testosterone levels and various dominant and male-typical behaviours (but see also 'The Role of Attractiveness' p. 18, for more details and caveats related to purported links between testosterone and genetic fitness). Higher testosterone levels have in turn been found to correlate with reduced parenting effort, greater relationship infidelity, a larger number of life-time sexual partners, higher chances of divorce and lower biological sympathy responses to crying infants (Booth & Dabbs, 1993; Fleming, Corter, Stallings, & Steiner, 2002; Folstad & Karter, 1992; Manning et al., 2000; Muller, Marlowe, Bugumba, & Ellison, 2009; Pollet, der Meij, Cobey, & Buunk, 2011).

Choosing a high quality or a dominant mate, therefore, may necessitate a trade-off: such partners are likely to bequeath offspring with more advantageous genes, but at the same time are less likely to provide long-term parental investment and support. Because of this, it may sometimes behave females to seek the best of both worlds – preferring pair-bonded relationships with males offering access to resources and long-term parenting support, while occasionally seeking extra-pair copulations (EPCs) with partners who can contribute superior genes (Baker & Bellis, 1994; Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; Kruger, 2006). Such variation in the use of short-term versus long-term mating tactics can vary within individual females over the phase of their menstrual cycle and its accompanying changes in hormonal levels (see also the Literature Review for Study 1, Chapter 4 p. 105, for more information on such menstrual cycle effects). Some researchers have argued that for females such conditional or mixed-mating strategies may

be the most prudent choice to guarantee optimal fitness outcomes in any given environmental situation (Gangestad & Simpson, 2000). The use of such conditional or mixed mating strategies provides one possible explanation for observed mating strategy diversity seen within the sexes. However, another possible explanation for such variation that has thus far not been explored is the potential role of genetic polymorphisms (Gross, 1996).

The Unanswered Question of Phenotypes

While the study of human mating strategy differences between the sexes has garnered considerable attention in the literature, less attention has generally been paid to mating strategy variation within the sexes, which can also be quite considerable (Gangestad & Simpson, 2000; Simpson et al., 1991). Some authors have attempted to examine observed intra-sexual variation in mating strategy by focusing on ‘conditional’ strategies, whereby the decision to pursue one mating strategy over another is guided by various local environmental cues (e.g. Gangestad & Simpson, 2000). Such conditional strategies, however, are still considered to be mono-strategic, with most of the research on strategies thus far ignoring the possibility that variation in mating strategies within the sexes may also be reflective of different underlying polymorphisms that are present in the population under study. It is quite possible that each sex is actually comprised of two phenotypes, one inclined towards the preferential pursuit of short term-mating opportunities, and one towards the pursuit of long-term, pair-bonded mating opportunities. Some past research has hinted at the possibility that mating strategies, both within males and within females, might actually be bi-modally distributed – with a distinct cluster of individuals within each sex preferentially pursuing either a short- or long-term strategy (Dunbar, 1993; Gangestad & Simpson, 1990). Furthermore, if these phenotypes are indeed present in human populations, then it is also likely that the relative distributions of such phenotypes may vary across populations, as the relative payoffs of each strategy for any one sex changes with local conditions. This is an extremely important issue to address in this field, since the existence of such within-

sex phenotypes differences may drastically alter our ability to accurately describe and interpret the mating strategy choices pursued by any one sex, and hence our ability to draw inferences and determine the ultimate and proximate drivers of these strategies.

In an attempt to address the uncertainty that exists when it comes to mating strategy distributions, Chapter 2 of this thesis examines the within-sex distribution of mating strategies in two mono-ethnic populations to determine whether they comprise one spectrum of mating strategies (potentially driven by conditional strategies), or alternatively whether two different strategies are being pursued preferentially by different individual phenotypes within each sex. Furthermore, this chapter also looks at purported biological underpinnings of mating strategy, namely prenatal testosterone exposure as indexed by 2D:4D digit ratio, to determine whether this too shows the same phenotypic divide and thus might be acting as the driver of differentiated mating strategies.

Mate Selection

Following the establishment of a mating strategy, the next step towards the establishment of mating pair-bonds involves the formation of mate preferences, the assessment of potential mates against those preferences, and finally the preferential choice of some mates over others – a process referred to as mate selection (Buss, 2002b). This process is directly influenced by the mating strategy being pursued by a particular individual, with short- or long-term mating strategies influencing the desirability of certain mate qualities over others (*ibid.*). During initial mate assessment, various cues are taken into account when selecting a suitable mate, including behavioural cues, visual cues signalling genetic fitness, olfactory cues to desirability and compatibility, and even cues discernable to other senses such as touch and hearing (e.g. Collins & Missing, 2003; Foster, 2008; Guéguen, 2007). As it has been previously proposed that some human courtship customs might have arisen to assist individuals in this process of assessing potential mates (Birdwhistell, 1970; Eibl-Eibesfeldt, 1972; D. Morris, 1971), Chapter 3 of this

thesis explores the idea that potentially useful reproductive functions might be served by one particularly prevalent and widespread courtship custom – that of ‘romantic kissing’. Chapter 4, in turn, further examines the custom of romantic kissing by looking at how attitudes towards the use of romantic kissing vary among females across the menstrual cycle, and at the effects of kissing-related information cues on mate desirability as well as the relative importance of such information as compared to traditional visual mate desirability cues.

Firstly, the following section provides a brief overview of the literature regarding general processes of human mate selection. Then, the potentially useful role of courtship customs is addressed, before an argument is introduced for the idea that the custom of romantic kissing is particularly well placed to serve several useful functions in the processes of mate assessment and pair-bonding. This argument is then developed in more detail, and tested using several experimental designs, in Chapters 3 and 4 of this thesis.

Sex Differences in Mate Selection

As with mating strategies, a considerable amount of sexual dimorphism is also present in the process of mate selection. Since the long-term mating strategy preferentially pursued by the majority of females involves establishing pair-bonds and making considerable investments in one mating partner and resulting offspring, the costs associated with making a poor choice are relatively high due the greater investments at stake. Consequently, and as predicted by parental investment theory (Trivers, 1972), individuals making this greater investment are also likely to be more selective when it comes to choosing a potential mating partner. Research in humans confirms that females undertake a more rigorous and selective mate-selection process, involving the careful assessment of a variety of different mate characteristics, while males, the less investing sex, pursue a much broader range of mating partners in a quest for sexual variety which often

values 'quantity' over 'quality' (Candolin, 2003; Furnham, 2009; Grammer, Kruck, Juette, & Fink, 2000; Kenrick, Sadalla, Groth, & Trost, 1990; Townsend & Wassermann, 1998).

Along with higher degrees of choosiness, females making higher parental investments are also likely to look for different qualities in a potential partner than males, who typically have lower minimum levels of parental investment. High-investing individuals are likely to value qualities suggesting that a potential partner is also likely to contribute high levels of parental investment (Bjorklund & Shackelford, 1999; Buss, 1989; Hatfield, Sprecher, Traupmann Pillemer, Greenberg, & Wexler, 1988; Shackelford, Schmitt, & Buss, 2005). A large body of evidence confirms this, with results showing that in most cultures females place particular value on cues signalling resource acquisition and parental investment potential in prospective mates, qualities which potentially improve a mate's ability to provide longer-term material support for the female and her offspring during her extended periods of gestation and lactation (Buss, 1989; Griskevicius et al., 2007; Kenrick et al., 1990; Shackelford et al., 2005; Townsend & Wassermann, 1998; Waynforth & Dunbar, 1995). Such increased male parental investment abilities and intentions not only match the female's large parental investments, but have also been found to affect offspring mortality rates significantly (Geary, 2000). Conversely, it has been shown that the qualities males value most in potential mates emphasise signs of female reproductive capacity and genetic fitness (and its proxies youth and physical attractiveness) when selecting for potential mates, in an attempt to ensure that a more limited parental investment might still lead to beneficial fitness outcomes (e.g. Buss, 1989; Townsend & Wassermann, 1998; Waynforth & Dunbar, 1995).

The Mating Market

The sex and mating strategy of an individual are not the only predictors of choosiness and assessment criteria use when it comes to selecting potential mates. Another important factor is an individual's understanding of their mating environment, or the 'biological market,' and their

relative worth within it – an understanding which will in turn affect their mating aspirations and behaviours (Back, Penke, Schmukle, & Asendorpf, 2011; Kavanagh, Robins, & Ellis, 2010; Koziel, Kretschmer, & Pawlowski, 2010; Noe & Hammerstein, 1994; Pawlowski & Dunbar, 1999; Regan, 1998). Real world mate selection is constrained by mate availability and interest, with mate interest partly determined by own attractiveness and genetic quality, which contributes to own ‘mate value’ and general desirability in the mating market. Using female attractiveness as a proxy measure for genetic fitness and desirability (as it is generally considered the most sought after trait among male suitors), it has been found that differing levels of a female’s attractiveness can lead to various condition-dependent mate selection criteria among females: attractive females, it seems, not only leverage their higher mate value by demanding higher standards of potential mating partners in areas such as resource acquisition potential and good parenting indicators, but at the same time show increased preferences for male masculinity and symmetry (purported good gene indicators) (Little, Burt, Penton-Voak, & Perrett, 2001; Shackelford et al., 2005; Todd, Penke, Fasolo, & Lenton, 2007; Waynforth & Dunbar, 1995).

Although mate value does seem to affect mate preferences, it must be noted that the subjective nature of own mate value assessments can sometimes make comparison difficult. The relative mate value of an individual will depend not only the criteria that are prized in a certain biological marketplace, but also on the extent and size of the market being used to make relative value comparisons. Comparing an individual’s relative value to that of competing mates locally, in a village or small city for example, will yield a different relative value than if making comparisons at a state or country level (as can be easily done in modern online dating ‘market places,’ or with the aid of mass media). Because of this, it can be difficult to compare self-perceived mate value and its influence on mating behaviour if some individuals are assessing their mate value and adjusting mate preferences based on their perceived relative value in the local biological market place, while others are doing so in the context of a much larger absolute market place.

The Role of Attractiveness

After initial mate preference criteria have been established, mate selection must also involve the assessment of potential mates on these criteria – with preference expressed for potential mates who are better at meeting such criteria than others. Research has found that mate assessment in humans seems to be finely tuned to interpreting various cues inherent in a potential mate's physical appearance and behaviour, particularly as they relate to mate fitness and suitability. Researchers examining mate desirability often focus on the construct of 'attractiveness,' which is generally considered to be a manifestation of the assessment outcomes of a potential mating partner (Buss & Greiling, 1999; Symons, 1990). Potential mates who best fulfil an individual's given mate choice criteria and possess valuable mate features tend to be rated as more 'attractive' than ones who do not, and are thus seen as more desirable potential mating partners.

Even though folk wisdom would have us believe that it is in the eye of the beholder that beauty is evaluated, a considerable body of research has demonstrated surprising agreement regarding some physical attributes which are thought to underlie attractiveness, both within and between cultures (Cunningham, Roberts, Barbee, & Druen, 1995; Gallup & Frederick, 2010; Langlois et al., 2000; Little, Jones, & DeBruine, 2011; Perrett, May, & Yoshikawa, 1994; Rhodes, 2006; Singh, 1993). An inherent ability to discern attractiveness in humans seems to even start at the earliest stages of development before any acculturation takes place, with infants showing preferential gaze towards more traditionally 'attractive' faces (Slater et al., 1998). Several lines of research have tried to explain the possible mechanisms by which attractiveness, particularly facial attractiveness, might universally signal underlying genetic quality or general health (for reviews see Fink & Penton-Voak, 2002; Gangestad & Scheyd, 2005; Little, Jones, & DeBruine, 2011).

It has been found that the symmetry of an individual's face is one factor which plays a role in predicting observer ratings of attractiveness (Gangestad, Merriman, & Emery Thompson, 2010; Grammer & Thornhill, 1994). Higher levels of facial and bodily asymmetry (or fluctuating

asymmetry, FA) are argued to be the result of a reduced ability of underlying genes to overcome parasitic/environmental perturbations and deleterious genetic mutations during development, leading to discernible asymmetry in the resulting phenotype. In other species, high levels of fluctuating body asymmetry are related to increased morbidity, slower growth rates and impaired reproductive success (Watson & Thornhill, 1994). In humans, low levels of fluctuating asymmetry have variously been associated with superior genetic fitness as indexed by general physical health, cognitive abilities and general intelligence, muscularity, sperm morphology and motility, and behavioural outcomes such as greater mating success (Baker & Bellis, 1994; Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997; Moller, 1997; Prokosch, Yeo, & Miller, 2005; Puts, Welling, Burriss, & Dawood, 2012; Soler et al., 2003).

Other features sometimes related to attractiveness and genetic quality are those associated with sexual dimorphism. In males, this includes the masculine traits of a pronounced jaw, prominent brow and more developed muscle mass, development of which is dependent on the hormone testosterone, acting both in-utero and throughout adolescent development (Hunter & Garn, 1972; Wells, 2007). Testosterone, in turn, has been found to interfere with the normal functioning of the immune system if present in high quantities (Folstad & Karter, 1992), to affect immunoglobulin production (Kanda, Tsuchida, & Tamaki, 1996) and reduce immune response to vaccinations (Furman et al., 2014; Rantala et al., 2012). Signalling theory states that potentially biologically 'costly' markers such as testosterone, called handicaps, can act as a signal of underlying physical condition since only individuals of superior genetic quality can afford the extra biological burden of such a handicap (Folstad & Karter, 1992; Hamilton & Zuk, 1982; Zahavi, 1975). Indeed, sexual dimorphism has been found by some studies to be related to aspects of general health (Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006), and findings from a large body of early research on male masculinity show that it can be

associated with opposite-sex ratings of male attractiveness (e.g. Barber, 1995; Buss & Barnes, 1986; Neave, Laing, Fink, & Manning, 2003; Perrett et al., 1998; Rhodes, 2006).

However, the link between testosterone, functional immunocompetence, and genetic quality may be more tenuous than this early research suggests (for a review see Scott, Clark, Boothroyd, & Penton-Voak, 2013). More recent findings show that the association between masculinity and attractiveness is more nuanced than first appears, with ratings of male attractiveness mediated, and in some instances even negated, by variables such as menstrual cycle phase of the rating female (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007), current health in the male as represented by face colour (Scott, Pound, Stephen, Clark, & Penton-Voak, 2010; Stephen et al., 2012), external pathogen cues (DeBruine, Jones, Crawford, Welling, & Little, 2010; Little, DeBruine, & Jones, 2011), a rater's current relationship status (Burriss, Marcinkowska, & Lyons, 2013; Little, Jones, Penton-Voak, Burt, & Perrett, 2002), and their own mate-value (Buss & Shackelford, 2008; Little et al., 2001). Difficulties in comparing the role of testosterone in various mating interactions are further compounded by the use of various methodologies when assessing testosterone levels, which have been found to have significant effects on measurement outcomes of testosterone levels (van Anders, Goldey, & Bell, 2014). It has also been suggested that the sexually dimorphic traits driven by testosterone in males, and found attractive by females, might actually be conveying information about social dominance and ability to engage in intrasexual competition – traits which are also desirable in a potential mating partner but not necessarily directly related to superior genetic 'fitness' (Puts, 2010).

In females, it has previously been suggested that waist-to-hip (WHR) ratios approaching 0.7 are more likely to be designated as attractive by the opposite sex, and may be signals of fecundity and underlying genetic fitness in females (Singh, 1993). The exact signals which are being conveyed by waist-to-hip ratio have been debated, with body attractiveness found to be also influenced by cultural factors, body mass index (BMI), and personality variables of the selecting

mate (Swami, Miller, Furnham, Penke, & Tovée, 2008; e.g. Tovée, Maisey, Emery, & Cornelissen, 1999). However, research has shown that some aspects of female body morphology mediated by sexually dimorphic hormones such as oestrogen, including adiposity and BMI, do seem to act as reliable proxy signals for female fertility and fecundity – correlating with a first child’s birth weight (a factor affecting infant survival rate) (Pawłowski & Dunbar, 2005) and hormones affecting female fecundity (Jasińska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004).

It must be noted that considerable debate still exists regarding the exact qualities that contribute to subjective ratings of attractiveness, and dissenting evidence exists regarding the purported universality of standards of beauty. Some recent research suggests, for example, that it may be fluctuating facial colouring, acting as a signal of current health, that is the driver of much attributed attractiveness, and not the kinds of permanent underlying morphological characteristics described above which purportedly represent underlying genetic fitness (Scott et al., 2013; Stephen et al., 2012). Other research suggests that universal agreement only exists about ‘un-attractiveness’ rather attractiveness (Sorokowski, Kościński, & Sorokowska, 2013), or even that such agreement is due to exposure to, and assimilation of, western standards of beauty in many parts of the world (Little, Jones, DeBruine, & Caldwell, 2011). The fact that the construct of attractiveness seems to encompass very different informational cues means that it is also possible that some inter-rater agreement about ‘attractiveness’ might actually be based on individuals assessing potential mating partners on completely different criteria. Furthermore, using the construct of attractiveness as a proxy for actual mate choice when conducting research might be problematic in itself. Several lines of research have found that while individuals may rate some mates as more attractive than others in experimental or artificial mate choice situation, such decisions sometimes have very little correspondence to actual mate choice decisions made in different, more ecologically valid, settings (e.g. Eastwick & Finkel, 2008).

Nevertheless, it appears that some form of mate quality and suitability information is being conveyed through the construct of attractiveness of potential mating partners, even if the details of what these qualities represent remain contested. Although vision dominates much of human interaction with the world (Levin, 1993), and much of this research on mate assessment and mate choice has focused primarily on various visual cues, cues which use other modalities to assess mate suitability have also been found to be a useful avenue for research. Since mate assessment is such an important decision to reproductive fitness, it is not surprising to find that all the other senses, including olfaction, touch, hearing and possibly even taste, seem to be utilised in this process. In fact, research on cues involving olfaction, which is an important sensory modality used by fellow mammals when assessing potential mates (Clutton-Brock & McAuliffe, 2009), suggests that this sense may still be important in human mate choice decisions.

Olfaction in Mate Assessment

The role of smell in both communication and mate selection has been recognized in insects and other animals (including mammals) for some time. Studies in rodents, for example, show that female mice prefer to mate with males endowed with a 'compatible' gene set (based on Major Histocompatibility Complex [MHC] compatibility), using mostly pheromonal cues to guide their decision making (Penn & Potts, 1999). It has been suggested that human olfactory receptor genes lost developmental influence with the evolution of trichromatic colour vision (Gilad, Wiebe, Przeworski, Lancet, & Pbo, 2004), leaving humans without vital neuronal elements in the vomeronasal organ (VNO) – an area critical to pheromone detection in other animals. Because of this, scientists have been sceptical as to whether humans can reliably detect pheromonal cues (Tirindelli, Dibattista, Pifferi, & Menini, 2009). However, recent observations that the human hypothalamus is activated by several pheromone-like substances via the olfactory mucosa have challenged arguments which had concluded pheromones could not be effectively detected by humans due to this VNO atrophy (Savic, Hedén-Blomqvist, & Berglund, 2009).

One of the first concrete examples of human pheromones in action was the reported synchronisation of female menstrual cycles, ostensibly via olfactory pathways, in dormitory-housed college women (McClintock, 1971). Since then, numerous studies have demonstrated the effects of pheromones on human sexual behaviour, suggesting that smell may play an important role in assessing the suitability of a potential mate. A seminal study in this field was carried out by Wedekind and colleagues (1995), who discovered that females asked to rate the attractiveness of males, based on the smell of the men's t-shirts alone, rated men who had dissimilar Major Histocompatibility Complex (MHC) genes as more attractive. MHC genes encode proteins involved in immunocompetence, or the ability to fight off infection. When pairing disassortatively with a mate whose MHC is different (i.e. a genetically 'compatible' mate), resulting offspring will be more heterozygous and will be better placed to ward off new infections, thus improving their odds of survival (for a review of MHC pheromones and mating see Havlicek & Roberts, 2009).

Since then, the role of olfaction in human mating assessment and selection has been explored in numerous other domains that relate to mate quality and compatibility. Results suggest not only that both male and female pheromones can have an effect on the timing of the female menstrual cycle (McClintock, 1971; Preti, Wysocki, Barnhart, Sondheimer, & Leyden, 2003), but that pheromonal cues may also betray information about a female's current ovulatory state (Doty, Ford, Preti, & Huggins, 1975; Singh & Bronstad, 2001; Thornhill et al., 2003; Tonzetich, Preti, & Huggins, 1978). Such information would be extremely useful to potential mating partners pursuing short-term mating strategies, increasing the odds that any one brief encounter may result in offspring. Although the exact composition of active pheromonal chemicals remains mostly unclear, one component of human pheromones which has been isolated and studied in detail is androstenol – with data suggesting that its presence can alter levels of sexual arousal, ratings of partner attractiveness, and influence reported frequencies of various sexual activities (Bensafi,

Brown, Khan, Levenson, & Sobel, 2004; Cutler, Friedmann, & McCoy, 1998; Saxton, Lyndon, Little, & Roberts, 2008; Thorne, Neave, Scholey, Moss, & Fink, 2002). Pheromones have also been found to convey a considerable amount of mate-relevant quality information, including information about aspects of a potential mate's personality (Butovskaya, Veselovskaya, Rostovtseva, Selverova, & Ermakova, 2013; Sorokowska, Sorokowski, & Szmajke, 2011), desirable non-verbal behaviour (Roberts et al., 2011), testosterone levels and dominance (Havlicek, Roberts, & Flegr, 2005; Thornhill, Chapman, & Gangestad, 2013), about levels of fluctuating symmetry (Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Thornhill et al., 2003, 2013), and even current health status (Durham, Malloy, & Hodges, 1993).

These results suggest that olfactory information can be highly relevant to mate choice decisions, with individuals seemingly even consciously aware of the important role olfaction might play in the process (Sergeant, Davies, Dickins, & Griffiths, 2005). While much of this mate-relevant information can also be conveyed through other senses such as vision, with olfactory cues merely assisting in a multi-modal communication of concordant information (e.g. Cornwell et al., 2004; Roberts et al., 2011), olfaction can also convey unique information, quickly and efficiently, which is less discernable to other senses (i.e. MHC-compatibility related information). Furthermore, it appears that sex differences exist in the utilisation of this information – females have been found to rely on olfactory mate cues more than males (Herz & Cahill, 1997; Herz & Inzlicht, 2002), even showing increased olfactory sensitivity at the time of their cycle where mating would be most likely to lead to conception (Doty, Snyder, Huggins, & Lowry, 1981; Pause, Sojka, Krauel, Fehm-Wolfsdorf, & Ferstl, 1996). This difference is likely to be related to increased mate selectivity commonly seen in females, who pay greater attention to a wider variety of mate cues when assessing potential mates due to their larger minimal parental investment levels (and the greater negative consequences of poor mate choice) (i.e. Candolin, 2003; Townsend & Wassermann, 1998).

Other Senses Used in the Assessment of Mates

Due to the importance of mate assessment to an individual's reproductive success, humans have been found to use nearly all the senses at their disposal to find, assess, and maintain relationships with desirable mates. When men were asked to judge the attractiveness of females based solely on listening to their voice pronouncing four vowels, strong agreement was found between ratings of their vocal attractiveness and their actual physical 'attractiveness' (Collins & Missing, 2003). Body movement has also been found to convey information about mate quality. Using biometric light-point analysis of dancing males, it was discovered that there is general agreement between female ratings of a male dancing ability, with males rated as 'good' dancers found to be displaying the sort of skilful variability of movement best achieved by particularly healthy and genetically fit specimens (Hugill, Fink, & Neave, 2010).

During the process of 'courtship', where in many cultures much of early mate assessment takes place, it has been found that men are more likely to initiate touching than women, and that touching leads to greater compliance with a male courtship request (Guéguen, 2007). Most interestingly, this difference in touching is reversed after the successful conclusion of initial courtship, with women married for more than one year more likely to initiate touching behaviours with their partners than men (Willis & Briggs, 1992). This research, combined with previous findings that women are more likely to infer 'commitment' from inter-sexual touching than men (K. L. Johnson & Edwards, 1991), and that social touch facilitates the release of neuropeptide oxytocin (Grewen, Girdler, Amico, & Light, 2005; Light, Grewen, & Amico, 2005; Uvnäs-Moberg, 1998) and potentially endorphins (Dunbar, 2010), suggests that individuals may be using touch to further their differing short-/long-term mating goals – men using touch to initiate sexual relations with a prospective partner, and females to establish/mediate pair-bond attachments.

Courtship Customs and Mate Assessment

Early researchers drew numerous parallels between courtship behaviours in other species, such as the dances of wild peacocks and turkeys, and some of the mating behaviours found in many of the world's human cultures (Birdwhistell, 1970; Eibl-Eibesfeldt, 1972; D. Morris, 1971). As the consequences of poor mate choice are potentially quite severe in terms of reproductive fitness, it seems quite likely that some human courtship customs and behaviours may be used to aid the important process of mate assessment, before any serious mating commitments are made (Givens, 1978; Grammer, 1989). It has been proposed that courtship in many cultures takes place over the course of multiple sequential stages, each increasing in intimacy, and designed to advance the progress of the mating process: attention, recognition, interaction, sexual arousal and resolution (Givens, 1978). Courtship behaviours have been variously found to be very effective at attracting the attention of potential mates, at accentuating desirable traits and general attractiveness, at aiding intra-sexual competition, and at increasing compliance in potential opposite-sex partners (Barclay, 2010; Grammer et al., 2000; Guéguen, 2007; Hirsch & Paul, 1996; Kenrick et al., 1990; Lycett & Dunbar, 2000; Moore, 2010; Neave et al., 2011). These behaviours can take many forms and range from subtle, non-committal activities (such as flirting and making eye contact), all the way to intense and directed behaviours (such as physical touching and caressing).

A Role for Romantic Kissing in Mate Assessment?

One courtship custom, which has received little attention from scientific researchers examining human mating, is kissing between mating partners – referred to as ‘romantic kissing.’ This is a custom which is present in some form in nearly all the world's cultures (Eibl-Eibesfeldt, 1972; H. E. Fisher, 1992; Ford & Beach, 1951), and at first glance seems to be a relatively high-risk behaviour – exposing relative strangers to numerous risks of infection (Cowan et al., 2002; Schoch-Spana, 1992; Tully et al., 2006). That such a potentially hazardous endeavour is so

prevalent and widespread suggests that its practice might serve some useful function in the context of human mating. In light of the literature on mate selection presented above, it seems that romantic kissing is particularly well placed to assist in several areas of mate selection. One of the primary consequences of this custom lies in the bringing together of two potential mating partners into very close proximity, which would facilitate olfactory sampling of another individual for cues of genetic compatibility, genetic and general health, fluctuating asymmetry, personality and dominance, or even signs of ovulation. Alternatively, the high levels of contact initiated by some forms of kissing might allow for the initiation of sexual relations, or alternatively for the mediation of pair-bond attachments between mating partners. If kissing served any of these functions, then it would follow that individuals who valued those functional outcomes more highly would also value kissing in relationship situations where kissing would best serve those purposes.

These as yet unanswered questions about the common courtship custom of romantic kissing are addressed in Chapters 3 and 4 of this thesis. The first of these chapters aims to determine what, if any, functional purpose romantic kissing might serve in processes of mate selection and retention. Three hypotheses relating to the function of kissing are tested against each other in this chapter in a 'critical tests' format: 1) that kissing's primary function is related to increasing arousal between partners and initiating sexual relations; 2) that it functions to help assess the quality and/or suitability of potential partners; 3) or that it serves to mediate feelings of attachment (the basis of pair-bonds) between partners in established long-term relationships. These questions are addressed in Chapter 3 by a study examining attitudes towards kissing in several relationship situations, and how these attitudes vary between individuals who differ on mate value, are following different mating strategies, and differ in respect to sex.

Since it can be useful to establish that a behaviour suspected of being shaped by evolutionary forces is linked to the kinds of biological processes upon which selection might act, Chapter 4

further examines the effect of a potential biological hormonal mediator of this courtship behaviour in females. In this case, attitudes towards kissing in romantic relationships in females are examined across the menstrual cycle to see whether patterns of menstrual cycle hormone fluctuations have any relationship with attitudes towards this courtship custom. Furthermore, also in this chapter, the role of kissing-related informational cues about potential mating partners is explored to see how they affect mate desirability in different mating situations, and the relative importance of such information in the presence of competing visual cues. The findings of these two chapters are an important step in establishing links between courtship customs found in many places of the world, which are sometimes seen as purely socio-cultural constructions, and evolutionarily functional purposes mediated by our shared biological underpinnings.

Pair-bonding

Establishing a mating strategy, prioritising relevant mate choice criteria, and selecting and mating with a suitable partner are the minimum steps required to influence an individual's long-term fitness outcomes. To ensure that these outcomes are significantly improved, however, any offspring resulting from these mating behaviours must also be reared to maturity. Individuals pursuing short-term mating strategies will expend energy siring multiple offspring, each with minimal parental investment, in the hope that some will survive to maturation. However, individuals who are pursuing a long-term mating strategy (see Chapter 2), and who have during the mate selection process preferentially chosen mates also willing to make long-term investments (i.e. Chapters 3 & 4), are also likely to attempt to improve offspring survival by co-ordinating parental investments under the auspices of bi-parental care (Clutton-Brock, 1989). In humans, the chances of individual offspring survival are greatly improved in the presence of such co-ordinated parenting activities (Geary, 2000), which are typically maintained through the formation of sexual pair-bonded attachments – also known in humans as ‘romantic love’ (H. E. Fisher, 1989; Mellen, 1981).

This section of the literature review briefly examines why bi-parental care is so important in humans, the role that pair-bonding attachments play in co-ordinating bi-parental investments, and the biological roots that are through underlie the creation and mediation of pair-bonds. Following this overview, a recent body of literature will be introduced that has attempted to understand the biological underpinnings of pair-bonding through the in-vivo examination of neural correlates associated with romantic love. This brain imaging literature has made some fascinating discoveries relating to localised neuronal ‘inhibition’ associated with pair-bonding, which researchers have hypothesised might inhibit certain cognitions and aid in this final process of pair-bonding – the formation and mediation of interpersonal attachments. A research question that aims to test the hypotheses arising from this fMRI research is then introduced at the end of this section, and further examined and empirically tested in Chapter 5 of this thesis.

The Need for Bi-parental Care

Human infants are secondarily altricial, requiring substantial support during rearing. The primary reason for this is brain size, which, though very large relatively to other primates, must still pass through the female birth canal, which is itself limited due to the constraints of bipedal locomotion (Rosenberg & Trevathan, 1995; Ruff, 1995). These constraints mean that infants are born with a brain which is relatively underdeveloped compared to other primates (requiring another 12 months of post-partum growth before catching up to primate development at birth), require nursing for up to 36 months, and need continued care in order to survive for several years after that (Bogin, 1999). These very high levels of dependency require intense levels of investment and place heavy physical demands on the mother, as well as demands on her time and resources. Because of this, strong selection pressures exist for both parents to contribute investment to the rearing of offspring, with bi-parental care playing a more important role human mating than in the mating processes of most mammals and many primates (Clutton-Brock, 1989; Flinn, Ward, & Noone, 2005). This kind of pressure in humans is relatively unique among mammals: in species

where females invest in offspring, male parenting occurs only 5% of the time (Clutton-Brock, 1989), although forms of allocare are commonly found in other large-brained non-human primate species with high infant investment requirements (Ross & MacLarnon, 2000). Research has shown that the presence of male parental investment, in humans as well as in other species where males make investments, does indeed significantly reduce offspring mortality rates and improves offspring survival and access to resources upon maturation (for review see Geary, 2000).

Since the survival of any offspring sired is also crucial to male reproductive success, it oftentimes makes sense for males to invest in a committed relationship with one partner and increase the long-term chances of survival of the resulting offspring. These disproportionately high parental investment requirements, however, necessitate that human males forfeit otherwise desirable short-term mating tactics, with parental investment typically carried out at the expense of additional mating opportunities due to constraints on time and energy (Marlowe, 2000). Various environmental variables may influence this decision by affecting the relative fitness payoffs associated with larger parental investments versus more diversified mating efforts. This has been shown to be the case within primate species such as callitrichids (Dunbar, 1995), with suggestions that either infanticide risk or mate guarding may have been contributing factors to the evolution of pair-bonded mating in non-human primates (Lukas & Clutton-Brock, 2013; Opie et al., 2013).

In humans, it is thought that three conditions must be met before such extra male investments take place, namely: 1) the existence of high levels of parental certainty (so as to ensure any investments made go towards own progeny); 2) paternal investment must be effective in improving offspring survival; 3) and a motivational system must exist which co-ordinates behaviours and efforts exclusively with one partner (Marlowe, 2000). Firstly, parental certainty in humans is enhanced by the presence of concealed ovulation, as well as evolved female norms placing restraints on promiscuous sex (Geary, 2000) – norms which are also present in other monogamous primate species (Dunbar, 1995). Secondly, the effectiveness of parental investment

in humans is assured by the vast improvements in offspring survival and success arising from male investment (see earlier). Finally, it has been proposed that human pair-bonding, colloquially referred to as romantic love, is the motivational system that has evolved to co-ordinate activities between mates, maintaining intense relational bonds between mating partners long enough to rear offspring (e.g. H. E. Fisher, 1989; Mellen, 1981). The formation and maintenance of interpersonal pair-bonds is the culmination of the pair-bonding process, arising to solve the problem of co-ordinating the kinds of bi-parental investments altricial human offspring require in order to improve their chances of surviving to maturity.

Pair-bonding in Humans

Interpersonal pair-bond attachments are found in nearly all human cultures, irrespective of whether the dominant mating system is monogamous, polygamous, or polyandrous (Brown, 1991; Murdock, 1967). Ethnographic evidence suggests that the concept of romantic love is experienced in some form by every recorded culture and is evident in even the earliest human oral and written records (Dunbar, 2012; Gottschall & Nordlund, 2006; Jankowiak & Fischer, 1992). This near-universal idea of romantic love is the cultural manifestation of a motivational and emotional biological mechanism that has historically been responsible for the initiation and maintenance of long-term attachments between mating partners (ibid.). Motivations associated with romantic love help direct an individual's interest towards one specific mating partner, reduce interest in the pursuit of other partners, and create a desire and drive for emotional intimacy and closeness with that individual (Dunbar, 2012; H. E. Fisher, 1992; McIntyre et al., 2006). Such intimacy and close attachment, in turn, aids in the process of aligning interests and co-ordinating behaviours for a period of time that is long enough to successfully rear offspring with the aid of bi-parental investment (Dunbar, 2014). Cognitions which have been associated with romantic love, and which are thought to help to facilitate the maintenance of these long-term relationships, are feelings of emotional dependency, security and comfort, commitment and reduced levels of

anxiety (H. E. Fisher, 1998). In humans, various affiliative behaviours are further thought to help reinforce and mediate these types of attachments, including high levels of social contact, joint coordination of behaviour, direct physical contact and various types of physically and psychologically arousal inducing activities (Dunbar & Shultz, 2010).

Because of its importance to offspring survival, the creation of pair-bonds is likely to have been under considerable evolutionary pressure. It has been suggested that this unique form of mating attachment may have originally evolved from the intense emotional and motivational bonds established between a mother and her infant, an attachment which is necessary for offspring survival (Bowlby, 1969; Broad, Curley, & Keverne, 2006). These two forms of attachment share many similarities, including feelings of security in the presence of the attachment object, longing when apart, and the desire to be together after separation – all of which permeate both mother-infant bonds and pair-bonded mating attachments (Shaver, Hazan, & Bradshaw, 1988). Most importantly, this evolutionary link is corroborated by similarities found in biological substrates which seem to underpin these two types of attachments, with the neuropeptide oxytocin thought to play the pivotal role in both mother-infant bonds, where it is released during parturition and lactation, as well as in mating pair-bonds (Carter, 1992; Hrdy, 1999; Insel, 1992; Soloff, Alexandrova, & Fernstrom, 1979; Uvnäs-Moberg, 1998). These purportedly shared biological origins have led researchers to examine in more detail the underlying physiology of these intense interpersonal bonds.

The Biological Roots of 'Romantic Love'

Research examining the underpinnings of human pair-bonds suggests that attachment behaviours such as these might be related to numerous physiological correlates (for reviews see Carter, 1998; de Boer, van Buel, & Ter Horst, 2012; Esch & Stefano, 2005; Kendrick, 2004; Saxe, 2006; Van Overwalle, 2009; L. J. Young, Murphy Young, & Hammock, 2005). Since the neuroanatomical

and neurochemical systems of much of human biological function is evolutionarily conserved among primates (and mammals in general), early animal models of neurobiological and endocrine function have proved to be instrumental to our understanding of the biological roots of human pair-bonding.

The earliest research on neuroendocrine systems associated with pair-bonding was carried out on prairie voles, who form monogamous bonds after mating, and who are taxonomically very closely related to montane voles, who are instead promiscuous maters. The difference in mating systems between these two closely related voles has been associated with differences in the expression of oxytocin and vasopressin receptor sites in the vole brain (Carter, 1992; Insel, 1992). Monogamous voles have higher densities of oxytocin receptors in regions of the brain associated with the dopamine reward system and in the amygdaloidal region (associated with memory and emotion), as well as higher vasopressin receptor densities in the lateral amygdala (Insel, 1992; L. J. Young & Wang, 2004). The role of these two peptides in the establishment of a mating system was corroborated by evidence that when their release was blocked in monogamous voles they failed to form pair-bonded attachments, while when vasopressin was expressed in promiscuous voles they formed monogamous pair-bonds (Lim & Young, 2006). These examples of the effects of simple neuropeptides on seemingly complex behaviours such as pair-bonding highlighted the value of examining links between various neural correlates and behavioural outcomes not only in mammals, but in humans as well.

A lot of the activity of these two neuropeptides in humans takes place in the dopaminergic reward system of the brain in pair-bonding species, with the dominant neurochemical of that region, dopamine, also thought to play a role in pair-bond formation and the mediation of oxytocin and vasopressin effects (L. J. Young & Wang, 2004). Because of this, it is perhaps not surprising to observe that romantic love behaviours can feel as addictive as other behaviours associated with dopaminergic reward pathways, such as gambling or drug addiction (Edwards & Self, 2006). The

neurotransmitter serotonin is yet another substance that has been associated with pair-bonding, with research suggesting that romantic love in its early stages may be associated with depleted levels of serotonin (Zeki, 2007). Similar levels of serotonin depletion are also found in psychiatric conditions such as obsessive compulsive disorders (Feygin, Swain, & Leckman, 2006; Marazziti, Akiskal, Rossi, & Cassano, 1999), depression (S. N. Young & Leyton, 2002), and anxiety (Leonardo & Hen, 2006), suggesting that behaviours associated with intense early-stage romantic love might share the same neural substrates as behaviours arising in individuals suffering from these disorders. Furthermore, endorphin activity is also known to be highly inter-correlated with dopamine activity, with endorphins also implicated in the formation and maintenance of various forms of social attachment and interpersonal bonding in humans as well as primates (Dunbar, 2010; Machin & Dunbar, 2011). Finally, other neuronal and hormonal changes that have been associated with early stage romantic love include the hypothalamic pituitary adrenal axis (HPA) and cortisol, which are also known to interact with oxytocin and vasopressin, nerve growth factor (NGF), and the hormone testosterone (for a review see de Boer et al., 2012).

What are the Cognitive Effects of The Brain on Love?

Evidence for the influence of various neurochemicals and hormones on human pair-bonding suggests that this evolved set of cognitions and behaviours may be mediated by a common and distinct set of biological substrates. More recent research has attempted to look deeper into the underlying neurobiology of pair-bonding using a different route – by using in-vivo brain imaging technology to try to localise love-related cognitions and processes within the brain. It is hoped that by observing regional activation patterns associated with pair-bonding, and by comparing this information to what is already known about the functional associations of those regions, the nature of various adaptive pair-bond associated cognitions and behaviours might be better understood.

Several Functional Magnetic Resonance Imaging (fMRI) based studies have uncovered some interesting neural correlates associated with romantic love cognitions, including brain activations in dopaminergic and reward and emotion processing centres of the brain. Some of these activations have been found to show a dose-response relationship between self-rated love intensity and activations patterns in those brain regions. Fascinatingly, some studies also show ‘deactivations’ in some areas of the brain among individuals in love. Such brain activity reductions have been found to occur in regions associated with mentalizing, the processing of negative emotions, and exercising cognitive self-control. It has been hypothesised that if these areas of deactivation represent neuronal inhibition, then cognitive functions that rely on those brain areas may be adversely affected in individuals who are in love. Such cognitive impairment has been hypothesised to explain various casually observed, love-typical behaviours that include anecdotal evidence that ‘love is blind’ or irrational, that it can instil feelings of fearlessness, and that it often involves obsessive, uncontrollable thoughts about a love object (Zeki, 2007). These predictions, however, have to date never been empirically tested. If we are to gain a clearer understanding of the nature of pair-bonding behaviour in humans, it is necessary to determine whether such fMRI based observations of neuronal deactivation can be relied on as an accurate predictor of love-related cognitions. Such a clarification would also determine whether in future research such fMRI commonly observed neuronal inhibitions might be relied upon to act as a predictor of general cognitions and behaviours.

The aim of Chapter 5, therefore, is to address this gap in our understanding of the effect of love-induced brain region deactivations on cognitions relying on those regions. By clarifying the existence of this link, we will be better placed to understand the kinds of cognitions that are associated with the motivational system of romantic love in humans and their biological basis, which is an important step to understanding how these cognitions might function to create and mediate pair-bond attachments. Chapter 5 firstly examines in more detail the research studies

that have so far looked at neural activations induced by love stimuli. Then, an experimental study is introduced that was designed to determine whether individuals in love show reduced functionality in regions previously observed to ‘deactivate’ during the presentation of a love prime. Using a controlled experimental design, following as closely as possible the methodology of previous fMRI studies where these brain deactivations were observed to take place, the study presented in Chapter 5 will set out to test empirically the effects of love on two distinct aspects of cognition that have been hypothesised to be affected by love, mentalizing ability, and regulation of self-control.

1.3 Thesis Outline

This chapter provided an outline of various processes across human mating interactions that lead up to the formation and maintenance of pair-bonds, namely mating strategies, mate selection, and pair-bonding cognitions. Within each phase of mating, a novel research question associated with a specific set of mating behaviours has been identified, the clarification of which would enhance our understanding of the process involved in pair-bonding within an evolutionary framework. The following chapters of this thesis elaborate further on the literature as it relates directly to each of these three research questions, and propose and execute an original set of experiments in an attempt to answer each of them in turn. The remainder of this thesis will examine, in more detail, the within-sex distribution of preferences for short- versus long-term mating and the distribution of a purported mediator of mating effort (testosterone) during the establishment of mating strategies, the possible functions of a common courtship custom (romantic kissing) in mate assessment and pair-bonding, and the effects of ‘romantic love’ on attachment-relevant cognitions within established pair-bonds.

Chapter 2 examines a dimension of human mating strategies referred to as ‘long-term’ versus ‘short-term’ mating. The choice between these two mating strategies has previously been shown

to impact reproductive fitness, and the pursuit of one strategy over another has been found to vary between different populations, between sexes within a population, and even within each sex in a population. The distribution of strategies within each sex, however, has typically been assumed to be continuous – with individuals following a strategy which is in part determined by environmental, cultural, and personal cues. This thesis proposes that these strategies might in fact be bi-modally distributed within each sex. If such bimodal distributions in strategy were found to be present, it would suggest that two distinct phenotypes might exist within the sexes, each a distinct driver of preferences towards either short-term or long-term mating strategies. The motivation of the research in this chapter is to address the current uncertainty that exists around the distribution of these strategies by determining statistically, using existing datasets, whether two phenotypes might actually underlie mating strategies within each sex. A secondary goal of this research was to examine whether these strategy distributions might be related to a purported biological driver of short-/ long-term mating strategy, namely prenatal testosterone (as indexed by 2D:4D digit ratios). This will be the first time that the nature of within-sex mating strategy differences will be examined in light of such phenotypic differences, and the first time an attempt will be made to show empirically a link between such differences and an underlying biological driver. The findings from this chapter will make an important contribution to our understanding of the underlying nature of human mating strategies, their biological substrates, and the implications of such strategy choices for the processes of pair-bonding. Furthermore, if such a phenotypic divide is found to exist, then our current understanding of mating strategy decisions may have to be adjusted to accommodate this newfound complexity, as the validity of using aggregate within-sex mating strategy indices to describe populations may be called into question.

Chapter 3 moves onto the next processes necessary for the establishment of pair-bonds, the assessment, selection and retention of potential mates. Although the courtship custom of romantic kissing is surprisingly prevalent in many cultures, it remains unclear at this stage whether

it serves a useful function in the processes of human mating, and more importantly, what exactly that function might be. It is possible that the primary role of kissing in relationship contexts is that of initial mate assessment, arousal and readying for coitus, or the mediation of interpersonal attachment in established relationships. The aim of this chapter of the thesis is to test these hypotheses to determine the most likely role that kissing plays in romantic relationships. Furthermore, this chapter will examine whether individuals pursuing the two different mating strategies might differ in their use of romantic kissing in various mating situations. The study detailed in this chapter examines variations in attitudes toward romantic kissing in a large, diverse multi-national sample of participants, looking at patterns of responses to survey questions and how they co-vary with participant characteristics (such as sex, sociosexuality, and relative mate value in the mating environment). Establishing what functional role may be served by this mating behaviour is essential to helping us further understand the complicated processes involved in the assessment of potential mates. Finding that this courtship custom serves useful functions in the process of pair-bond formation and maintenance would influence future research in this field by paving the way for the examination of other common courtship customs through an evolutionary framework in order to determine whether they too have arisen to solve evolutionary problems faced by individuals in their attempts to improve their long-term fitness.

Chapter 4 of the thesis includes three follow-up studies examining two different aspects of romantic kissing as it relates to mate selection. The aim of this chapter is to look at whether any evidence can be found for a biological driver underlying the utilisation of romantic kissing in certain relationship situations, to determine whether purported kissing abilities have an effect on mate desirability in different mate assessment situations, and to examine the relative importance of mate information derived from kissing as compared to traditional visual cues of mate information. The chapter is divided into three sections, detailing three experimental studies that address these aims. The first study in this chapter examines how biological mechanisms might

affect the role of romantic kissing in mating relationships by looking at variation in attitudes towards kissing among females over the course of the menstrual cycle and how this varies with estimated menstrual cycle hormone levels. The following two studies attempt to discern whether purported kissing abilities in a hypothetical mating partner affect the desirability of mating partners in various mating situations, and examine the relative importance of this information in light of competing visual cues of mate quality.

Chapter 5 examines the nature of human pair-bonding and its effect on cognition. Recently, brain imaging technologies such as fMRI have been utilised to examine the neural correlates of romantic love in order to improve our understanding of the biological substrates linked to emotions and cognitions associated with such attachment pair-bonds. While interesting activations have been found in various brain regions, including dopaminergic reward centres of the brain, several studies have also found what appears to be ‘deactivations’ in individuals presented with a love prime in regions of the brain associated with mentalizing and inhibition of self-control. Researchers have theorised that such deactivations may be responsible for impaired cognitive function in domains associated with these regions among individuals in a state of romantic love. The motivation of this chapter of the thesis is, therefore, to examine whether such previously observed deactivations in individuals presented with a love prime might lead to impaired cognitive abilities in areas linked to those regions, namely mentalizing and exhibiting self-control. These predictions are tested using an experimental design where individuals are primed by thoughts of a loved one and asked to complete the requisite cognitive tasks. This is the first time that such hypotheses regarding love-induced brain deactivations and their relationship to love-relevant cognitions are empirically tested, with this experiment potentially enhancing our understanding of the complex interplay between fMRI observed brain activity and real-world cognitions within established mating pair-bonds.

Finally, Chapter 6, synthesises the results of the six studies carried out in this thesis, and describes how the diverse mating behaviours examined here are interconnected prerequisite processes affecting human pair-bond formation and maintenance. The original contributions of this thesis not only extend our understanding of some of the functional purposes served by mating behaviours such as mating strategies and courtship customs like romantic kissing, but also have implications for future methodological approaches to studying human mating, and for our understanding of the evolution of pair-bonding in humans. An exploration of how these findings provide new and interesting directions that might be fruitfully explored by future research is also presented at this point in the thesis.

The collection of analyses, experimental and behavioural studies presented in this thesis represent a wide range of research problems and techniques that are brought to bear on the broad topic of processes of pair-bonding. Although each chapter addresses very different behavioural aspects of human mating, each of these interrelated mating behavioural outcomes forms an integral part of the pair-bonding process. Each behaviour, therefore, must be not only be understood in its specific functions and detail, but it must also be examined in the wider context of its role in the creation and maintenance of pair-bonds so that they can be ultimately understood from an evolutionary perspective. These studies help us understand the evolutionary pressures affecting motivations and cognitions behind our seemingly complicated and conflicting mating behaviours, behaviours which play not only an integral role in our everyday lives, but ultimately drive reproductive success.

Chapter 2 – Mating Strategy Phenotypes

2.1 Introduction

One of the first necessary processes in the formation of mating pair-bonds relates to the search for suitable mates, which begins with an initial allocation of mating effort. At this early stage in the process mating effort can be directed towards one of two strategies when it comes to pursuing mates: either towards the search for multiple, short-term mating interactions; or towards the search for a single partner with whom to pursue long-term mating opportunities (Buss & Schmitt, 1993). It is individuals pursuing such long-term mating strategies who are more likely to go on to establish mating pair-bonds with mating partners, making greater resource and parental investments in any resulting offspring. To assess the relative allocation of effort towards one of these two main strategies, the concept of ‘sociosexuality’ has been established, which consists of behavioural, attitude and desire sub-components that assess the degree to which any one individual is likely to pursue non-committal (short-term) sexual encounters (Penke & Asendorpf, 2008; Simpson et al., 1991).

Past research looking into mating strategies in humans has focused primarily on sex differences in strategies. Parental investment theory suggests that the sex making the greater minimal parental investment (in humans, females) is more likely to pursue long-term mating opportunities than the less investing sex (males) (Trivers, 1972). A large body of research across diverse cultures bears these predictions out, showing that males are universally more likely to have more ‘unrestricted’ sociosexuality (i.e. more likely to pursue short-term mating strategies) than females (e.g. Buss, 1989). It has been found that these differences in sociosexuality between the two sexes in a given population are also related to various environmental factors being faced by each population (e.g. Lippa, 2009; Schmitt, 2005b). Furthermore, mating effort and aspects of sociosexuality are thought to have a significant genetic component driving their expression

(Bailey, Kirk, Zhu, Dunne, & Martin, 2000; Buss & Greiling, 1999), with testosterone emerging as the most likely biological candidate responsible for strategy establishment (Ellison, 2001).

Research looking at sociosexuality differences within the sexes has thus far focused on the idea of conditional mating strategies, whereby individuals within a given sex pursue either short- or long-term mating strategies adaptively depending on the local conditions faced (e.g. Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Schmitt, 2005a). However, it is also possible that alternate mating strategies within the sexes are reflective of different polymorphisms present in each sex, each driving strategy choice in one of two directions (Gross, 1996). This possibility, however, has never been empirically investigated.

The main motivation of this chapter is to explore this gap in our understanding of human mating strategies and their underlying drivers. The aim here is to use mathematical and statistical modelling techniques to determine whether the distribution of within-sex mating strategies in a given population (as indexed by sociosexuality), and the distribution of a purported driver of mating strategy (prenatal testosterone, as indexed by 2D:4D digit ratios), shows signs of being driven by two distinct underlying phenotypes in the form of bimodal strategy/driver distributions. This chapter also examines how these distributions differ both within and between the sexes, and whether these differences might be suggestive of the existence of an evolutionary stable strategy set.

2.2 Literature Review – Male and Female Mating Strategies

Some uncertainty exists as to whether humans are predisposed to be primarily monogamous, polygamous or promiscuous, with physiological and anthropological data suggesting that humans possess considerable flexibility when it comes to the structure of their mating systems (Low, 2001). While the vast majority of known cultures have predominant mating systems which are based on some form of polygyny, in practice various different mating strategies are also

simultaneously pursued within these cultures (Mealey, 2000; Murdock, 1967) (for more details see also Chapter 1, 'Mating Systems,' p. 7).

As introduced in Chapter 1, parental investment theory suggests that the sex undertaking the greater level of minimal parental investment (in humans females) will prioritize the pursuit of long-term relationships (M. B. Andersson, 1994; Trivers, 1972). Research indeed confirms that across various cultures, females more than males prioritize long-term mating relationships, preferring potential mates who possess traits signalling the ability to invest resources into parental care (Buss, 1989; Kenrick et al., 1990; Townsend & Wassermann, 1998) and who show willingness to enter into long-term pair-bonded relationships (Baumeister & Bratslavsky, 1999; Ellis & Symons, 1990; Symons, 1979). As the potential fitness advantages of promiscuous mating preferentially benefit the sex with lower minimum parental investment requirements (in humans males), males more than females generally prioritise the pursuit of short-term mating strategies with multiple partners (Buss, 1989; Schmitt, 2003; Symons, 1979).

The Construct of Sociosexuality

The extent to which an individual is likely to engage in uncommitted sexual relationships has been conceptualised as their sociosexuality by early researchers into human sexual behaviour (Kinsey, Pomeroy, & Martin, 1948; Kinsey, Pomeroy, Martin, & Gebhard, 1953). Since then, attempts have been made to operationalise this concept using a short self-report inventory known as the Sociosexuality Orientation Inventory (SOI), which takes into account an individual's sexual history and general attitudes towards noncommittal sex (Simpson et al., 1991). This scale has since been expanded into a longer self-report scale (the 9-item SOI-R), which further isolates sociosexuality into three component dimensions, namely: noncommittal sexual behaviours; attitudes towards noncommittal sex; and general desire for noncommittal sexual encounters (Penke & Asendorpf, 2008). Interpretations of this scale typically describe individuals scoring

highly on sociosexual orientation as being sociosexually ‘unrestricted,’ demonstrating behaviours and attitudes in favour of sexual encounters in the context of noncommittal, short-term relationship situations, while individuals scoring relatively low on this scale are classed as having ‘restricted’ sociosexuality, preferentially pursuing and desiring sexual encounters within the context of committed, long-term pair-bonded relationships. These differences are generally thought to be reflective of long-term (monogamous) or short-term (promiscuous) mating strategies respectively. Each mating strategy in turn leads to differentiated use of mate assessment and mate selection behaviours in later phases of mating (see also ‘Mate Selection,’ p. 14). Recent research even suggests that sociosexuality may affect responsiveness to strategy-relevant mate cues within individuals – with unrestricted individuals, for example, showing increased sensitivity to fluctuating asymmetry in female faces (Sacco, Hugenberg, & Sefcek, 2009), improved episodic memory function for male sexually dimorphic cues (D. S. Smith, Jones, & Allan, 2013), and biases in the perception of signs relating to sexual interest (Howell, Etchells, & Penton-Voak, 2012).

Sex Differences in Sociosexual Orientation

Extensive research on sex differences and sexuality confirms that males, the lesser-investing sex, almost uniformly demonstrate behaviours and attitudes consistent with short-term mating strategies as compared to females. Research has found that males have higher sex drive (Lippa, 2009), desire a larger number of partners and have more extra-pair copulations (Buss & Schmitt, 1993; Symons, 1979; Wiederman, 1997), have more favourable attitudes towards noncommittal sex (H. E. Fisher, 1989; Oliver & Hyde, 1993; Townsend, 1995), are more likely to fantasize about sex with multiple partners (Ellis & Symons, 1990), are more likely to be attracted to opposite sex friends (Bleske-Rechek et al., 2012), are more likely to consent to sex with strangers (R. Clark & Hatfield, 1989), and are considerably more likely to have sex with prostitutes (Symons, 1979).

Studies which have examined the construct of sociosexuality directly, as assessed by the SOI and SOI-R, have also found sex differences, whereupon males universally display more unrestricted sociosexualities (e.g. Bailey et al., 2000; A. P. Clark, 2004; Penke & Asendorpf, 2008; Simpson et al., 1991). While many studies in psychology are limited by their overreliance on research based on Western, educated, industrialized, rich, and democratic populations (WEIRD, Henrich, Heine, & Norenzayan, 2010), the study of sociosexuality is quite unique in the cultural breadth in which it has been studied. Examining sociosexuality scores in a large international sample of 14,059 individuals from 48 countries, Schmitt (2005b) showed that these sex differences were indeed cross-culturally universal. Distributions of sociosexuality across these cultures also seemed to vary with several ecological variables, with countries with male-biased sex ratios or more demanding or stressful environments showing a greater overall bias towards long-term mating strategies. Furthermore, this data suggests that the differences between the sexes in their sociosexuality scores, while consistently skewed in the same direction, nonetheless varied according to both environmental stress and political and economic gender equality. It seems that differences in sociosexuality scores between males and females are accentuated in more demanding environments, and conversely reduced in countries with higher levels of gender equality. These results were replicated in a similarly large study, conducted online, which found even stronger sex sociosexuality effects (using the SOI attitudinal subscale only) in a sample of 200,000 individuals drawn from 53 nations, with environmental stress and political/economic equality having even more robust mediating effects on sociosexuality scores (Lippa, 2009). However, this larger study, while attracting a larger sample, suffered from sampling flaws by being presented only online and in English, unlike the previous study that used translated materials and face-to-face interviews wherever possible.

These findings demonstrate the existence of a scalar relationship between environmental pressures and mating strategies. Interestingly, these, and other studies, all show converging

evidence that it is mean female sociosexuality, rather than male sociosexuality, that shifts adaptively to changes in the socio-cultural and physical environment (Baumeister, 2000; Lippa, 2009; Murray, Jones, & Schaller, 2013; Schmitt, 2005b). It appears that in harsh or demanding environments, where raising offspring is more challenging and the dual investments of bi-parental care mediated long-term relationships are more important to offspring survival, females are more likely to pursue long-term mating strategies while males remain relatively promiscuous, increasing the between-sex sociosexuality gap. Meanwhile, greater political and economic equality, where females might be expected to have greater access to resources and thus be less reliant on males for additional parental investments, is associated with higher sociosexuality scores in females, with male sociosexuality scores once again remaining relatively unchanged.

Such findings are corroborated in other research, with interest in long-term mating opportunities among females found to vary across cultures with differing levels of environmental stress (DeBruine et al., 2010; Gangestad & Buss, 1993; Schaller & Murray, 2008; Thornhill, Fincher, & Aran, 2009), operational sex ratios (Stone, Shackelford, & Buss, 2007), and mating systems and cultural norms (Buss, 1989). These findings have been interpreted as support for strategic pluralism theories of mating strategy sex differences, where males and females follow strategies that are conditionally adaptive to local environments. It seems that cultural and environmental variables need to be taken into consideration when examining at sociosexuality in different human populations.

Within-sex Variation in Sociosexual Orientations

Although aggregate differences in sociosexuality between males and females attract a considerable amount of research attention, it is also apparent that the propensity to engage in and desire casual sexual encounters versus long-term mating relationships shows very high levels of variation *within* the sexes, as well as considerable overlap between the sexes (Simpson et al.,

1991). It has been estimated that the effect of sex on sociosexual orientation may actually only account for about 10-20% of the population variance, with intra-sexual variation accounting for a large part of the remaining variance (Gangestad & Simpson, 2000; Simpson et al., 1991).

While males typically display more unrestricted sociosexualities than females overall, the wide distribution of sociosexual orientation scores within males suggests that while some males in a given population pursue short-term mating, others still pursue relatively long-term mating strategies, a divide colloquially referred to as 'cads vs. dads' (Buss & Schmitt, 1993; Cashdan, 1996; Draper & Harpending, 1982; Gangestad & Simpson, 2000). Long-term mating strategies among males typically involve some form of increased parental investment, both in a particular mating partner and in resulting offspring, which are likely to increase the chances of that offspring's survival and hence improve reproductive success (Geary, 2000; K. Hill & Hurtado, 1996). However, such investments must usually be made at the expense of other mating opportunities, which also improve reproductive success through multiple sirings, although with potentially lower offspring survival rates of due to reduced paternal investments made in each additional offspring (Trivers, 1972). Because of this trade-off, increased male parental investment may be a more effective strategy for males in some environments more than others, for example where bi-parental care is more crucial to the survival of an infant (M. B. Andersson, 1994). While research on sociosexuality across multiple countries has already shown that ecological variables primarily affect the average mating strategies of females (Lippa, 2009; Schmitt, 2005b), it is quite possible that the relative within-sex distribution of male mating strategies might also be affected, without altering mean male sociosexuality scores.

Other mediating factors that can affect within-sex variation in male mating strategies relate to the 'quality' of the male in question. Short-term mating strategies are preferentially pursued by males of higher genetic quality (as assessed by various purported proxy measures including physical attractiveness, masculinity, social dominance or fluctuation asymmetry) (A. P. Clark, 2006;

Gangestad & Simpson, 2000; Landolt, Lalumière, & Quinsey, 1995; Rammsayer & Troche, 2013), with such males found to be generally more successful in attracting a greater number of mates (Langlois et al., 2000; Manning et al., 2000; Pollet et al., 2011; Rhodes, Simmons, & Peters, 2005). High quality males are able to pass on any superior morphological traits to their offspring, thus potentially improving the odds of any one offspring's survival even in the absence of male parental investment (Mousseau & Roff, 1987). Conversely, research also finds that males of higher quality make poorer long-term partners, showing greater relationship infidelity, higher chances of divorce and lower biological sympathy responses to crying infants (Booth & Dabbs, 1993; Fleming et al., 2002). Such differences mirror findings in classic animal mating research, where zebra finch mating effort was found to be contingent on the male's genetic quality as indexed by their 'attractiveness' (Burley, 1986).

Similar levels of within-sex variation seem to exist in female populations. A focus on long-term mating among females may oftentimes necessitate making some trade-offs in partner choice – between male partners of high genetic quality and those willing and/or able to commit to long-term relationships (see also above). Although environmental pressures might increase the need for bi-parental care and hence favour long-term mating strategies among females, short-term mating strategies may still offer favourable long-term fitness benefits if pursued with mates of higher genetic quality, as any resulting offspring would be endowed with these genes and have increased odds of survival. As is the case with males, female mating can also vary according to a female's 'mate value', with attractive females demanding even higher overall standards in potential mating partners, pursuing more unrestricted mating strategies, and achieving greater overall mating success (Little et al., 2001; Perilloux, Cloud, & Buss, 2013; Rhodes et al., 2005; Shackelford et al., 2005; Todd et al., 2007; Waynforth & Dunbar, 1995). Female preference for short-term mating with high quality partners also shows some within-individual fluctuation across the

menstrual cycle, and can be further mediated by the quality of the relationship a female finds herself in currently (see also Chapter 1, 'Variation within the Sexes' p. 11).

Ultimately, the extent to which any one mating strategy is pursued, either within or between the sexes, will depend on the fitness benefits that the strategy accrues to the individual, and thus strategy may vary between and within populations as those benefits change (Gross, 1996; Low, 1978). As discussed above, fitness benefits can be dependent on environmental stressors, operational sex ratios, or political/economic gender equality. While it is possible for individuals to alter their strategies across their mating life (and has been found to vary to some degree within females across the menstrual cycle), research actually finds that mating strategies remain relatively stable over the lifetime of any one individual (Bleske-Rechek, VandenHeuvel, & Vander Wyst, 2009). Rather, these strategies seem to vary conditionally between individuals, shaped by long-term changes in the mating environment (Kaplan & Lancaster, 2003) and most likely driven by underlying biological factors.

Biological Drivers of Mating Strategy

The drivers for mating strategy, and in turn sociosexual orientation, are thought to have genetic underpinnings (Buss & Greiling, 1999). Extensive research on sociosexuality in a large twin sample, for example, found that while some aspects of the early external environment have a moderate association with sociosexuality, it was additive genetic factors that were the best predictors of adult sociosexuality levels (Bailey et al., 2000). The most obvious candidate physiological mechanism underlying mating strategies is the hormone testosterone (Ellison, 2001). Research has found that mating effort and general sexual desire, fundamental components of promiscuity and sociosexuality, are most closely related to basal testosterone levels in both males and females, with males having considerably higher overall baseline levels of testosterone

(Bribiescas, 2001; A. P. Clark, 2004; Ellison, 2001; Regan & Berscheid, 1999; Wingfield, Hegner, Dufty, & Ball, 1990).

In both humans and primates, 2D:4D digit ratio (that is the relative length of the fourth digit as compared to the second digit) is thought to be a reliable proxy measure for prenatal levels of testosterone exposure, due to the androgen sensitivity of the homeobox gene cluster which is responsible for both sexually-dimorphic reproductive development and variation in digit length (Manning, Bundred, Newton, & Flanagan, 2003; Manning, Scutt, Wilson, & Lewis-Jones, 1998; Manning, 2002). It must be noted that some gene-wide association studies have suggested that the gene variant LIN28B is responsible for 2D:4D digit length rather than prenatal testosterone exposure (Medland et al., 2010). However, such correlational studies cannot establish causality, and research using more thorough experimental methods (on mice) has indeed shown that the link between prenatal testosterone exposure and digit ratios is likely to be robust (Manning, 2011; Zheng & Cohn, 2011).

In various primate species, greater prenatal testosterone exposure as indexed by 2D:4D digit ratios, has been found to correlate with promiscuous, as opposed to pair-bonded, mating systems (E. Nelson & Shultz, 2010), with baseline primate testosterone levels also found to be related to general mating effort (Muller & Wrangham, 2004). In humans 2D:4D digit ratios have been associated with several traits related to genetic quality and mate desirability (such as dominance, status seeking and physical strength), which in turn also co-vary with higher promiscuity (Fink, Thanzami, Seydel, & Manning, 2006; Manning & Fink, 2008; Millet & Dewitte, 2008). High testosterone can also influence mating behaviours by increasing perceptions of body and face attractiveness of potential mating partners, thus increasing motivation to pursue mating encounters with a wider range of potential mates (Manning & Quinton, 2007). Furthermore, high levels of both prenatal and adult baseline testosterone have been associated with increased sex ratios (proportion of males at birth) (James, 1996; Manning, Martin, Trivers, & Soler, 2002),

which in turn mediate cross-cultural sex differences in sociosexuality (Fink, Manning, & Neave, 2005; Harts & Kokko, 2013; Schmitt, 2005b).

This evidence would suggest that testosterone levels are an excellent candidate for being a primary biological driver of mating strategy and sociosexuality. To that end, some evidence supports the notion that prenatal testosterone levels as indexed by 2D:4D digit ratios are directly related to male and female promiscuity and sociosexuality (Hönekopp, Voracek, & Manning, 2006; McIntyre et al., 2006; Udry, Talbert, & Morris, 1986). Not all studies, however, have been able to replicate such direct links (e.g. Charles & Alexander, 2011; Delecce, Polheber, & Matchock, 2014; Manning & Fink, 2008; Puts, Gaulin, Sporter, & McBurney, 2004). It has been suggested that wide variation in measurement methodology is one reason that inconsistencies are often found in 2D:4D ratios and other variables, with ratios measured from photocopies resulting in ratio differences to those measured from live measurement or x-rays, and right-hand ratios showing greater association with sociosexuality than left hand ratios (e.g. Manning, Baron-Cohen, Wheelwright, & Fink, 2010; Xi, Li, Fan, & Zhao, 2014). Furthermore, a more detailed examination of the link between 2D:4D ratio and sociosexuality suggests that while a relationship does exist, it is dependent on the sub-component of sociosexuality being measured (behaviours, attitudes or desires) (Edelstein, Chopik, & Kean, 2011).

Is Mating Strategy Driven by Underlying Phenotypes?

The wide variance in intra-sex sociosexuality, and the implication that both short- and long-term mating strategies may offer differing fitness payoffs in different situations, has thus far been examined primarily in light of conditional mating strategies – whereby mating strategy is dependent on environmental cues and continuously distributed within each sex (i.e. Gangestad & Simpson, 2000). However, alternate strategies within humans could also be reflective of different underlying polymorphisms driving this variation in mating strategy (Gangestad &

Simpson, 1990; Gross, 1996; D. S. Wilson, 1994). If this were the case, then one would expect sociosexuality within each sex to be distributed multi-modally around multiple means, or in this case bi-modally around two means, with one mean representing individuals with a phenotype favouring a long-term mating strategy (restricted sociosexuality), and one a phenotype favouring a relatively short-term mating strategy (unrestricted sociosexuality). Indeed, some researchers have hypothesized that sociosexuality and its genetic drivers, in large and complex societies such as ours, might in fact be bi-modally distributed and represent two alternate mating strategies maintained through frequency-dependent payoffs (Beckerman, 2005; Gangestad & Simpson, 1990). Such competing strategies would exist under frequency-dependent selection if the value, in terms of fitness outcomes, of a particular strategy decreases as its relative frequency increases, thus keeping both strategies stable in a particular environment (Allen & Clarke, 1984). Early research into male mating strategies and their predicted fitness payoffs hinted at the existence of distinct long-term and short-term mating strategies (Perusse, 1993), with their frequency in a sampled population of Quebecois men inversely related to their respective estimated fitness payoffs – thus forming the basis of an evolutionary stable strategy (Dunbar, 1993).

2.3 Aims

The vast majority of literature thus far on human mating strategies has focused on average differences in strategy between the sexes. When researchers have looked at variation in mating strategies within the sexes, it has typically been presumed that any within-sex variation remains normally distributed, with mating effort driven by conditional strategies that reflect various environmental pressures. As suggested above, it is possible that strategies within the sexes are also driven by underlying genetic polymorphisms. If within-sex phenotypic differences exist, then it is vital that they are identified as such differences will provide us with a much more nuanced understanding of the nature of mating strategy decisions within and between the sexes. Furthermore, such a finding may call into question the validity of making population

sociosexuality comparisons based on just within-sex sociosexuality aggregate means, since such metrics may not accurately portray the true nature of these strategies.

This chapter of the thesis was motivated by this very gap in our understanding of human mating strategies, and thus aims to explore the possibility that human within-sex mating strategies might be reflective of two different underlying phenotypes. This chapter involves mathematical and statistical examination of the distribution of both male and female mating strategies (as assessed by sociosexual orientation) in two mono-cultural/mono-ethnic populations. The aim of this analysis is to determine whether these distributions show signs of being driven by the existence of two underlying phenotypes. Furthermore, as any such phenotypes are likely to be driven by underlying biological substrates, the chapter will also examine the within-sex distributions of a candidate biological driver, namely testosterone (in particular, prenatal testosterone exposure as indexed by 2D:4D digit ratios), in one of these mono-cultural/mono-ethnic populations. It is hypothesised that the distributions of within-sex mating strategies, and of a purported underlying genetic driver, follows a bi-modal distribution pattern that is suggestive of the existence of two phenotypes. A secondary aim of this chapter is to examine how these distributions differ both within and between the sexes, and to speculate whether these differences might be suggestive of the existence of an evolutionary stable strategy set.

2.4 Methods

The analysis of sociosexuality distributions in this study was carried out on sociosexuality data which had been previously collected for the study which is presented in Chapter 3 of this thesis (see also page 83 for more details of that study and methodology). This data had been collected using an online questionnaire, approved by Oxford University's Research Ethics Committee, and distributed to several international online psychological testing repository websites. Responses

were voluntary, restricted to individuals over 18 years of age, and completely anonymous. Participants were offered the chance to enter a prize draw for an online shopping voucher.

Although sociosexuality data was available for 902 participants, analyses in this study were restricted to two mono-ethnic and mono-cultural populations, since population-wide environmental factors are known to affect sociosexuality scores (Lippa, 2009; Schmitt, 2005b), and hence data was analysed only from participants who reported they were ethnically Caucasian/white and were either of British or North American nationalities. This analysis, therefore, included data from 134 male and 186 female British participants (aged 18 to 58 years, $M = 22.5$, $SD = 6.4$), and 68 male and 187 female North American participants (aged 18 to 63 years, $M = 27.1$, $SD = 9.9$).

To measure participants' preference for short-term versus long-term mating, six items were selected from the 9-item Sociosexual Orientation Inventory Revised (SOI-R), making up the two subscales which evaluate an individual's attitudes and desires as they relate to non-committal sex (Penke & Asendorpf, 2008; Simpson et al., 1991). Sample questions included '*Sex without love is OK*' in the attitude component (rated on 9-point agreement scales ranging from 'Strongly disagree' to 'Strongly agree') and '*How often do you have fantasies about having sex with someone you are not in a committed romantic relationship with?*' in the desire component (rated on 9-point frequency scales ranging from 'Never' to 'At least once a day') (full scale available in Appendix A, p. 258). Answers to the remaining 3 items of the SOI-R, relating to actual sexual behaviours (e.g. *With how many different partners have you had sex within the past 12 months?*), were omitted from these analyses for two reasons: 1) attitudes and desires are more likely to be reflective of ultimate, long-term mating strategies being pursued by a particular individual, irrespective of the culturally dominant mating system in place or variable personal circumstances facing different individuals (such as religious restrictions or mate availability); and 2) previous research has found that attitudes and

desires are more closely related to biological drivers thought to be responsible for affecting mating strategy, namely testosterone levels (Edelstein et al., 2011; Lippa, 2009).

As female menstrual cycle phase is known to have an effect on both sexual desire and mate selection criteria (see Chapter 4, 'Literature Review – Mate Assessment across the Menstrual Cycle' on p. 104 for more details on these effects), a possibility exists that the sociosexual attitudes and desires reported by the females in these British and North American samples might be affected by their current cycle phase. To test this possibility, the distribution of sociosexual orientations among females in this sample who were either in the late follicular (i.e. within the 5 days prior to estimated ovulation) or the luteal (i.e. within 10 days of the next estimated day of menses onset) phase of their menstrual cycle at the time of the survey was examined. Estimations of cycle phase were calculated from self-report answers to questions about menstrual cycle phase regularity, duration, and date of last menses onset (for exact details on the methodology used in estimating cycle phase, see 'Estimations of Menstrual Cycle Phase and Risk of Conception' in the Methods section of Study 1, Chapter 4 p. 110). Of the total female sample, a subsample of 51 females were normally cycling at the time of the survey (not on any hormonal contraception) and were estimated to be in one of these two cycle phases. Chi-squared analyses found that among females in the luteal phase of their cycle (29 females) there were no significant differences in the number of females who reported restricted (14 females) versus unrestricted (15 females) sociosexuality based on median-splits of their sociosexuality scores, and no differences among females in the late follicular phase of the cycle reporting unrestricted (13 females) versus restricted (9 females) sociosexuality ($\chi^2(1, N = 51) = 0.587, p = .443$).

Data used in analyses of the distribution of prenatal testosterone levels (as indexed by 2D:4D digit ratio) comprised of previously unpublished data collected in as part of a study concerned with establishing British population 2D:4D digit ratio norms, and were measured from photocopies of participants' right hands (Manning, 2013). This dataset included data on 2D:4D

ratios from a representative sample of Caucasian/white British participants, including 572 males and 742 females. 2D:4D ratio has been found to correlate with baseline testosterone levels in adult males (Manning et al., 2000) and has been linked to many sexual and sex-specific behavioural traits, although some disagreement does exist in the literature regarding the reliability of these measures (see 'Biological Drivers of Mating Strategy,' p. 49, for more on this debate).

All statistical analyses were carried out using the R statistical program (version 3.01, R Development Core Team, 2013) and the 'mixtools' statistical package for analysing finite mixture models (version 0.4.6, Benaglia, Chauveau, Hunter, & Young, 2009). The mixtools analysis package utilizes statistical modelling methods to carry out model-based clustering on finite data sets. Exploratory analyses of the data to determine whether a mixture model may be present were carried using a likelihood ratio test ('test.equality' analysis) of the existence of a mixture of k (i.e. 2) means versus the model of a single, normally distributed mean. The alternative hypothesis in this analysis is that each k -component has its own mean, while the null hypothesis is that all means are equal (i.e. the distribution is not multi-modal), with the results presented in the format of an asymptomatic chi-square statistic. Further analyses were carried out to model the detailed nature of the composition of the two mixture components ('normalmixEM' analysis). This modelling procedure utilizes maximum likelihood estimation (MLE) to iteratively estimate Gaussian distribution models that maximize the model fit to the observed data, providing estimates of component mixing proportions (λ), the component distribution means (μ), and the estimated component standard deviations (σ) if more than one component is found to be the best descriptor of the observed data. Mean model parameter estimates and their standard errors were further estimated using a parametric bootstrap procedure ('boot.se' analysis), with 1000 realizations created to produce bootstrap samples of the parameters for each mixture model. The results section below displays the bootstrapped parameter means and standard errors.

2.5 Results

Sociosexuality – A British Sample

For Caucasian males and females from the British sample, mixtool chi-square analyses were firstly run testing for equality of means to determine whether the data are likely to comprise of two components. Furthermore, for each sex best-fit bi-modal models were then calculated, estimating mixing proportions, means, and variances. The results of these analyses are presented in Table 1.

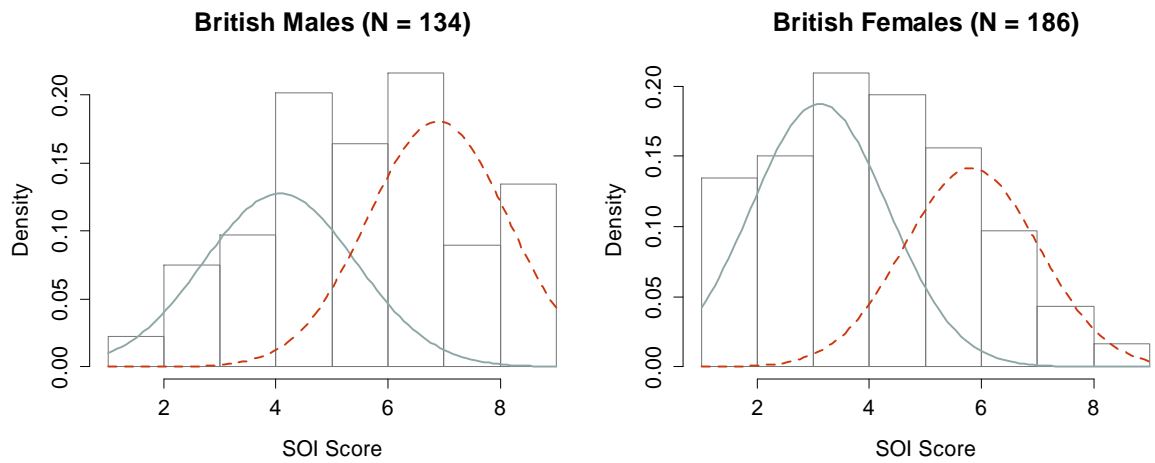
Table 1. Modelled component estimates for sociosexuality in a British sample

	Restricted Sociosexuality (bootstrap mean \pm SE)	Unrestricted Sociosexuality (bootstrap mean \pm SE)
British Males		
<i>Test for bi-modality: ($\chi^2(1, N = 134) = 4.88, p = .027$)</i>		
Mixing Proportions (λ)	.434 \pm .245	.566 \pm .245
Means (μ)	4.07 \pm 0.89	6.89 \pm 0.63
Variances (σ)	1.36 \pm 0.39	1.25 \pm 0.34
British Females		
<i>Test for bi-modality: ($\chi^2(1, N = 186) = 15.08, p < .001$)</i>		
Mixing Proportions (λ)	.573 \pm .262	.426 \pm .262
Means (μ)	3.11 \pm 0.68	5.82 \pm 0.98
Variances (σ)	1.22 \pm 0.34	1.20 \pm 0.40

As can be seen from the table, the chi-square tests for bimodality confirm that the British male and female sociosexuality data consist of bi-modal distributions. Modelling analyses detected the existence of two underlying phenotypes within each sex, one of restricted sociosexuality and one of unrestricted sociosexuality, with unrestricted sociosexuality males making up a slightly larger proportion of the male distribution, and restricted sociosexuality females making up a slightly

larger proportion of the female distributions. Figure 1 charts the best-fit model estimates of these bi-modal distributions.

Figure 1. Modelled bimodal distribution of sociosexuality in a British sample



Note: Solid line represents a low sociosexuality (restricted) phenotype, dashed line a high sociosexuality (unrestricted) phenotype. Histograms represent underlying data distribution.

Sociosexuality – A North American Sample

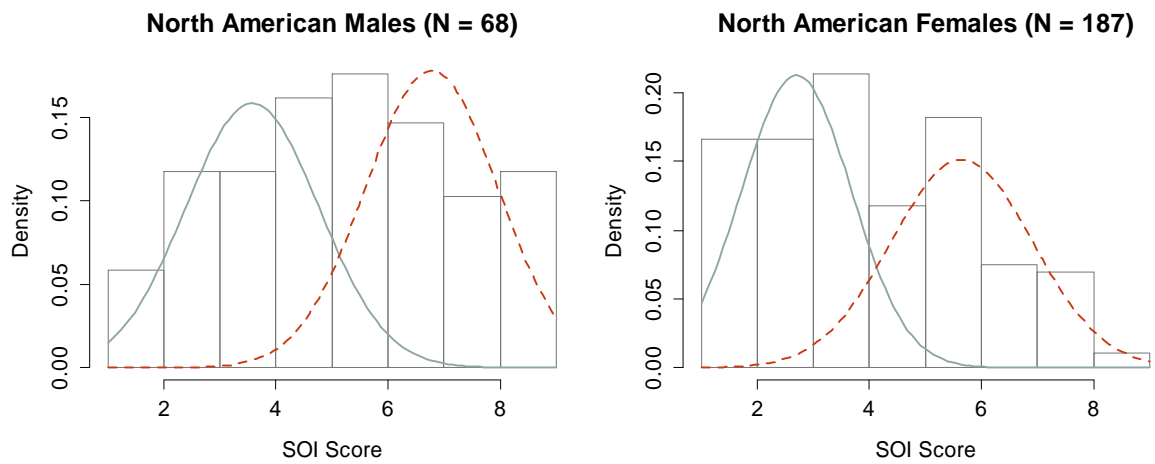
For Caucasian males and females from the North American sample, mixtool chi-square analyses were again run testing for equality of means to determine whether the data are likely to comprise of two components. For each sex, the best-fit bi-modal estimates were then calculated, estimating mixing proportions, means, and variances. The results of these analyses are presented in Table 2.

Table 2. Modelled component estimates for sociosexuality in a North American sample

	Restricted Sociosexuality (bootstrap mean \pm SE)	Unrestricted Sociosexuality (bootstrap mean \pm SE)
North American Males		
<i>Test for bi-modality: ($\chi^2(1, N = 68) = 8.87, p = .003$)</i>		
Mixing Proportions (λ)	.473 \pm .232	.527 \pm .232
Means (μ)	3.58 \pm 0.89	6.78 \pm 0.75
Variances (σ)	1.19 \pm 0.44	1.18 \pm 0.40
North American Females		
<i>Test for bi-modality: ($\chi^2(1, N = 187) = 9.75, p = .002$)</i>		
Mixing Proportions (λ)	.522 \pm .124	.478 \pm .124
Means (μ)	2.70 \pm 0.28	5.65 \pm 0.45
Variances (σ)	0.98 \pm 0.17	1.26 \pm 0.24

As can be seen from the table, the chi-square tests for bimodality confirm that the North American male and female sociosexuality data consists of bi-modal distributions. Modelling analyses confirmed the existence of two underlying phenotypes within each sex, one of restricted sociosexuality and one of unrestricted sociosexuality, with unrestricted sociosexuality males making up a larger proportion of the male distribution, and restricted sociosexuality females making up a larger proportion of the female distributions. Figure 2 charts the best-fit model estimates of these underlying bi-modal distributions.

Figure 2. Modelled bimodal distribution of sociosexuality in a North American sample



Note: Solid line represents a low sociosexuality (restricted) phenotype, dashed line a high sociosexuality (unrestricted) phenotype. Histograms represent underlying data distribution.

2D:4D Digit Ratio – A British Sample

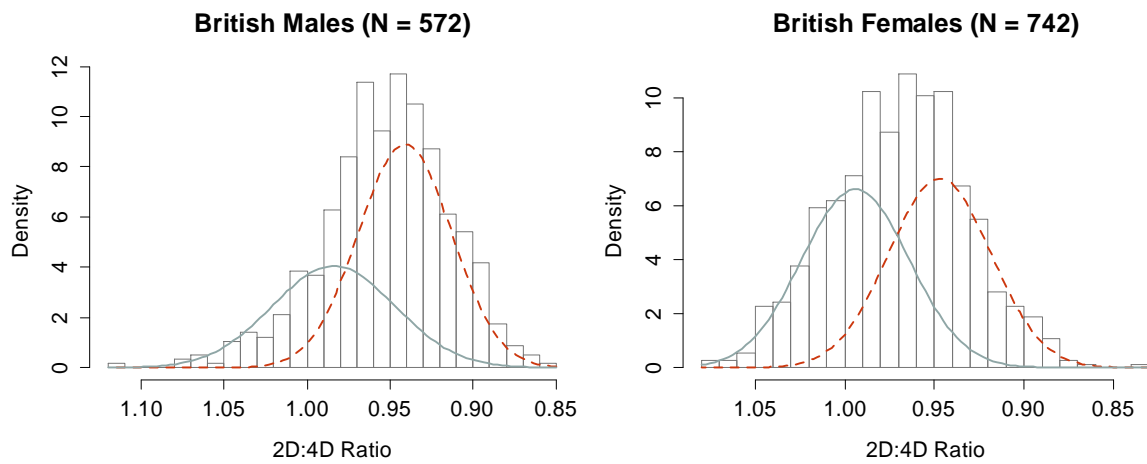
For British Caucasian males and females mixtool chi-square analyses were run, testing for equality of means to determine whether the data are likely to be comprised of two components. For each sex, the best-fit bi-modal model estimates were also calculated to estimate mixing proportions, means, and variances. The results of these analyses are presented in Table 3, with the low testosterone component representing high 2D:4D digit ratios and the high testosterone component low 2D:4D digit ratios.

Table 3. Modelled component estimates for 2D:4D ratio in a British sample

	Low Testosterone (bootstrap mean \pm SE)	High Testosterone (bootstrap mean \pm SE)
British Males		
<i>Test for bi-modality: ($\chi^2(1, N = 572) = 15.17, p < .001$)</i>		
Mixing Proportions (λ)	.376 \pm .235	.624 \pm .235
Means (μ)	0.984 \pm 0.027	0.941 \pm 0.006
Variances (σ)	0.037 \pm 0.009	0.028 \pm 0.005
British Females		
<i>Test for bi-modality: ($\chi^2(1, N = 742) = 3.07, p = .079$)</i>		
Mixing Proportions (λ)	.498 \pm .326	.501 \pm .326
Means (μ)	0.994 \pm 0.023	0.947 \pm 0.020
Variances (σ)	0.030 \pm 0.008	0.0285 \pm 0.009

The chi-square test for bimodality confirmed that the British male 2D:4D data consists of a bi-modal distribution, however, it failed to confirm this for the female data (although only by a small statistical margin). Modelling analyses, however, still converged on bi-modal distribution models in both sexes as ‘best-fit’ descriptions of the data, one of low 2D:4D (high testosterone) and one of high 2D:4D (low testosterone), with high testosterone males making up a larger proportion of the male data, and both testosterone phenotypes evenly distributed in the female data. Figure 3 charts the modelled within-sex bimodal distributions of 2D:4D ratios (reversed x-axis) in a British sample.

Figure 3. Modelled bimodal distribution of 2D:4D ratios in a British sample



Note: Solid lines represent a low testosterone (high 2D:4D ratio) phenotype, dashed lines a high testosterone (low 2D:4D ratio) phenotype (plotted on reversed x-axes). Histograms represent distribution of underlying data.

2.6 Discussion

In this study, computationally intensive statistical analyses were used to establish whether the within-sex distribution of sociosexuality might actually be comprised of a mix of two distinct mating strategies, reflecting two underlying phenotypes. The results showed that sociosexuality was bimodally distributed within each sex, with Caucasian British and North American males and females each comprising of two sub-populations, of either restricted or unrestricted sociosexuality. In both the British and North American samples, restricted sociosexuality males made up a slightly smaller proportion of males (~45%) than unrestricted sociosexuality males. Females exhibited a reverse distribution, with restricted sociosexuality females making up a slight majority (~55%) across both samples. Analysis of a purported driver of sociosexuality (prenatal testosterone as indexed by 2D:4D digit ratio) also found statistical support for the existence of bimodal within-sex distributions in a large sample of Caucasian British nationals. The mixing proportion estimates suggest that while the majority of males belong to a high-prenatal

testosterone group (~62%), females appear evenly split (~50%) between high- and low-testosterone groups.

The Existence of Two Phenotypes

These analyses of distribution of sociosexuality found that, as hypothesised by early research into sociosexuality (Gangestad & Simpson, 1990), mating strategy within each sex clusters around two distinct phenotypes. One of these revolves around having a more restricted sociosexuality (i.e. focusing on long-term mating opportunities and the possibility of forming pair-bonds), the other on a relatively unrestricted sociosexuality (which prioritizes short-term mating with multiple partners). As a considerable body of previous research has shown, males have a more unrestricted sociosexual orientation than females overall. However, these analyses show that two distinct mating strategies also exist *within* each sex. For alternative mating strategies to coexist in this way, it suggests that unique fitness benefits must accrue to each strategy (Dunbar, 1983; Gross, 1996; Low, 1978). In mammals, and humans in particular, the co-existence of divergent strategies of this kind typically reflect the fact that males may gain fitness benefits by either pursuing short-term mating opportunities, or by pursuing long-term mating opportunities involving more extended parental investments (Buss, 1989; Perusse, 1993; Schmitt, 2003; Symons, 1979). Among males, the two phenotypes might represent individuals of differing mate quality, since mate quality is one factor influencing mating strategy (Burley, 1986; A. P. Clark, 2006; Gangestad & Simpson, 2000; Pawlowski & Dunbar, 1999; Waynforth & Dunbar, 1995). Similar considerations might attend female phenotypes, with female mating decisions to pursue benefits acquired by mating with multiple (possibly genetically high quality) males, or alternatively being resourced over a longer term by a particular male, a decision potentially mediated by the mate value of each female (Little et al., 2001; Rhodes et al., 2005; Shackelford et al., 2005; Todd et al., 2007; Waynforth & Dunbar, 1995). Individuals of different sociosexual orientations, in turn, are likely to desire and go on to choosing partners with different attributes, with unrestricted individuals

preferentially valuing mates with high genetic fitness and restricted individuals preferring mates showing signs of long-term commitment and resource acquisition potential (Simpson & Gangestad, 1992).

These results also show that in each sex the proportional split in the two sociosexuality phenotypes is skewed in opposite directions for males and females, with males on average showing evidence of polarisation towards an unrestricted strategy (on average for the two datasets, a 55:45 split in favour of the unrestricted strategy) and females the opposite polarisation (45:55 split reflecting restricted/unrestricted strategies). While it is not possible to say anything about the fitness consequences of the two mating strategy phenotypes in these particular populations, an earlier study of French-Canadian sample of males (Perusse, 1993) found that the distribution of mating strategies in that population was inversely related to their respective estimated fitness payoffs, suggesting the existence of an Evolutionary Stable Strategies (Dunbar, 1993; Maynard Smith, 1984). As the female data suggest a split that favours a reversed ratio to that of males, it is likely that this distribution also reflects the relative fitness payoffs in the populations under study. However, due to a lack of relevant data on fitness differentials in females in these populations it is difficult to make any statements about these payoffs. This is the first time that experimental methods have been able to clearly show the existence of these two phenotypes in humans, and suggests that sociosexuality may result from discrete alternate mating strategies driven by two underlying phenotypes in human populations, potentially sustained by frequency dependent selection (Gross, 1996).

Exact fitness payoffs are likely to be driven by the unique combination of socio-cultural and environmental factors faced by any one population. Since past research has found that mean differences in sociosexuality between sexes within a population vary with levels of environmental stress, gender equality, operational sex ratio, and cultural norms (Buss, 1989; DeBruine et al., 2010; Gangestad & Buss, 1993; Harts & Kokko, 2013; Lippa, 2009; Pedersen, 1991; Schmitt,

2005b; Stone et al., 2007), it seems likely that the equilibrium of mating strategy distribution within and between the sexes might also co-vary with these variables. The slight differences in the within-sex sociosexuality distributions in British and North American males and British and North American females may well reflect small differences in the two regions' socio-cultural, demographic, and physical environments. These small differences in environment will lead to differing fitness payoffs for different strategies, potentially explaining the small observed differences in phenotypic distribution ratios within each sex. Data from a wider range of cultures facing different environmental environments, which would lend itself to analysis and comparison with relative phenotypic ratios found in those populations, may potentially be able to illuminate the extent to which contextual variables influence these distributions.

Biological Underpinnings of Mating Strategy Phenotypes

Since it is generally believed that sociosexuality has a strong genetic component (Bailey et al., 2000; Buss & Greiling, 1999), it was hypothesized that a similar bimodal distribution might exist in a purported biological driver of sociosexuality, prenatal testosterone levels (as indexed by 2D:4D digit ratios). These analyses found that in a large sample of British nationals, prenatal testosterone was also bimodally distributed, with the male sample comprising a larger high testosterone (low 2D:4D) sub-population and a smaller low testosterone (high 2D:4D) sub-population, whereas the female sample was evenly split between the two phenotypes. Since testosterone levels are related to mating effort and sexual desire (Bribiescas, 2001; A. P. Clark, 2004; Ellison, 2001; Regan & Berscheid, 1999; Wingfield et al., 1990), in both humans and primates (Manning et al., 2003; Muller & Wrangham, 2004; E. Nelson & Shultz, 2010), it is likely that testosterone is related to sociosexuality, particularly the sub-components of sociosexuality relating to desires and attitudes towards promiscuous sex, as measured here (Edelstein et al., 2011). The fact that bimodal distributions were found in both sociosexuality and 2D:4D ratios

provides corroborating evidence that testosterone may be one important factor mediating human mating strategies.

These analyses also suggest the existence of differences in relative proportions of these two phenotypes within the sexes between the sociosexuality data and the underlying 2D:4D ratios. In the British sample, for which a direct comparison can be made, the proportional split in sociosexuality in males favours an unrestricted (short-term) mating strategy, with a 57:43 split, with females having a reversed split favouring a restricted strategy (47:53). However, the mixing proportions for the two strategies in the 2D:4D digit ratio data suggest that a relatively higher proportion of a high prenatal testosterone phenotype (driving short-term mating strategies) exists in both sexes (males 62%, females 50%). While evidence exists that additive genetic factors are better predictors of adult sociosexuality scores than environmental variables (Bailey et al., 2000; Baumeister, 2000), such observed behavioural differences may in part still reflect cultural or environmental fine tuning of underlying genetic strategies in response to local circumstances, as each sex tries to maximise their overall fitness in their local environment.

It may be that an initial 50:50 split among female 2D:4D ratio phenotypes may provide the most versatile foundation from which the greatest variety of sociosexuality distribution outcomes can arise based on environmental pressures. This could explain regular observations that it is females who make the greater adaptive shifts to environmental pressures (Baumeister, 2000; Lippa, 2009; Murray et al., 2013; Schmitt, 2005b), and are thought to have more fluid sexuality than males (Diamond, 2003). Among males, however, the 2D:4D ratio phenotype split is in favour of a much larger high-2D:4D subpopulation, which may translate into a more consistent skew in favour of a larger proportion of males pursuing a high-sociosexuality mating strategy irrespective of environmental pressures. Such a consistently larger sub-population of males pursuing short-term mating strategies could be the reason that males are consistently found to show higher sociosexuality scores in every population studied thus far, the larger proportion consistently

skewing results in favour of higher mean sociosexuality scores. Among different populations with varying environmental pressures, it is possible that the within-sex sociosexuality phenotypic proportion splits, and the underlying 2D:4D phenotypic proportion splits, may be affected in differing ways by the same environmental pressures. It is possible that environmental variables have an effect on population testosterone distributions over many generations, but also have short-term effects on behavioural phenotype outcomes, further mediating adaptive shifts in mating strategy within a given culture.

2.7 General Discussion

These findings have important implications for future research into sex and population differences in sociosexuality and mating strategy. The fact that within-sex phenotypic differences exist, and might vary in their relative splits within sexes of a given population, suggests that the use of mean sociosexuality scores to describe any one sex may miss-represent the true nature of sociosexual orientations within that population (Voracek, 2005). The data also show that considerable overlap exists between these phenotypes across the sexes, with the mean sociosexuality and testosterone scores of females in the short-term mating phenotype being much higher than the mean scores of males in the long-term mating phenotype. Using aggregate within-sex indices of mating strategy to make comparisons between the sexes, therefore, ignores this extreme overlap in mating strategy that may be more dependent on within-sex phenotype than it is on the sex of the individual. It is vital that, in future, these phenotypes and their relative proportions are identified as they can provide us with a much more nuanced understanding of the exact nature of mating strategies both within and between the sexes.

2.8 Chapter Summary and Outlook

This study is the first to show quantitatively that males exhibit two phenotypes when it comes to sexual strategies ('cads vs. dads') (Gangestad & Simpson, 1990), both at the behavioural level and

at the anatomical/physiological level. More importantly, it has been shown here that there may be a similar, but previously unsuspected, division into two phenotypes among females as well. These phenotypic splits drive the formation of different mating strategies, which in turn direct mating effort towards either short-term or long-term mating strategies. The establishment of these strategies forms an integral part of the pair-bonding process, determining the likelihood that future mating encounters will result in the formation of pair-bond attachments. These differing strategies will drive not only the expenditure of mating effort, but will also lead to the establishment of different criteria on which potential mating partners will be assessed. These findings have implications for our understanding of the nature of sociosexuality and the sexes, demonstrating for the first time that heretofore typical assessments of sociosexuality in the two sexes may be glossing over important, although nuanced, within-sex distributional differences which may be more representative of the true mating strategy landscape.

The next chapter deals with another process integral to the establishment of mating pair-bonds, namely the assessment and selection of a suitable mate. As introduced in Chapter 1, mate selection in humans is an extremely involved process, where multiple senses are brought to bear on the important task of assessing, selecting, and mating with a suitable partner, one who is likely to maximise long-term fitness outcomes and complement the mating strategy being pursued. Because of the importance of accurate assessment and selection of a suitable mate, it has been proposed that various courtship customs may exist in human populations to aid in this process. One such prevalent custom, romantic kissing, is examined in detail in the following chapter to determine whether it serves a useful function in human mating.

Chapter 3 – Functions of Romantic Kissing¹

3.1 Introduction

Having established a fitness maximising mating strategy, the next step towards establishing pair-bonds with a suitable mate involves selecting an appropriate mating partner. The mating strategy being pursued will have a direct influence on the mate selection process that follows, affecting both the amount of mating effort to be expended and the mate selection criteria that will be utilised to select a mating partner. As mentioned in Chapter 1 ('Mate Selection,' p. 14), mates can be preferentially assessed on numerous dimensions, including their genetic fitness (as conveyed by their 'attractiveness' and other purported fitness cues), genetic compatibility, resource acquisition potential, interest in the establishment of long-term relationships and parental investment, and so forth. Individuals will utilise various senses to assess potential mates on these traits, taking note of different morphological and behavioural cues and deciding whether they are desirable in light of the particular mating strategy being pursued. Furthermore, males and females with different mating strategies are not only likely to pay attention to different mate cues, but are also likely to engage in differential courtship behaviours which might better aid the pursuit of their particular mating strategy.

It has been previously observed that many human courtship behaviours might actually be analogous to those found in other species, who use various courtship practises to communicate the presence of desirable traits, assess potential mates, and gain preferential access to mating partners (Birdwhistell, 1970; Eibl-Eibesfeldt, 1972; D. Morris, 1971). In light of the reproductive value inherent in accurately assessing a potential mate's suitability among humans, it seems

¹ The results of this study have been published as the following peer-reviewed journal article: Wlodarski, R., & Dunbar, R. I. M. (2013). Examining the possible functions of kissing in romantic relationships. *Archives of Sexual Behavior*, 42(8), 1415-1423. doi:10.1007/s10508-013-0190-1.

prudent to also look at common human courtship practices to determine whether they might be playing a similar role human pair-bonding processes (Givens, 1978; Grammer, 1989). ‘Romantic kissing’ is one such cross-culturally prevalent courtship custom, which has been hypothesised to be potentially useful in early processes of pair-bonding involving the initial selection and eventual retention of desirable mates (Harrison, 2006; Hughes, Harrison, & Gallup, 2007; Kirshenbaum, 2011).

This section of the thesis examines whether romantic kissing serves a useful function in human mating. The chapter firstly introduces the literature as it relates to kissing in the context of mating relationships, demonstrating that it is a unique and pervasive human custom, common in some form to most cultures of the world and prevalent throughout recorded human history (Eibl-Eibesfeldt, 1972; H. E. Fisher, 1992; Ford & Beach, 1951). The literature suggests that the mechanics of romantic kissing leave it particularly well placed to serve several potentially useful functions in the processes comprising pair-bonding, including: 1) the facilitation of visual, olfactory, gustatory, and/or tactile assessment of a potential mating partner; 2) increasing arousal and initiating coitus; or 3) the direct mediation of established relationships and pair-bonds. Since, to date, no research has yet convincingly managed to establish which of these functions is most likely to be served by romantic kissing, this chapter of the thesis sets out to determine whether kissing is likely to be used primarily for the purpose of mate assessment, arousal, or the mediation of pair-bonds.

In order to answer this question, an experiment was carried out looking at variations in attitudes toward romantic kissing in a large, diverse, multi-national sample of participants. Patterns of participant responses were examined to see how they varied between different participants (according to their sex, mate value, and sociosexuality); with these patterns compared to predictions made by the three competing hypotheses that attempt to explain the primary function

of romantic kissing. A ‘critical tests’ approach is utilised to compare the evidence against the predictions of each hypothesis and reach conclusions as to the primary function served by kissing.

3.2 Literature Review – The Role of Kissing in Human Mating

Nearly all human cultures partake in the custom of kissing, with kissing between romantic partners found in nearly all the world’s cultures where ethnographic records exist (Eibl-Eibesfeldt 1972, p. 141). In the 10% of societies where mouth-to-mouth partner contact is unknown or frowned upon, sexual partners still often practice analogous ‘kissing’ traditions of close face-to-face contact involving sniffing, licking or rubbing (H. E. Fisher, 1992; Ford & Beach, 1951). The first written accounts depicting romantic kissing date back to humanity’s earliest surviving records, with ancient Sanskrit Hindu texts, known as the Vedas, depicting a ritual involving the ‘sniffing’ of faces between romantic partners (Hopkins, 1907). Some anthropologists believe that this is a social custom imported from India to Ancient Greece by Alexander the Great, with ancient Romans further popularising the types of mouth-to-mouth kissing behaviours inherited by many modern societies (Bryant & Grider, 1991). This account of kissing as a purely social construct, however, does not explain its appearance and re-emergence among various disparate and historically isolated cultures around the world. Depictions of romantic kissing-type behaviours have been found in archaic cultures that pre-date the Indian-Greek-Roman account, such as those of ancient Egypt (Parkinson, 1999). Portrayals of romantic kissing also exist in the Greek poetry of Sappho, written in the 7th century BC (300 years before the time of Alexander) (Reynolds, 2003), and in the Old Testament of the Bible in the ‘Song of Solomon,’ whose composition dates to around 900 BC and includes the statement “*O that you would kiss me, with the kisses of your mouth!*” (Sparks, 2008).

In the 1960s, zoologist Desmond Morris postulated that kissing may actually be a ‘relic gesture’ leftover from the hominoid practice of pre-masticating food to feed young (D. Morris, 1967), a

practice common in today's apes and still practiced in some contemporary hunter-gatherer societies (Eibl-Eibesfeldt, 1972). It is quite possible that such face-to-face contact in its various guises has since then become an exaptation, co-opted by natural selection pressures either to serve as a litmus test of romantic partner suitability, or perhaps to invoke between romantic couples the types of intimate mother-infant bonding processes that are known to take place during early influential developmental periods.

Our closest genetic relatives, chimpanzees, occasionally practice light mouth-to-mouth kissing and embracing, though often in the context of post-conflict reconciliation between two primates (de Waal, 2000). In this context, kissing communicates positive intentions and/or submissiveness through implied vulnerability, since exposure during such an activity opens up the opportunity to be bitten or attacked. Our other close cousins, bonobos, have also been observed to partake in extended, sloppy, mouth-to-mouth kissing, including (uniquely) tongue-kissing, during play and in various sexual contexts – though it most often forms part of a strategy, alongside promiscuous sex, to reduce tension between individuals (de Waal & Lanting, 1997). Similarly, in Rhesus monkeys mother-infant interactions have been observed to sometimes take the form of mutual gazing, lip-smacking and kissing (Bard, 2009). It seems, therefore, that although our closest primate relatives sometimes partake of this custom, kissing is uniquely pervasive and widespread among human populations, particularly between potential and actual mating partners. If this courtship custom is indeed so prevalent, it begs the question whether it serves any useful purpose in the human context.

Why Do Humans Kiss?

It has been suggested that when individuals kiss there is a “rich and complicated exchange of visual, tactile, postural, and chemical information based on olfactory and gustatory cues” (Gallup & Frederick, 2010). So far, there has been only limited research on the possible functions that

might be served by various acts of kissing between mating partners, and on what role exactly it plays in the extended processes of mating and pair-bonding. Various hypotheses have been proposed: that kissing acts as a chemosensory test of a partner's genetic suitability and desirability – facilitating mate assessment via olfactory and/or gustatory pathways: or alternatively that kissing serves to merely intensify physiological arousal of mating partners to induce coitus; or that is utilised in the process of pair-bond maintenance (Hughes et al., 2007). The literature examining how these three functions might work is discussed in some detail below.

Olfactory, Gustatory & Physiological Mate Assessment

One important consequence of all forms of romantic kissing is the physical proximity it provokes between two potential mating partners. Since it appears that smell plays an important role in human mate assessment (see also Chapter 1, 'Olfaction in Mate Assessment' p. 22 for more details), kissing behaviours may function to facilitate olfactory sampling of a potential mate's distinctive body odours and pheromones. Kissing behaviours may be particularly useful in this regard as they may be one of the few socially acceptable methods of invading another's 'personal space' in many cultures, allowing unacquainted individuals to get close enough to each other to engage in olfactory assessment before making deciding whether to make any more costly mating commitments (Eibl-Eibesfeldt, 1972; Ford & Beach, 1951). Such smell-based appraisal of a mate's Major Histocompatibility Complex (MHC) compatibility, genetic or general fitness, or even personality, may guide subconscious mate assessment decisions by mediating subjective ratings of attractiveness attributed to that mate. The fact that MHC in humans is typically only assessable via olfactory channels, and that mate MHC compatibility has important implications for offspring genetic fitness and survival (see also 'Olfaction in Mate Assessment' p. 22), suggests that smell-based appraisal can make unique contributions to the assessment process. The fact that 'face sniffing' is more pervasive than mouth-to-mouth kissing historically and in some of the world's contemporary cultures (H. E. Fisher, 1992; Ford & Beach, 1951; Hopkins, 1907;

Parkinson, 1999) provides further *prima facie* evidence for the potential importance of olfaction in the context of kissing.

It has also been hypothesised that kissing might be, quite literally, a taste test. Sebum, an oily substance secreted by microscopic sebaceous glands in skin, is regulated by endogenous hormones, varies greatly in its composition between individuals, and is found in greater quantities in humans than any other mammal – particularly in the area of the face (Floyd et al., 2009). Acting as a semiochemical in primates, it has been suggested that sebum may play a similar role in humans to help them assess various underlying genetic qualities of potential mates, either through the surreptitious exchange of sebum during mouth-to-mouth contact or via olfactory assessment of sebum odours (Nicholson, 1984).

Alternatively, the myriad of compounds found in saliva (including proteins, electrolytes, antibacterial compounds, enzymes, MHC gene markers, hormones and various pheromone-like substances) may also serve as a proverbial acid test of a potential mate's compatibility and/or suitability. It may be that the exchange of saliva facilitated by mouth-to-mouth kissing allows an individual to make some kind of surreptitious gustatory or olfactory assessment of mate quality by sampling the unique composition of its chemicals and hormones. The contents of saliva have similarly been found to play a significant role in the mating behaviours of some other mammals. In wild boar populations, for example, the male boar produces substantial amounts of a pungent drool upon arousal (also containing the human pheromone androstenone) that is irresistibly attractive to any nearby female boar in oestrus (Tirindelli et al., 2009). It been suggested that in humans saliva can act as a vehicle for hormones and pheromones, particularly testosterone, which might be passed between individuals and have a semiochemical effect on the opposite sex – mediating their behaviour and sexual responsivity (Hughes et al., 2007). While this testosterone transport hypothesis seems unlikely, since testosterone is rapidly inactivated by the first-pass

hepatic metabolism (Nieschlag et al., 2004), salivatory testosterone still emits olfactory cues which might be detectable to potential mates (Gröschl, 2009).

A final way that romantic kissing behaviours might be used to assess mate quality is by means of the physical coordination required between two individuals. Physical awkwardness during a kissing encounter, demonstrated through poor coordination during such an intimate courtship behaviour or poor kissing ‘technique’, might be a signal of inferior genetic quality – analogous to substandard genetic quality that seems to be signalled by poor coordination of dance-related behaviours (Hugill et al., 2010).

Arousal

Human lips are densely populated with dermal and epidermal touch receptors, with a disproportionately large section of the somatosensory cortex dedicated to processing tactile information from this region – more cortex area is devoted to receiving sensations from the lips than even from the genital region (Penfield & Boldrey, 1937). With so much tactile information being conveyed to the brain, the lips act as a very effective erogenous zone, and romantic kissing behaviours (particularly mouth-to-mouth kissing) are uniquely placed to leverage these biological responses to facilitate states of elevated physiological arousal. Heightened arousal, in turn, can be instrumental in preparing the body for coitus – inducing the penile erection necessary for intercourse and lubricating vaginal walls to facilitate sexual penetration (Zuckerman, 1971). Levels of arousal induced by kissing may be so intense, that some women have been reported to experience orgasm through kissing alone (Kinsey et al., 1953). It is possible, therefore, that the primary purpose served by kissing is the provisional escalation of arousal levels between romantic partners in preparation for imminent acts of sexual intercourse.

The increased arousal levels stimulated by the act of kissing are also likely to set a particular intimate interaction on a typical ‘sexual trajectory,’ where relatively less intimate behaviours (like

kissing) increase the chances of imminent progression to more intimate behaviours, up to and including sexual intercourse (de Graaf, Vanwesenbeeck, Meijer, Woertman, & Meeus, 2009). Research has found that an increase in levels of affectionate behaviours such as kissing in mating encounters is related to expectations of the encounter leading to a casual sex relationship (Grello, Welsh, & Harper, 2006). Such progression is likely the direct result of increased arousal levels, since arousal has been previously found to influence decision making abilities regarding the appeal of further sexual activities, as well as willingness to engage in unsafe sex (Ariely & Loewenstein, 2006). Married and cohabitating couples have been found to frequently use kissing, amongst other non-verbal behaviours, to initiate sexual intercourse (Byers & Heinlein, 1989). Kissing, a relatively innocuous act with few parental investment consequences in and of itself, may be used by individuals as a tool for initiating sexual relations and increasing the chances of mating with a potential romantic partner, possibly being used preferentially by individuals pursuing short-term mating strategies to facilitate multiple mating goals.

Attachment and Pair-Bonding

Numerous chemicals (including endorphins, dopamine, cortisol, and the neuroendocrines serotonin, vasopressin and oxytocin) are released endogenously during intimate physical and sexual behaviours (such as hugging and kissing), acting in concert to reduce stress levels, increase arousal, and mediate feelings of attachment between two individuals (Floyd et al., 2009; Grewen et al., 2005; Light et al., 2005; Uvnäs-Moberg, 1998; C. A. Wilson & Hill, 2007). These intimate behaviours and their effects on attachment can directly affect the creation and maintenance of pair-bonds. This kind of physical and sexual intimacy and its effect on attachment is sometimes referred to as the tightly integrated ‘sexual behaviour system’, which affects pair-bond initiation, continuing motivation to remain in a pair-bond, and pair-bond maintenance (Birnbaum & Gillath, 2006). Research has shown that the mere subliminal suggestions of sexual interest or arousal can also increase the kinds of cognitive-behavioural responses that are associated with

initiating and maintaining close relationships in both males and females (Gillath, Mikulincer, Birnbaum, & Shaver, 2008).

The physiological mechanics of mouth-to-mouth kissing closely imitate mouth movements used by infants when breast-feeding, a period in early development associated with the formation of intense emotional attachments and bonds between mother and child (Hrdy, 1999). Since it is known that these early maternal-infant bonds are mediated by neurochemicals such as oxytocin, released in large quantities during birth and during breastfeeding, the act of kissing in later life outside of the mother-infant context may activate similar mechanisms, and consequently facilitate similarly intense feelings of attachment between individuals (Insel & Young, 2001; E. E. Nelson & Panksepp, 1998; Uvnäs-Moberg, 1998). Feelings of mild dopamine-induced euphoria and a state of relaxation associated with romantic kissing may also create rewarding associations with the individual being kissed, motivating further intimate contact with that them, which in turn allows further pair-bonding mediation to take place.

Previous research has found not only that mouth-to-mouth kissing is considered more “intimate” than nearly all other acts of physical affection (not including sex), but also that the amount of ‘kissing, hugging, stroking or cuddling’ between romantic partners is highly correlated with levels of self-reported relationship satisfaction (Gulledge, Gulledge, & Stahmann, 2003; Jonason, Li, & Richardson, 2011). Among both adolescent couples and adults, it has been found that kissing frequency often correlates positively with relationship satisfaction (Aron & Henkemeyer, 1995; Welsh, Haugen, Widman, & Darling, 2005). In one young adult population, ‘casual sex’ situations between friends or acquaintances were found to involve more affectionate behaviours, such as kissing or hugging, than between strangers – again suggesting these behaviours are related to emotional intimacy (Grello et al., 2006). Further anecdotal evidence for the role of kissing in attachment lies in the business practices of working prostitutes, who need to distance themselves emotionally from their clients in order to efficiently carry out their work and therefore refuse to

kiss clients on the basis that it is “too intimate” or “it smacks too much of genuine desire and love for the other person” (Brewis & Linstead, 2000).

Perhaps another part of the reason that romantic kissing is seen as an intimate behaviour is because the saliva exchanged during mouth-to-mouth kissing, which may also contain trace amounts of blood, can expose the individuals involved to multiple health risks. Kissing can facilitate in the transmission of infections such as influenza (Schoch-Spana, 1992), herpes simplex virus (Cowan et al., 2002), meningococcal meningitis (Tully et al., 2006) and can even expose partners to foreign fragments of food which may trigger life-threatening food allergy responses (Maloney, Chapman, & Sicherer, 2006). Since it would seem unwise to expose oneself to such potential health hazards without good reason, kissing another individual may act as a significant psychological and behavioural signal of commitment, both to the mating partner and to society. Alternatively, biologically risky behaviours such as kissing may induce cognitive dissonance in individuals (Festinger, 1957), creating discomfort between a hazardous behaviour and trivial initial feelings towards a new romantic partner, which could be most easily resolved by modifying feelings of attraction, attachment or sexual interest to match these behavioural outcomes.

Sex Differences in Romantic Kissing

Early research into human mating, some of which also touched upon romantic kissing as a courtship custom, has suggested that some interesting differences might exist in how kissing is viewed and utilised by the sexes. Research into jealousy in multiple cultures around the world has found that females, almost universally, showed greater jealousy than males when thinking about the prospect of their partner kissing another individual (Buunk & Hupka, 1987). Furthermore, when actually partaking in extra-pair activity, i.e. sexual contact outside of an established and exclusive relationship, while males and females were both as likely to partake in kissing behaviours, females were less likely to also experience and pursue fondling, oral sex or vaginal

sex (Wiederman & Hurd, 1999). In a similar vein, in a young adult population boys indicated that they desired more 'breast petting' and genital contact at even the earliest stages of a relationship, whereas females preferred to just kiss until more developed stages of the relationship (McCabe & Collins, 1984).

When viewed through an evolutionary framework, such observed sex differences in attitudes towards romantic kissing shed some light on the role kissing may play in romantic relationships, since in general the sexes also utilize many other courtship and relationship behaviours in divergent ways. An evolutionary approach to studying such differences predicts that the sex making the greater minimal parental investment will be more discerning when it comes to selecting a mate (Bjorklund & Schackelford, 1999; Trivers, 1972). In humans the female pays the higher metabolic cost of parenting, with a considerable body of research confirming that females do indeed undertake a more rigorous and selective mate-selection process than males (Buss, 1989; Candolin, 2003; Grammer et al., 2000; Kenrick et al., 1990; Townsend & Wassermann, 1998). This process of selecting mates may involve the assessment of various physical and behavioural cues, many of which putatively convey information about genetic quality and include fluctuating asymmetry (Grammer & Thornhill, 1994), sexually dimorphic traits of masculinity/femininity (Little et al., 2001), voice pitch/quality (Collins & Missing, 2003), and olfactory cues (Grammer, Fink, & Neave, 2005; Rikowski & Grammer, 1999) (see also Chapter 1, 'Mate Selection' on p. 14 for discussion). If romantic kissing assisted in some way in the process of assessing and selecting a desirable mate, it follows then that the more selective sex, females, would place greater value on romantic kissing than males.

However, human females have also been found to place greater value than males on traits signalling a willingness and ability to invest resources and time into parental care (Buss, 1989; Kenrick et al., 1990; Townsend & Wassermann, 1998) and on the creation and maintenance of pair-bonded relationships (Baumeister & Bratslavsky, 1999; Ellis & Symons, 1990; Symons,

1979). Since it is believed that courtship behaviours like physical touching may act to strengthen pair-bond attachments, it is not surprising to find that females also place greater value than males on these types of relationship activities (Denney, Field, & Quadagno, 1984; Hughes et al., 2007; Hughes & Kruger, 2011; K. L. Johnson & Edwards, 1991; Symons, 1979). Romantic kissing may be one of the more effective bond-mediating courtship behaviours, with both males and females rating it as the type of physical affection “most expressive of love” (Gulledge et al., 2003). Recent neurological evidence suggests that romantic physical contact may function to mediate romantic pair-bonds by elevating levels of arousal (see also review of kissing and arousal above, p. 73), by activating the brain’s reward and motivational systems, or by initiating the release of neurotransmitters, opioids, and other neurohormones (Aron, Norman, Aron, McKenna, & Heyman, 2000; Carter, 1998; Dunbar, 2010; Esch & Stefano, 2005; H. E. Fisher, Aron, & Brown, 2006; H. E. Fisher, Brown, Aron, Strong, & Mashek, 2010; Light et al., 2005; Macdonald & Macdonald, 2010; Marazziti & Canale, 2004; Uvnäs-Moberg, 1998; C. A. Wilson & Hill, 2007). In light of this, it is again not surprising that females have previously been found to place a greater premium on romantic kissing and show greater jealousy than males when thinking about their partner kissing another individual, although such aggregate sex difference in attitudes alone are not always able to distinguish between whether kissing is being valued for its potential to facilitate mate assessment or pair-bond initiation and maintenance.

Leveraging some these evolutionarily informed predictions, a recent self-report based study (Hughes et al., 2007) found that females placed greater general importance on kissing as a mate selection device than males, emphasising the importance of kissing before a sexual encounter and stating that they would be considerably less likely to have sex with a potential mate without kissing first than males. Males, on the other hand, were found to report few qualms with kiss-free sexual escapades and were significantly more likely than females to have sex with someone who they had consciously evaluated as a ‘bad kisser’. As a testament to its potentially pivotal role in mate

assessment, around 60% of both male and female respondents said that their attraction to an individual had somehow changed after an initial kiss. In the same study, females also stated that they utilise kissing behaviours to assess a partner's level of commitment throughout the relationship, while males more typically used kissing to either initiate sex or as a reconciliation strategy. When it comes to initiating kissing, similar research has found that males are more likely to initiate kissing before sex, whereas females were more likely to initiate kissing after sex (Hughes & Kruger, 2011), the authors suggesting that males use kissing for arousal and sexual purposes, while females preferentially utilise it as a pair-bonding device. These early results seem to suggest that romantic kissing variously serves all the functions in human mating which have been previously predicted: to assess the suitability of potential mates; to increase levels of autonomic arousal (and initiate coitus); and to mediate feelings of attachment in pair-bonded relationships.

3.3 Aims

While recent research on romantic kissing managed to exploit sex differences in attitudes towards romantic kissing to shed some light on how kissing is used in mating relationships, the research methodology of this research was not without shortcomings. As is typical of much psychological research, the population used to examine kissing in this research was a very young sample of U.S. participants from the same university, which is a population with limited sexual experience as is only recently graduated from the period of hormonal upheaval known as puberty – hardly representative of the rest of the U.S. population, let alone of other cultures (Henrich et al., 2010). Secondly, using sex as the main and only predictor variable of attitudes towards romantic kissing raises issues regarding demand characteristics. As gender stereotypes in many cultures are associated with the most pervasive and prescriptive expectations, the self-report answers of this mono-cultural sample may be reflecting gender-stereotypical answers more than an individual's actual beliefs about, and experiences with, romantic kissing. Questions also remain as whether it is just one or two of the hypothesised functions of romantic kissing that are the primary

explanation for its prevalence, or whether all these functions are equal in importance when it comes to romantic relationships.

The current research was motivated by the need to address the limitations of past research into the role of romantic kissing and to establish which of the proposed functions of romantic kissing is the primary driver of this courtship custom. These unresolved issues need to be addressed if we are to have a more complete understanding of the contribution of this custom to the process of pair-bonding, either in the early stages involving the assessment of suitable mates with whom to pursue pair-bonds, or later where it might help mediate pair-bond attachments directly.

The aim of the study presented in this chapter was to distinguish between the three competing hypotheses that attempt to ascribe a function to kissing in romantic relationships: that of mate assessment; arousal; and pair-bond maintenance. This research study aimed to achieve this distinction by examining attitudes towards romantic kissing among a large, diverse and multi-national study population that varied by sex, sociosexual orientation and mate value.

Hypothesis 1 of this study predicted that, if kissing serves a mate-assessment function, individuals who typically demand higher standards of mate quality from potential mating partners, including females, individuals high in mate value (see Kavanagh et al., 2010; Little et al., 2001; Noe & Hammerstein, 1994; Pawlowski, 1999), and those with unrestricted sociosexuality (Sacco et al., 2009; Simpson & Gangestad, 1992; Simpson et al., 1991), should place greater importance on kissing in romantic partner interactions, particularly at initial relationship stages. Furthermore, this hypothesis also predicts that these more selective individuals (again females, high mate value participants, unrestricted sociosexuality participants) will be more likely to have had their attraction to a potential romantic partner affected by an initial kissing experience.

Hypothesis 2 predicted that, if kissing plays a primary role in arousal and the physiological preparation of the body for coitus, individuals should find kissing more important immediately

before sexual intercourse than during or after sexual intercourse, particularly within short-term (casual sex) romantic partners. This hypothesis also predicts that males, who have been previously shown to prioritize short-term mating interactions more than females, will place greater value on kissing before sex where it might be most useful in arousal and initiating sexual relations.

Hypothesis 3 predicted that, if kissing plays a significant role in mediating pair-bond attachments between established romantic partners, then individuals who prioritize the pursuit of long-term mating relationships over short-term mating interactions (i.e. females and individuals with a restricted sociosexual orientation) would find kissing to be more important in the established relationship phase than in the initial relationship phase. Furthermore, this hypothesis predicts that, with long-term partners, kissing will be valued at times not related to sex, particularly for females, where it would be most useful in mediating pair-bonds. Furthermore, this hypothesis predicts that kissing frequency in a relationship should be positively related to pair-bond attachment strength (as indexed by relationship satisfaction).

3.4 Methods

Participants

An online questionnaire, approved by Oxford University's Research Ethics Committee, was distributed to various international online psychological testing repository websites and the University of Oxford. The study was advertised as being about 'romantic attraction,' and responses were voluntary, restricted to individuals over 18 years of age, and anonymous. All participants were offered the chance to enter a prize draw for an online shopping voucher.

In total, 902 participants took the survey to completion, of which 308 were male and 594 were female, ranging in age from 18 to 63 years ($M = 24.7$, $SD = 7.9$). The majority of participants self-identified as being ethnically Caucasian/white (78.7%), 4.6% were Latino, and 3.1% South

Asian. The sample was mostly made up of nationals of British (39.1%), North American (36.7%), and Western European (6.6%) origin. High school education was completed by 99.2% of participants, with 46.9% having attained a Diploma or some college experience, and 30.6% completing a Bachelor's degree or higher. Of the sample, 55.2% of participants were in some kind of long-term/committed relationship (either living apart, living together or married) at the time of the survey.

Procedure

Participants were asked to complete questions about their attitudes towards romantic kissing in various romantic partner situations. Throughout the survey, romantic partners were defined as persons with whom the participant could be romantically involved (with or without the involvement of sex), with short-term relationships defined as involving 'casual, short-term partners (i.e., one night stands)' and long-term relationships defined as those with a 'committed, long-term romantic partner (i.e., someone you are in a relationship with).' Kissing was defined as 'kissing on the lips or open-mouth ("French") kissing.' Participants were also asked to provide general demographic information. In all cases, responses were collected using 5-point Likert-type scales with endpoints labelled either 'Extremely unlikely/Extremely likely,' 'Not at all important/Extremely important,' or 'Strongly disagree/Strongly agree' as appropriate.

Participants in a relationship at the time of the survey were also asked to complete a version of the Relationship Assessment Scale (RAS) (Hendrick, 1988) to assess the quality of their relationship. This 7-item scale asked for participants' levels of agreement with questions such as *'My partner meets all my needs'* and *'There are many problems in my relationship,'* with responses collected using 7-point Likert-type scales which had endpoints ranging from 'Strongly disagree' to 'Strongly agree.' Responses were reverse scored where necessary and averaged to calculate a mean RAS score ranging from 1-7. Participants were also asked about how 'good' at kissing their partner

was, how often they kissed their partners, had sexual intercourse with them, and whether they were satisfied with the amount of kissing and sexual intercourse in their relationship, with responses collected on 5-point Likert-type scales.

To measure participants' preference for short-term, casual sexual encounters versus committed, close sexual relationships, referred to as their sociosexual orientation (Simpson et al., 1991), questions were included from the 9-item Sociosexual Orientation Inventory Revised (SOI-R) to evaluate an individual's behaviours, attitudes, and desires as they relate to non-committal sex (Penke & Asendorpf, 2008). Sample questions included *'With how many different partners have you had sexual intercourse on one and only one occasion?'* in the behavioural component (rated on 9-point frequency scales ranging from '0' to '20 or more'), *'Sex without love is OK'* in the attitude component (rated on 9-point agreement scales ranging from 'Strongly disagree' to 'Strongly agree'), and *'How often do you have fantasies about having sex with someone you are not in a committed romantic relationship with?'* in the desire component (rated on 9-point frequency scales ranging from 'Never' to 'At least once a day'). Mean sociosexual orientation scores were derived from participants' answers to the nine items (with reverse scoring as necessary), which were then median-split into restricted/unrestricted sociosexual orientation for use in some of the ANOVA analyses.

Each participant's mate value was approximated by their self-rated attractiveness, which has previously been found to be highly correlated to peer-rated attractiveness (Feingold, 1988) and to act as a suitable proxy for genetic quality and hence mate value in a biological mating market (Barber, 1995). Answers to the questions *'How do you think other people would rate you on physical attractiveness?'* and *'How do you think other people would rate you on sexual attractiveness?'* were collected using a 7-point Likert-type scale ranging from 'Very low' to 'Very high.' Mean mate value scores were calculated and median-split into a high/low mate value score for use in some ANOVA analyses. A copy of all questions and scales used in this study is included in Appendix A (p. 253). Analyses were carried out in SPSS (version 22.0, SPSS Inc., 2013).

3.5 Results

Importance of Kissing, Relationship Phase, Sex, Sociosexual Orientation and Attraction

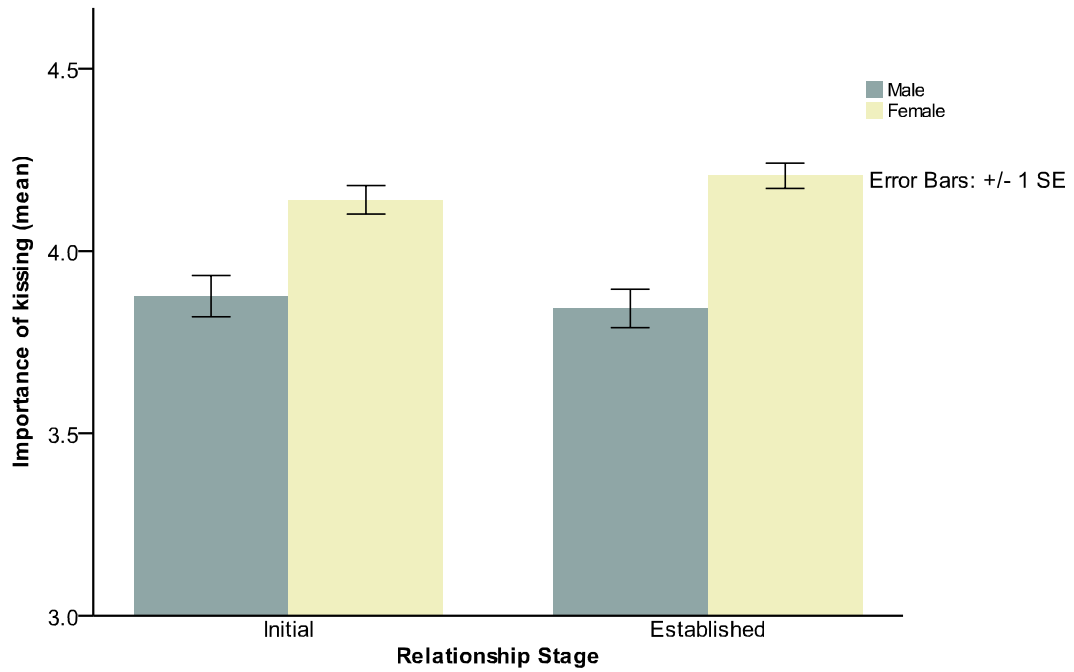
Participants were asked ‘*How important do you think kissing is . . . at the very initial stages of a relationship/ during the established phases of a committed, long-term relationship?*’ A 2 x 2 x 2 x 2 mixed design ANOVA was conducted with sex (male/female), sociosexuality (restricted/unrestricted), and mate value (low/high) as between subjects factors and time in the relationship (initial stage versus established phase) as a within-subjects factor. Table 4 shows the results of this ANOVA analysis.

Table 4. ANOVA results for ratings of kissing importance at initial/established relationship phases by sex, sociosexual orientation, and mate value

	<i>df</i>	<i>F</i>	<i>p</i>	<i>partial η²</i>
<i>Within subject effects</i>				
Relationship phase	882	0.96	.328	.001
Relationship phase × Sex	882	0.05	.823	.001
Relationship phase × Sociosexuality	882	17.34	.001	.019
Relationship phase × Mate Value	882	1.55	.214	.002
Relationship phase × Sex × Sociosexuality	882	2.32	.128	.003
Relationship phase × Sex × Mate Value	882	0.16	.689	.001
Relationship phase × Sociosexuality × Mate Value	882	0.85	.357	.001
Relationship phase × Sex × Sociosexuality × Mate Value	882	0.23	.630	.001
<i>Between subject effects</i>				
Sex	882	32.53	.001	.036
Sociosexuality	882	5.05	.025	.006
Mate Value	882	11.55	.001	.013
Sex × Sociosexuality	882	4.42	.036	.005
Sex × Mate Value	882	0.48	.487	.001
Sociosexuality × Mate Value	882	0.50	.479	.001
Sex × Sociosexuality × Mate Value	882	1.06	.304	.001

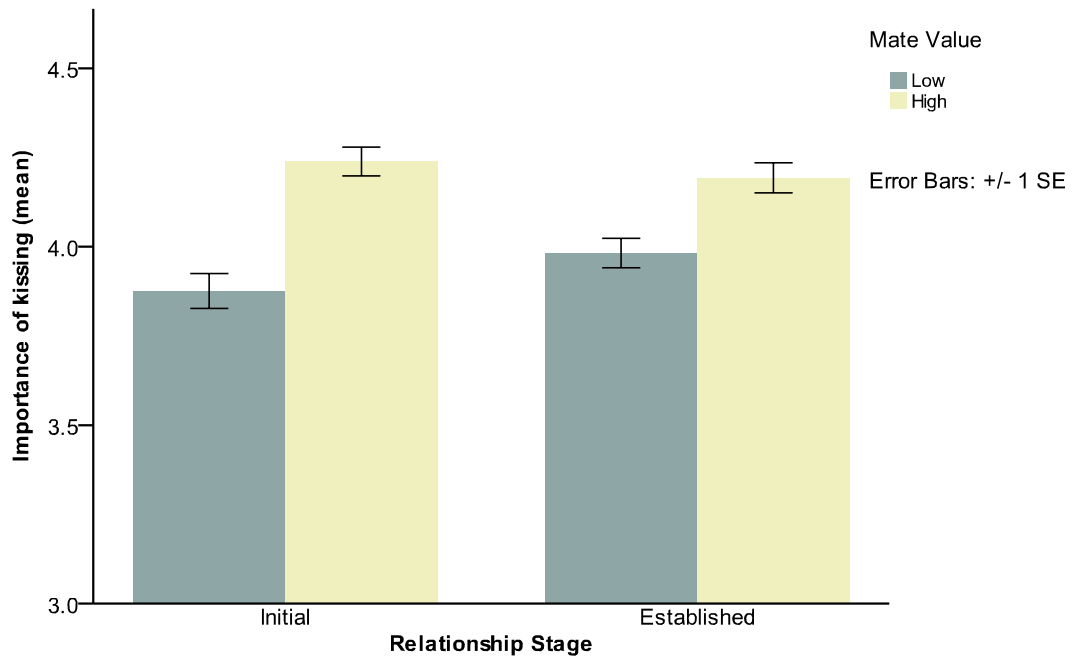
The main effect for sex suggests that females ($M = 4.17, SE = 0.03$) rated kissing as more important than males ($M = 3.83, SE = 0.05$) (Figure 4) in all partner interactions.

Figure 4. Importance of kissing at different stages of a relationship by sex



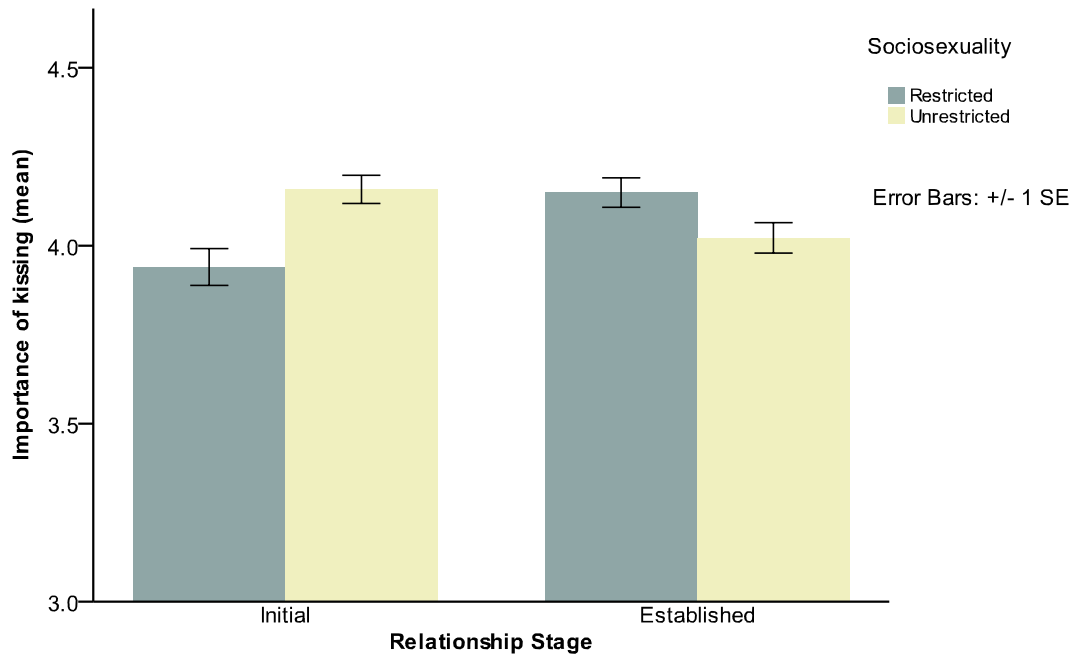
The main effect for mate value indicated that participants high in mate value ($M = 4.10, SE = 0.05$) rated kissing as more important than low mate value participants ($M = 3.90, SE = 0.04$) in both relationship stages (Figure 5).

Figure 5. Importance of kissing at different stages of a relationship by own mate value



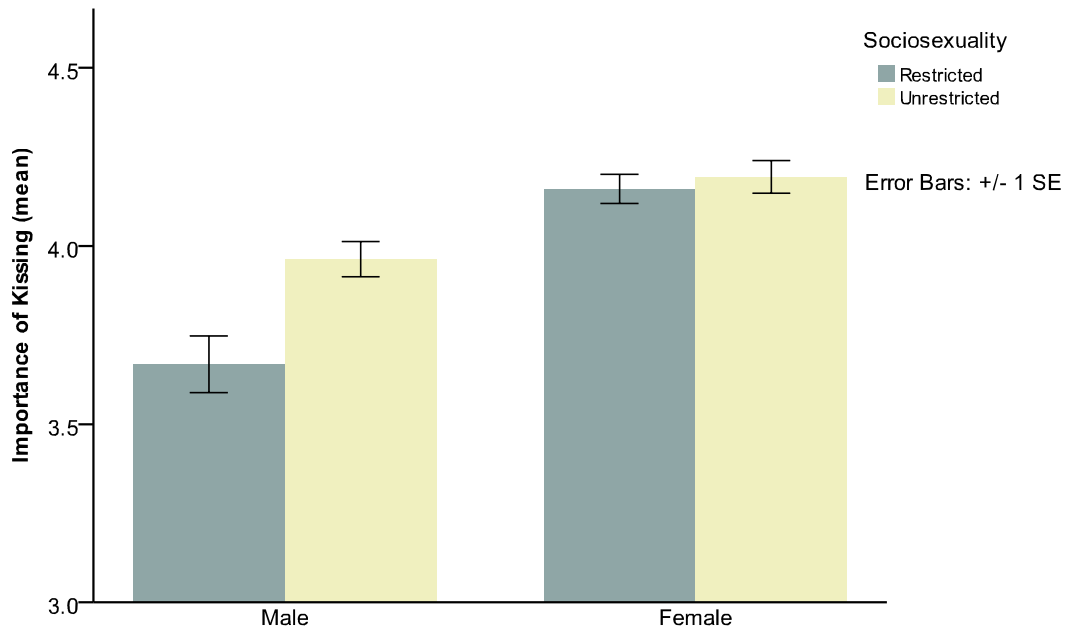
The interaction effect between relationship stage and sociosexuality suggests that at initial relationship stages, participants with restricted sociosexuality scores believed kissing was less important ($M = 3.82$, $SE = .06$) than participants with unrestricted sociosexuality ($M = 4.14$, $SE = .05$), while at established relationship stages the opposite was true, with participants with restricted sociosexuality believing kissing was more important ($M = 4.04$, $SE = .06$) than participants with unrestricted sociosexuality ($M = 4.00$, $SE = .04$) (Figure 6).

Figure 6. Importance of kissing at different stages of a relationship by sociosexual orientation



The interaction effect between sex and sociosexuality suggested that among males, unrestricted males felt that kissing was more important ($M = 3.96$, $SE = .05$) than restricted males ($M = 3.70$, $SE = .09$), while all females felt that kissing was more important than males, with no differences between restricted ($M = 4.17$, $SE = .04$) and unrestricted females ($M = 4.18$, $SE = .05$) (Figure 7).

Figure 7. Importance of kissing at any stage of a relationship by sex and sociosexual orientation



Importance of Kissing around Sexual Intercourse with Short- and Long-Term Partners by Sex

Participants were asked the question ‘*How important do you think kissing is with a [casual, short-term romantic partner/committed, long-term romantic partner] in the following situations: Immediately before sex; During sex; After sex; At all other times (not related to sex)?*’ A 2 x 2 x 4 mixed design ANOVA was conducted with participant sex (male/female) as a between subject factor and romantic partner type (short-term/long-term) and time in relation to sex (before, during, after, ‘other times’) as within-subject factors. The results of this analysis are shown in Table 5.

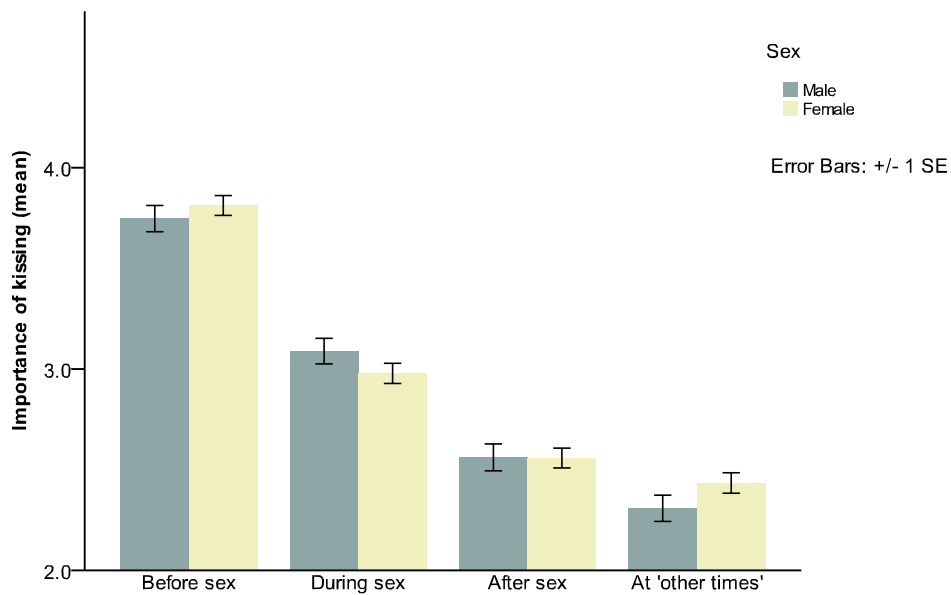
Table 5. ANOVA results for ratings of kissing importance with short/long term partners at different times around sexual intercourse by sex

	<i>df</i>	<i>F</i>	<i>p</i>	<i>partial η²</i>
<i>Within subject effects</i>				
Short/Long Term Partner	867	1052.12	.001	.548
Short/Long Term Partner × Sex	867	2.98	.085	.003
Time Around Sex	867	447.96	.001	.341
Time Around Sex × Sex	867	4.50	.034	.005
Short/Long Term Partner × Time Around Sex	867	658.89	.001	.432
Short/Long Term Partner × Time Around Sex × Sex	867	0.27	.274	.001
<i>Between subject effects</i>				
Sex	867	2.40	.121	.003

The results suggest that an interaction effect was present between sex and time around sex, with post-hoc tests (adjusted for multiple comparisons, differences significant at $p < .005$) revealing that females thought kissing was more important than males ‘at other times not related to sex’ (females $M = 3.39$, $SE = 0.03$, males $M = 3.16$, $SE = 0.05$), but did not differ from males in rating the importance of kissing before, during or after sex (all $ps > .05$).

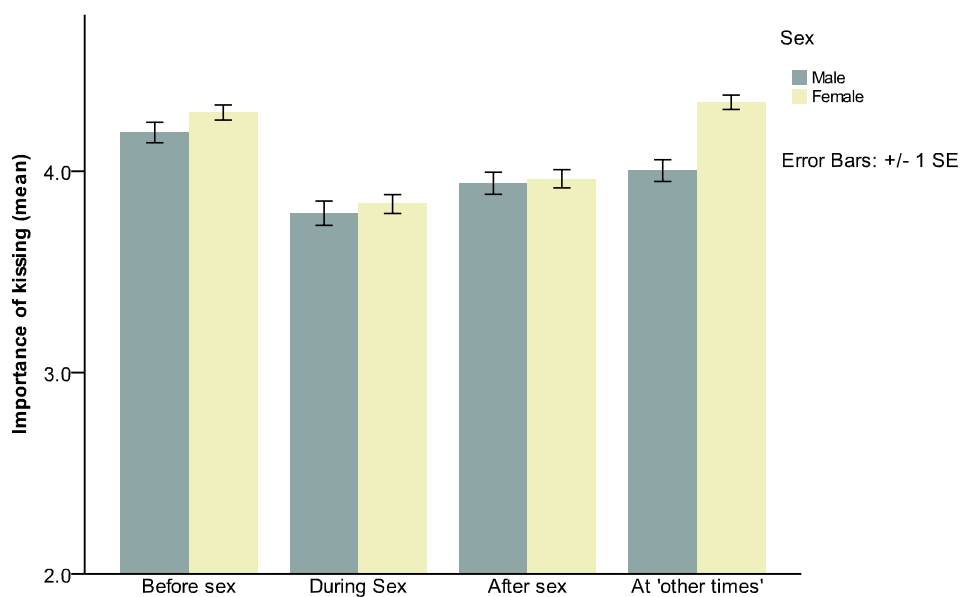
Another interaction effect was found between romantic partner type and time around sex, with post-hoc pairwise comparisons (adjusted for multiple tests, all differences significant at $p < .005$) indicating that overall kissing was seen as much more important with long-term partners ($M = 4.05$, $SE = 0.03$) than with short-term partners ($M = 2.94$, $SE = 0.03$). Furthermore, kissing short-term partners was seen as most important before sex ($M = 3.79$, $SE = 0.04$), less important during sex ($M = 3.04$, $SE = 0.04$), even less important after sex ($M = 2.57$, $SE = 0.04$), and least important at ‘other times’ ($M = 2.37$, $SE = 0.04$) (Figure 8).

Figure 8. Importance of kissing short-term partners at various times around sex, by sex



When it came to long-term romantic partners, kissing was seen as equally important before sex ($M = 4.24, SE = 0.03$) and at 'other times not related to sex' ($M = 4.18, SE = 0.03$), while it was significantly less important after sex ($M = 3.96, SE = 0.04$) and least important during sex ($M = 3.82, SE = 0.04$) (Figure 9).

Figure 9. Importance of kissing long-term partners at various times around sex, by sex



Change in Attraction after an Initial Kiss

Multiple regression analysis was conducted regressing answers to the question ‘*Have you ever felt attracted to someone, only to find that your attraction to them had changed after an initial kiss?*’ onto the three main predictor variables of sex, mean mate value, and mean sociosexuality (and their interactions). None of the interaction terms were found to improve the model fit significantly, and were therefore not included in the final analysis, the results of which are shown in Table 6.

Table 6. Multiple regression analysis results for predictors of change in attraction after an initial kiss

	<i>B</i>	<i>SE B</i>	β
Constant	1.72	0.11	
Sex	0.38	0.07	0.18***
Self-rated Attractiveness	0.23	0.03	0.23***
Sociosexuality	0.11	0.02	0.19***

Note: $r^2 = .126$, *** $p < .001$

The results showed that females were more likely than males to have experienced a change in attraction after an initial kiss, that participants with higher mate value were more likely to have had a kiss alter their feelings of attractiveness, and that a more unrestricted sociosexuality was associated with greater changes in post-kiss attraction.

Kissing and Relationship Satisfaction

A multiple regression analysis was conducted to see to what extent romantic partner kissing ability, frequency of kissing and sexual intercourse, and satisfaction with the amount of kissing and sexual intercourse in the relationship predicted relationship quality. As shown in Table 7, having a partner who was a ‘good’ kisser, greater frequency of kissing in the relationship, greater

satisfaction with the amount of kissing, and greater satisfaction with the amount of sex in the relationship were all positively associated with relationship quality, while the frequency sex in the relationship was not significantly related to relationship quality.

Table 7. Multiple regression analysis results for predictors of relationship quality

	<i>B</i>	<i>SE B</i>	β
Constant	2.072	0.256	
How 'good' at kissing partner is	0.405	0.052	0.321***
Frequency of kissing partner	0.116	0.049	0.111*
Satisfaction with amount of kissing	0.155	0.062	0.132*
Frequency of sex with partner	0.065	0.050	0.066
Satisfaction with the amount of sex	0.168	0.057	0.161**

Note: $r^2 = .331$, * $p < .05$ **, $p < .01$, *** $p < .001$

3.6 Discussion

This study explored the potential functions of romantic kissing by examining attitudes towards kissing in the context of various human mating situations. The three main hypotheses predicting the potential function of romantic kissing were: mate assessment – either via sebum, saliva or auxiliary pheromone sampling for signs of fitness or genetic (MHC) compatibility; arousal – mediating readiness for sex and inducing sexual interaction; and pair-bonding – the initiation and mediation of feelings of attachment between individuals. Table 8 compares the results of this study against the predictions made by the three competing hypotheses for several different research questions in a ‘critical tests’ format (see also Calhim, Shi, & Dunbar, 2006; van Schaik & Dunbar, 1990).

Table 8. Critical tests analysis between competing hypotheses for the function of kissing

Research Question	Predictions of each hypothesis			Observed Result
	Mate Assessment (Hyp. 1)	Arousal (Hyp. 2)	Pair-Bonding (Hyp. 3)	
Females believe kissing is more important in relationships than males do	<u>YES</u>	NO*	<u>YES</u>	YES
High mate value participants believe kissing is more important than low mate value participants	<u>YES</u>	NO*	<u>YES</u>	YES
Kissing importance at early (E) vs. late (L) stages of relationship	$E > L^*$	$E = L^*$	$E < L^*$	$E = L$
Unrestricted sociosexuality participants value kissing more at early stages of a relationship	<u>YES</u> *	NO	NO	YES
Restricted sociosexuality participants value kissing more at late stages of a relationship	NO	NO	<u>YES</u> *	YES
Unrestricted sociosexuality male participants value kissing more than restricted male participants	<u>YES</u> *	NO	NO	YES
Females more likely to have attraction change after an initial kiss than males do	<u>YES</u> *	NO	NO	YES
High mate value participants more likely to have attraction change after an initial kiss	<u>YES</u> *	NO	NO	YES
Unrestricted sociosexuality participants more likely to have attraction change after an initial kiss	<u>YES</u> *	NO	NO	YES
With ST partner: kissing more important before sex than at other times	NO	<u>YES</u> *	NO	YES
With LT partner: kissing important at all times around sex	NO	NO	<u>YES</u> *	YES
Males find kissing more important before sex than during/after sex	<u>NO</u>	YES*	<u>NO</u>	NO
Females find kissing more important at times not related to sex than males	NO	NO	<u>YES</u> *	YES
Frequency of kissing predicts relationship satisfaction	NO	NO	<u>YES</u> *	YES
Number of correct predictions	8	2	7	
Number of critical tests confirmed (no. available)	5 (6)	2 (5)	4 (5)	

Notes: prediction that matched the observed result is underlined

* Critical test that yields a unique prediction in favour of one hypothesis only

If the mate assessment hypothesis is true, then females and high mate value participants would value kissing more at early relationship stages, since all these individuals are known to be more selective when it comes to assessing genetic quality (see also Chapter 1, Mate Selection p 14). Additionally, unrestricted sociosexuality males should also value kissing more at early stages – such males have been shown to place greater value on, and show improved sensitivity to, easily assessable signs of genetic quality in potential mates (e.g. Sacco et al., 2009; D. S. Smith et al., 2013), and are generally uninterested in pursuing the establishment of relationships. Furthermore, if these three types of individuals rely on kissing as an initial mate assessment device, then they are also more likely to have had their attraction affected by an initial kiss. Conversely, if the bonding hypothesis is true then individuals who are known to value the creation and maintenance of mating pair-bonds, which again included females and high mate-value participants as well as restricted sociosexuality individuals, are likely to value kissing more – particularly at later relationship stages. The bonding hypothesis would also be supported by findings showing that kissing is valued most with long-term partners at times not related to sex, (particularly for females), where it would mediate pair-bonds, and by findings suggesting that kissing frequency is positively related to pair-bond attachments. The arousal hypothesis would suggest that kissing is most important immediately before sexual intercourse, particularly within short-term (casual sex) romantic partners, with males placing greater value on kissing before sex aid in initiating sexual relations.

The critical tests comparison found that the data generally supported the predictions made by the mate assessment hypothesis (Hypothesis 1) and bonding hypothesis (Hypothesis 3), while showing very little support for the arousal hypothesis (Hypothesis 2).

Kissing and Mate Assessment

Support for Hypothesis 1, that kissing aids in mate assessment, was provided by the finding that both females and participants high in mate value believed kissing was more important in relationships than either males or low mate value participants, and responded that they were more likely to have had their attraction to an individual change after an initial kiss. It was also found that sociosexually unrestricted individuals thought kissing was more important at early stages of a relationship than restricted sociosexuality individuals, that they reported greater changes in attraction after an initial kissing encounter, and that males with unrestricted sociosexuality thought kissing was more important than males with restricted sociosexuality.

Previous research suggests that females and participants high in mate value are generally more selective when it comes to choosing a mate and are more likely to place value on both cues signalling underlying genetic fitness/compatibility and on cues signalling long-term commitment and resource-acquisition potential (Buss, 1989; Candolin, 2003; Grammer et al., 2000; Kenrick et al., 1990; Little et al., 2001; Regan, 1998; Shackelford et al., 2005; Todd et al., 2007; Townsend & Wassermann, 1998). The fact that kissing was seen as more valuable in a relationship setting and more likely to mediate initial attraction in these populations suggests that it may also act as a cue to mate assessment. These results provided further support for this hypothesis with the finding that unrestricted sociosexuality participants more than restricted sociosexuality participants valued kissing in initial relationship stages, were more likely to have had their attraction mediated by a kiss, and that unrestricted sociosexuality males valued kissing more than sociosexually restricted males. Previous research on sociosexual orientation has found that such individuals, and in particular unrestricted males, show greater sensitivity to and interest in cues signalling genetic quality (Sacco et al., 2009; Simpson & Gangestad, 1992).

Kissing and Attachment Pair-Bonds

Strong support was also found for Hypothesis 3, that kissing aids in the mediation of long-term attachments, or pair-bonds. Restricted sociosexuality participants believed kissing to be more important at established rather than initial stages of a relationship compared to unrestricted sociosexuality participants. In addition, with short-term casual sex partners, participants responded that kissing was primarily important immediately before sex, whereas with long-term romantic partners kissing was very important before, during, and after sex (as well as at other times not related to sexual intercourse). With long-term partners, it was found that females more than males felt kissing was important at ‘times not related to sex.’

Since restricted sociosexuality participants have previously been found to prioritize the pursuit of long-term, committed mating relationships (Sacco et al., 2009; Simpson & Gangestad, 1992), valuing kissing at later stages of a relationship suggests that it may prove useful in mediating such relationships. Further evidence in support of kissing’s role in affecting long-term attachment lies in the finding that females felt kissing was more important at times where it could not possibly affect initial attraction or arousal levels, i.e. at times unrelated to sex with long-term partners. Since past research has shown that females tend to prioritize activities which aid in the creation and maintenance of relationship pair-bonds (Denney et al., 1984; Ellis & Symons, 1990; Hughes et al., 2007; Hughes & Kruger, 2011; K. L. Johnson & Edwards, 1991; Symons, 1979), it follows that kissing is being utilized for this purpose among these participants.

This research also found that the frequency of kissing in established relationships was significantly related to relationship satisfaction, a result which echoes similar research which had previously found that various physically intimate partner activities were related to relationship satisfaction and feelings of attachment (Floyd et al., 2009; Grewen et al., 2005; Gullede et al., 2003; Heiman et al., 2011; Light et al., 2005). In this study it was found that the frequency of more ‘intimate’ partner activities (i.e., sexual intercourse) had no association with relationship

satisfaction – suggesting that there may be something unique about romantic kissing that is related to attachment and relationship satisfaction, even more so than ostensibly more physiologically arousing behaviours such as intercourse. It has been previously proposed that bonding may be at least partly mediated through the touch-initiated mediation of neurochemicals such as oxytocin, dopamine or endorphins (Dunbar, 2010; Machin & Dunbar, 2011; L. J. Young & Wang, 2004), and since there is more sensory cortex area devoted to receiving sensations from the lips than from the genital area (Penfield & Boldrey, 1937), kissing may be an extremely efficient process mediating pair-bond attachments. These findings build upon and extend research which has previously found that kissing is more “intimate” than other forms of physical affection, and that many forms of physical affection, including kissing, are related to relationship satisfaction (Aron & Henkemeyer, 1995; Gullede et al., 2003; Jonason et al., 2011; Welsh et al., 2005).

Kissing and Arousal

These findings provided very little evidence to support Hypothesis 2: that the primary function of kissing was to elevate levels of arousal and initiate coitus in romantic encounters. The data suggested that with short-term romantic partners kissing was seen as most important immediately before sex, but less so during sex, after sex, and at other times not related to sex. While in these circumstances it seems that kissing serves an arousal function, support for the arousal hypothesis only arises in this situation since the possibilities of kissing for the potentially more useful functions of mate assessment or bonding are not possible in this context – during short-term sexual interactions any initial assessment of a mate is already likely to have occurred, and mediating attachment is not a goal of short-term sexual encounters. While it is highly likely that one of the consequences of kissing is indeed autonomic arousal, these data did not support the hypothesis that arousal was a driving factor associated with the prevalence of kissing.

3.7 General Discussion

The research presented in this chapter was motivated by a gap in our current understanding of the exact role that the pervasive courtship custom of romantic kissing plays in processes of pair-bonding, namely mate assessment and the mediation of pair-bond attachments. While past research on sex differences in attitudes towards kissing has hinted that it may be variously used for mate assessment, arousal, and pair-bonding purposes, the inability to differentiate between the relative importance of these three functions and the use of unrepresentative study populations has meant that only limited conclusions regarding kissing could be drawn to date. The aim this study was to address these limitations and to extend our knowledge in regards to the exact role that kissing plays in human mating.

The data presented here suggests that kissing in romantic relationships serves two primary functions – that of mate assessment and the mediation of attachment pair-bonds, with little support for the hypothesis that arousal is a primary function of kissing. It seems likely that kissing can function to both assess mates, as well as to facilitate attachment, by leveraging different physiological mechanisms associated with kissing at different stages of mating. This also evident in the findings that individuals pursuing different mating strategies, either short- or long-term, valued kissing at times of a relationship where it was most likely to serve a strategy-relevant purpose, i.e. either mate suitability assessment or mediation of pair-bonds. This opens up an interesting question: whether, during the evolutionary process, one preceded the other. Kissing may have appeared first to aid mate assessment and was later utilised for bonding purposes or, alternatively, it may have been useful in mediating bonding initially and then been exploited for mate choice purposes. Unfortunately, this study is not amendable to testing between these two alternative scenarios, although one can speculate that the first seems logically the more likely, if only because pair-bonding is relatively rare, and relatively recent, among mammalian and primate species (Kleiman, 1977; E. Nelson, Rolian, Cashmore, & Shultz, 2011; Opie, Atkinson, & Shultz,

2012; van Schaik & Dunbar, 1990), and evolutionary problems related to mate selection, common to all mammals, would have likely preceded those surrounding pair-bonded relationships.

It still remains unclear whether kissing aids in the process of mate assessment by facilitating the evaluation of pheromonal cues for overall health, genetic fitness, or menstrual cycle phase and fertility, or alternatively by aiding gustatory assessment of skin oils and saliva compounds. While it was not within the scope of this thesis to determine the exact mechanisms by which kissing achieves its proposed functions, it is possible to speculate. Since a considerable body of work has previously found that olfactory processes play a significant role in the process of mate assessment (see Chapter 1, 'Olfaction in Mate Assessment,' p. 22), and since it has been observed that one of the more common attributes of kissing present throughout history and across diverse cultures typically involves deep inhalation or 'sniffing' of another individual (H. E. Fisher, 1992; Ford & Beach, 1951; Hopkins, 1907; Parkinson, 1999), it seems highly probable that olfaction is the primary mechanism by which kissing aids the assessment of potential mates. Although a considerable amount of general mate information can be ascertained from olfactory cues, it is only cues related to genetic (MHC) compatibility which are most efficiently assessable through olfactory means (see also 'Olfaction in Mate Assessment' p. 22). Because of this, MHC assessment seems like the most likely evolutionary driver for the initiations of this custom for mate assessment purposes. This assessment mechanism may also help explain why only limited kissing behaviours are observed in our closest primate cousins bonobos and chimpanzees (de Waal & Lanting, 1997; de Waal, 2000), rarely occurring in mate assessment situations. This is most likely because primates are much more sensitive to olfactory and pheromonal cues than humans (Tirindelli et al., 2009), and most likely do not need to establish such close physical proximity to in order to assess potential mates using this sensory modality.

Similarly, while it is likely that kissing forms an integral process in human pair-bonding, mediating attachment in a similar fashion to other forms of close physical affection (such as hugging or

touching), it is not yet known whether kissing works by affecting arousal levels, by reducing stress, by instigating the release of various neuropeptides and neurotransmitters (including oxytocin/vasopressin), by directly affecting the dopaminergic reward or opioid centres of the brain, or by merely mediating levels of trust and psychological intimacy. It is likely that in this instance kissing acts as a form of intense social touch, possibly stimulating the release of endorphins directly affecting social attachment, as endorphins have been proposed as one of the likely mechanisms by which attachment is mediated among our primate cousins during social grooming behaviours (Machin & Dunbar, 2011).

3.8 Chapter Summary and Outlook

These data suggest that kissing in mating relationships serves two main functions: mate assessment and the mediation of pair-bond attachments. Data was presented to support the hypothesis that kissing serves a useful mate-assessment function, with females, high mate value participants, and unrestricted sociosexuality participants placing greater importance on kissing in romantic relationships and stating that an initial kiss was more likely to affect their attraction to a potential mate than did males, low-mate value or restricted sociosexuality participants. Kissing also forms part of the pair-bonding process, utilized in the mediation of pair-bond attachments: kissing was seen to be more important at established stages of relationships by restricted sociosexuality participants, kissing was generally rated as more important in long-term relationship contexts (particularly by females), and kissing frequency was found to be related to relationship satisfaction. These findings have potential implications for our approach to understanding of various other common courtship customs, which although often examined as socio-cultural constructs, may also serve evolutionarily useful purposes

Chapter 2 of this thesis discussed how the different mating strategies pursued by the two within-sex strategy phenotypes could influence mating effort and thus the types of mating partners that

are preferentially pursued. This chapter demonstrated that these two phenotypes also seem to utilise the courtship customs of romantic kissing in divergent ways – with individuals interested in short-term mating with high genetic quality partners using kissing to help assess the quality of potential mates, and individuals interested in long-term mating commitments favouring the use of kissing in established relationships to help mediate and maintain pair-bonds.

The following chapter follows up on the research presented in this chapter and examines in more detail the role of romantic kissing in human mating decisions. In order to help establish that a set of behavioural outcomes is driven by evolutionary pressures, it is useful to examine if any links exists between that behaviour and some kind of underlying biological substrates. As female mate preferences has been previously shown to change across the menstrual cycle alongside the fluctuation of menstrual cycle related hormones, the following chapter examines how attitudes towards romantic kissing also change across the cycle among females, and whether this variation can be predicted by fluctuating levels of menstrual hormone oestrogen or progesterone. Furthermore, as the research carried out on kissing thus far has mostly looked at self-report attitudes towards kissing in different situations, a second study is carried out in the following chapter that looks at the effects of mate information conveyed by romantic kissing on the desirability of potential mates. Finally, the following chapter also looks at the relative importance played by kissing-related informational cues versus traditional visual information in the process of assessing a potential mate.

Chapter 4 – Romantic Kissing: Biological substrates and effects on Mate Desirability

4.1 Introduction

The study presented in the previous chapter established that the courtship custom of romantic kissing plays two important roles in the process of pair-bonding: that of mate suitability assessment at initial relationship stages, and that of the mediating of pair-bond attachments in established relationships. The current chapter follows up on this initial research and goes on to examine the functional uses of romantic kissing in more detail.

The first study in this chapter attempts to determine whether the use of romantic kissing in mating relationships might be mediated by potential biological substrates by examining variation in attitudes towards kissing among females over the course of the menstrual cycle. A considerable body of research has previously found that the menstrual cycle, and the underlying hormones which fluctuate in tandem with the cycle, has a significant effect on female mating behaviour and mate preferences (for reviews see Gangestad & Thornhill, 2008; Jones et al., 2008). By comparing attitude changes towards kissing across the cycle to previously established cyclical changes in mating behaviour, it may be possible to make further conclusions regarding the purpose served by this courtship custom. Furthermore, by comparing changes in attitudes towards kissing across the menstrual cycle to fluctuations in underlying estimated levels of various menstrual hormones (namely oestrogen and progesterone), it may also be possible to determine whether kissing in the mating context has any biological covariates which might be mediating its use and expression.

The aim of the second study in this chapter was to explore the effects of kissing-related informational cues on mate desirability. This study used an experimental design to present participants with various third-hand informational cues about potential mating partners,

including kissing-mediated information, to determine whether such information has an effect on mate desirability in various mating situations. Furthermore, as the relative role of different modal cues used in mate assessment have been found to vary between situations (e.g. Foster, 2008; Kovacs et al., 2004; Saxton et al., 2008), this study also aimed to examine the relative utility of such kissing-based information in the presence of traditional visual cues, which in humans dominate much of our interaction with the world (Levin, 1993), including mate choice, and have been the traditional focus of much mate assessment research (see also Chapter 1, ‘The Role of Attractiveness’ p. 18).

These results of these studies are examined in light of the role of biological substrates in mediating courtship custom use, the relative role of the various senses in aiding mate assessment, and the variation in mating partner desirability among individuals pursuing different mating strategies and of differing mate values. This chapter concludes by elaborating further on the possible proximate mechanisms by which kissing might work to assess potential mates and mediate attachment.

4.2 Study I – Menstrual Cycle Effects on Attitudes toward Romantic Kissing²

Literature Review – Mate Assessment across the Menstrual Cycle

Hormonal changes associated with the human menstrual cycle seem to have a significant effect on female sexual and mating behaviour. While it has been known for some time that female sexual desire spikes in the days surrounding ovulation (Regan, 1996), it has recently been discovered that preferences for certain types of mating partners also co-vary with phases of the

² The results of this study have been published as the following peer-reviewed journal article: Wlodarski, R., & Dunbar, R. I. M. (2013). Menstrual cycle effects on attitudes toward romantic kissing. *Human Nature*, 24(4), 402-413. doi:10.1007/s12110-013-9176-x.

menstrual cycle. For example, females in the late follicular phase of their cycle (in the days immediately preceding ovulation, when risk of conception from a single act of intercourse is at its peak) report elevated levels of general attraction to men (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006) and show increased preferences for sexually dimorphic (i.e. 'masculine') faces, masculine body shapes (Little, Jones, & Burriss, 2007; Penton-Voak et al., 1999), 'typical male behavioural displays' (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004), for the scents of symmetrical males (Gangestad & Thornhill, 1998) and of men who have greater genetic (MHC) compatibility (Wedekind et al., 1995), as well as for men who are socially dominant (Havlicek et al., 2005) and high in creative intelligence (Haselton & Miller, 2006). Females in this cycle phase have also been found to be more accurate at judging male sexual orientation (Rule, Rosen, Slepian, & Ambady, 2011) and at interpreting and paying attention to cues signalling status (Lens, Driesmans, Pandelaere, & Janssens, 2012).

Many of the preferences affected by the menstrual cycle relate to purported mate signals of underlying genetic fitness (for reviews see Gangestad & Thornhill, 2008; Jones et al., 2008; Rhodes, 2006). Mating with a partner who possesses a robust gene set increases the odds that resulting offspring will be endowed with similar genetic advantages. However, as a negative relationship seems to exist between genetic fitness indicators such as these and behaviours associated with long-term parental investment (see also Chapter 1, 'Variation within the Sexes,' p. 11), choosing a mate of superior genetic fitness may necessitate a trade-off when it comes to parental investment potential. It is because of this trade-off that females may seek to improve long-term reproductive fitness outcomes by pursuing a mixed-mating strategy: preferring long-term partnerships with males willing to provide resources and parental support; while being open to pursuing short-term sexual relationships with partners able to contribute superior genes to resulting offspring (Baker & Bellis, 1994; Foerster et al., 2003). Such a mating strategy explains the plethora of data found thus far on shifts in mate preference across the menstrual cycle,

whereby genetically fit sexual partners are preferentially favoured at a time of the cycle when copulation is most likely to lead to conception (i.e. the late follicular phase of the cycle), while sexual partners offering the greatest long-term resource investment potential are favoured at times less likely to lead to conception (i.e. the luteal phase of the cycle).

Research on female mate preference shifts during luteal cycle phases goes some way to corroborating theories about such mixed-mating strategies. When females are in the luteal phase of the cycle, i.e. at lowest risk of conception from a single sexual encounter (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001), they have been found to show preferences for males displaying cues associated with kinship, such as pheromones indicating a similar MHC genetic makeup and faces with higher levels of self-resemblance, as well as for cues of present health (for a review see Jones et al. 2008). It has been proposed that because mating in the luteal phase of the menstrual cycle involves little risk of conception, females at this time pursue decision strategies geared towards affiliating with individuals likely to provide a supportive social environment, such as kin (DeBruine, Jones, & Perrett, 2005; Jones, Perrett, et al., 2005). However, the mate-preference shifts driven by luteal phases of the cycle do not appear to be as robust as mate-preference shifts seen during late follicular phases. DeBruine et al. (2005) found that the cyclic shift for self-resemblance was considerably stronger for female (non-mate) faces than for male faces, while Jones et al. (Jones, Perrett, et al., 2005) found that preference shifts for signs of health were stronger in pregnant women and women using hormonal contraception than in normally cycling women in the luteal phase, suggesting that similarity/kin affiliations might be strongest during hormonal profiles associated with pregnancy (and its associated hormonal surge).

The drivers behind a behavioural adaptation such as this are likely to be related to the steroid hormones that fluctuate in tandem with the menstrual cycle, particularly estradiol (oestrogen) and progesterone. Indeed, the probable reason that mate preference differences seem to be at their

most pronounced between the late follicular and luteal phases of the menstrual cycle is due to the fact that the two phases are associated with the most extreme spikes in levels of oestrogen and progesterone hormones respectively (Durante & Li, 2009; Jones et al., 2008; Meston & Frohlich, 2000). Furthermore, menstrual cycle fluctuations in mate choice preferences are typically only observed among normally cycling females not using any kind of hormonal contraception (e.g. Penton-Voak et al., 1999), presumably due to the moderating effects of these prophylaxes on the conventional fluctuation of oestrogen and progesterone, and hence menstrual-cycle-related behaviour shifts.

Aims

Since multiple lines of research have already established the existence of menstrual cycle effects on preferences for cues related to mate quality, and as the study carried out in the previous chapter found that kissing can convey information about mate quality, the current study aims to determine whether attitudes towards kissing might vary at different phases of the menstrual cycle. If romantic kissing indeed serves some useful mate assessment functions, then one would expect to observe menstrual cycle effects on attitudes toward kissing on par with attitudes toward other cues that convey information regarding mate quality. Furthermore, it would be illuminating to see if a link exists kissing behaviours and a biological mediator that might potentially be influencing these behaviours, such as menstrual cycle hormones.

The present study explored, for the first time, whether menstrual cycle shifts can be seen in female attitudes towards romantic kissing at different stages of a relationship. It was predicted that normally cycling females in the late follicular (high risk of conception) phase of their menstrual cycle would place greater importance on kissing during the initial stages of a relationship, where it would be most useful as a preliminary mate assessment device, than females in the luteal (low risk of conception) phase of their cycle. It was further predicted that this shift

would be mediated by biological substrates, namely one or both of the two hormones that show the greatest fluctuation across the menstrual cycle: oestrogen and progesterone. In addition, if such cycle shifts were found to be present, then it was further predicted that menstrual variation would also exist in females' ratings of various factors associated with a romantic kiss, particularly olfactory factors which are the most likely mechanism by which potential mates can be assessed during romantic kissing encounters.

Methods

Participant Recruitment

An online questionnaire, approved by Oxford University's Research Ethics Committee, was distributed via international public online psychological testing repository websites. Participants were required to be over 18 years of age to complete the survey; no identifying personal data were collected and participants were informed that their responses were completely voluntary and anonymous. Participants were required to provide informed consent, and were offered the chance to enter a prize draw for an online shopping voucher upon completion of the questionnaire.

Questionnaire Design

Participants were informed that they to be were completing questions about their 'attitudes towards kissing with romantic partners.' Participants were firstly asked '*How important do you think kissing is . . . at the very initial stages of a relationship / during the established phases of a committed, long-term relationship?*' They were also asked about various factors associated with kissing: '*In deciding whether someone is a 'good kisser', how important are the following factors: How pleasant their breath is / The scent of their body / The taste of their lips/skin / How 'wet' the kiss is / How much touching/physical-contact/caressing is involved / How physically aroused it makes you / Whether their kissing style is the same as yours?*' Responses

to these questions were collected using 5-point Likert-type scales, with endpoints ranging from 'Not at all important' to 'Extremely important.' For menstrual cycle phase estimation purposes, participants were asked whether they were currently taking any hormonal contraception, whether they experienced a 'regular' menstrual cycle, the average length of their menstrual cycle, and the date of onset of their last menses (see Appendix B, p. 260 for list of all questions used). Basic demographic information was also collected.

Estimations of Menstrual Cycle Phase and Risk of Conception

For all the analyses described below, data were only used from females who reported having a regular menstrual cycle, whose cycle length fell within the 'normal' ranges of 22 to 36 days (Chiazze, Brayer, Macisco, Parker, & Duffy, 1968), who were not on any form of hormonal contraception, and who provided the all the information required to make cycle phase estimations. To estimate the menstrual cycle phase at the time of answering the survey, information was used about the last date of menses onset and typical cycle length to estimate day of ovulation using the reverse cycle day method – approximated as 15 days prior to next estimated onset of menses (as per Pillsworth, Haselton, & Buss, 2004; Thornhill & Gangestad, 1999). This method is preferable to forward-counting methods, as previous research has found that the follicular phase of the menstrual cycle is where much of the variation in average cycle length takes place, with average luteal phase length remaining relatively constant (Fehring, Schneider, & Raviele, 2006; Lenton, Landgren, & Sexton, 1984). For analyses involving a binary measure of cycle phase, participants undertaking the experiment either on the estimated day of ovulation or within the 5 days prior to ovulation were classed as being in the late follicular phase of their cycle (i.e. at 'high risk of conception'), and participants within 10 days of the next onset of menses were classed as being in their luteal phase (i.e. at 'low risk of conception') (Jones, Perrett, et al., 2005; Pillsworth et al., 2004; Wilcox et al., 2001). These particular cycle days were used as they represent the greatest differences in progesterone and estradiol (oestrogen) levels throughout the

menstrual cycle (Durante & Li, 2009; Jones et al., 2008; Jones, Little, et al., 2005; Meston & Frohlich, 2000).

For analyses investigating the hormonal mechanisms which might be driving menstrual cycle behaviour shifts, estradiol and progesterone levels on any given day of the cycle were estimated using mean serum estradiol and progesterone reference values previously derived from a large sample of normally cycling females within 15 days of ovulation (Stricker et al., 2006). All analyses were carried out in SPSS (version 22.0, SPSS Inc., 2013).

Participants

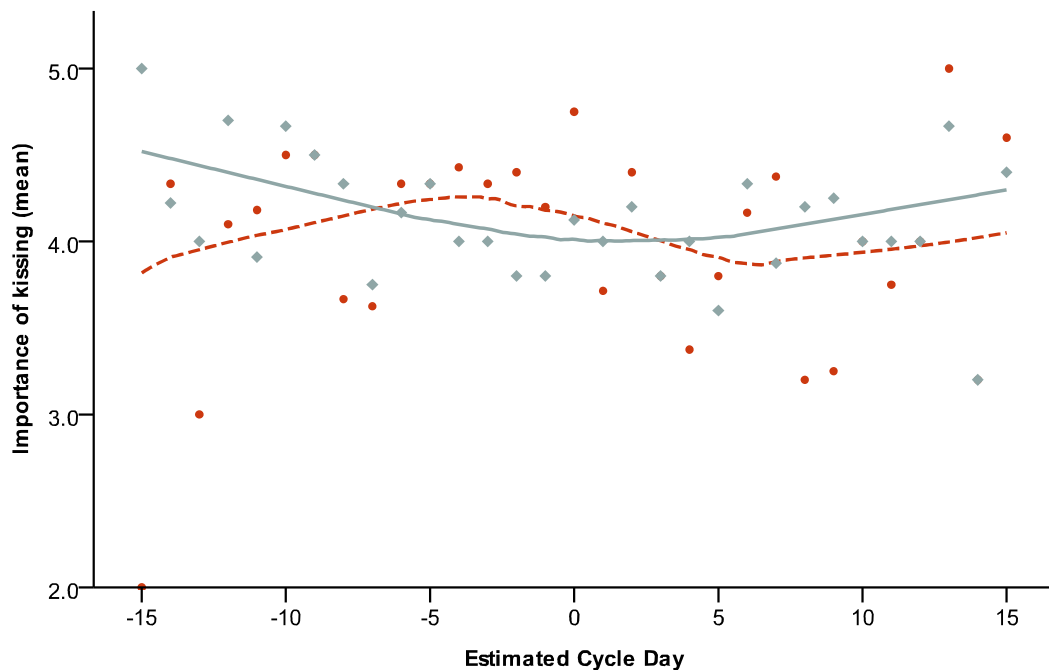
For analyses looking at estimated estradiol and progesterone levels, data was utilised from all eligible participants, who could be in any phase of their menstrual cycle as long as it was within 15 days of estimated ovulation (since estimated estradiol and progesterone levels were only available for these days). This sample had 173 females aged 18 to 51 ($M = 24.7$, $SD = 6.5$), with menstrual lengths varying between 23 to 36 days ($M = 28.9$, $SD = 2.1$) and comprising primarily of North American (39%), British (25%), and Western (10%) and Eastern (5%) European nationalities.

For analyses which were restricted to looking at females in either their late follicular or luteal cycle phases only, a subset of these participants was used which included 50 females who were in the luteal phases of their cycle (within 10 days of estimated onset of next menses) and 34 females in the late follicular phases of their menstrual cycle (day of ovulation plus 5 preceding days). These participants' ages ranged from 18 to 47 ($M = 24.7$, $SD = 6.6$), their menstrual cycle length varied from 23 to 35 days ($M = 28.9$, $SD = 2.2$), and the sample was predominantly made up of North American (33%), British (28%), and Western (8%) and Eastern (6%) European nationals.

Results

Participants' responses to questions about the importance of kissing at both initial and established relationship stages across the entire menstrual cycle can be seen plotted in Figure 10.

Figure 10. Variation in ratings of kissing importance during initial and established phases of a relationship across the menstrual cycle

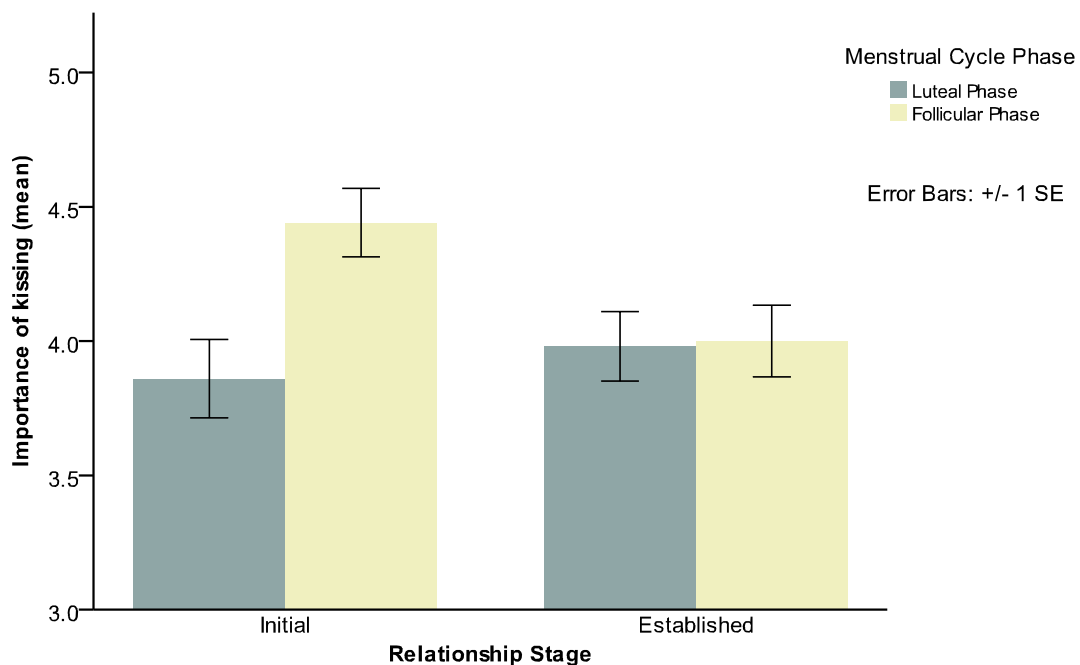


Note: Importance of kissing during initial relationship stages (circular markers, dashed line) versus established relationship phases (diamond markers, solid line) across the menstrual cycle, $N = 173$. Day '0' represents reverse-day-count estimated day of ovulation, trend curves fitted using Loess curve estimation, 65% points fit, Epanechnikov kernel.

A 2 x 2 mixed design ANOVA was carried out on answers to this question, with the binary variable of follicular/luteal cycle phase as a between-subject factor, and stage of the relationship (initial stage/established phase) as a within-subject factor. It was found that while there was no significant main effect of cycle phase on overall ratings of the importance of kissing ($F(1,82) = 3.55, p = .063, \text{partial } \eta^2 = .041$), and no main effect of relationship stage on ratings of kissing importance ($F(1,82) = 1.83, p = .180, \text{partial } \eta^2 = .022$), a significant interaction existed between

cycle phase and relationship stage ($F(1,82) = 5.58, p = .021, \text{partial } \eta^2 = .064$). That is, during the initial stages of a relationship participants in the follicular (high risk of conception) phase of their cycle ($M = 4.10, SD = .97$) believed that kissing was more important than participants in the luteal (low risk of conception) phase ($M = 3.86, SD = 1.03$), while at established stages of a relationship both follicular and luteal phase participants stated that kissing was equally important (follicular phase $M = 4.00, SD = 0.78$, luteal phase $M = 3.98, SD = 0.92$) (Figure 11).

Figure 11. Ratings of kissing importance at initial versus established phases of a relationship by menstrual cycle phase



To determine if the two primary hormones associated with the menstrual cycle might be acting as mediators of participant responses, linear regression analyses were also carried regressing answers to the above two questions onto estimated levels of estradiol and progesterone. As seen in Table 9, progesterone levels were found to be a significant negative predictor for ratings of the importance of kissing, though only during the initial stages of a relationship.

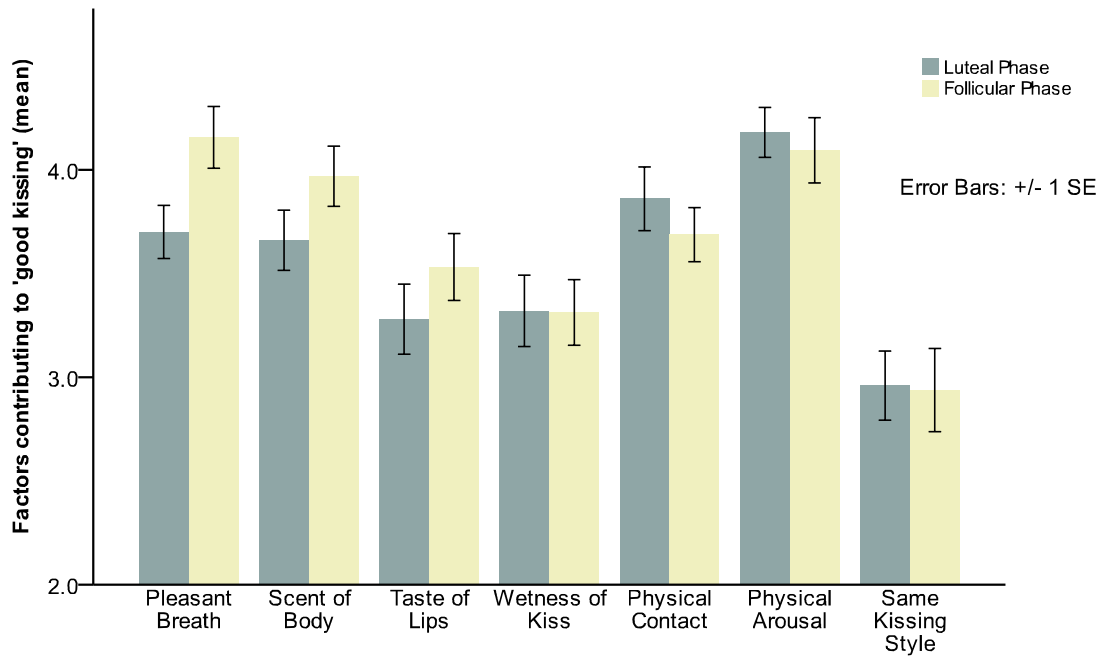
Table 9. Multiple regression analysis of hormone levels as predictors of kissing importance at initial and established relationship stages

	<i>B</i>	<i>SE B</i>	β
Importance of kissing at initial stages			
<i>r</i> ² = .039 (<i>p</i> = .033)			
Constant	4.021	0.150	
Estimated Estradiol Levels	0.001	0.000	0.120
Estimated Progesterone Levels	-0.014	0.006	-0.211**
Importance of kissing at established stages			
<i>r</i> ² = .016 (<i>p</i> = .262)			
Constant	4.274	0.150	
Estimated Estradiol Levels	0.000	0.000	-0.115
Estimated Progesterone Levels	-0.001	-0.005	-0.023

***p* < .01

Next, answers by females at the two distinct phases of their cycle to questions about the importance of factors contributing to a good kiss were examined. It was initially found that females in late follicular (high risk of conception) phases of the cycle believed that ‘pleasant breath’ was a more important component of a good kiss than females in luteal (low risk of conception) cycle phases (follicular *M* = 4.15, *SD* = 0.82, luteal *M* = 3.70, *SD* = 0.91, *t*(82) = 2.34, *p* = .022), and while there was a trend towards females in the follicular phase rating ‘scent of body’ and ‘taste of lips’ as more important than females in the luteal phase, these trends did not reach significance (see Figure 12). No significant differences were found between participants’ ratings of any other factors associated with kissing. However, after these analyses were corrected for multiple comparisons using Bonferroni correction, this main significant finding was edged out of the range of statistical significance.

Figure 12. The importance of various factors in deciding whether someone is a ‘good kisser’ by menstrual cycle phase



Multiple linear regression analyses found that estimated progesterone levels were a negative predictor when rating ‘pleasantness of breath’ as an important component of a good kiss (constant $B = 3.867$, $SE B = 0.131$, Estradiol $B = 0.000$, $SE B = 0.000$, $\beta = 0.111$ $p = .174$, Progesterone $B = -0.011$, $SE B = -0.005$, $\beta = -0.189$ $p = .022$, $r^2 = .032$), while similar regression analyses did not find progesterone or estradiol levels to be significant predictors for importance ratings of any other kissing factors ($0.29 < t < 1.91$, $.056 < p < .875$). After these analyses were Bonferroni corrected for multiple comparisons, however, the one significant finding again fell outside the traditional range of statistical significance.

A Principal Component’s Analysis (PCA) with orthogonal (varimax) rotation was also conducted on answers to the seven factors contributing to ‘good kissing’. Table 10 shows the results of the PCA, with factor loadings for the three main extracted components shown after rotation (coefficients over 0.5 displayed in bold). Linear regression analysis indicated that neither

estimated estradiol nor progesterone levels were significant predictors for any of the three PCA-extracted components ($0.01 < t < 1.80$, $.075 < p < .990$), with progesterone coming closest to significance when predicting answers to Component 1 ($B = -0.010$, $SE B = 0.006$, $\beta = -0.149$ $p = .075$).

Table 10. Principal components analysis results for factors contributing to a ‘good’ kiss

	Components		
	1	2	3
Pleasant breath	.783	-.058	.050
Scent of body	.843	.097	-.112
Taste of lips/skin	.704	.112	.210
Wetness of kiss	.216	.405	.536
Physical contact	.003	.804	.148
Amount of arousal	.059	.768	-.047
Same kissing style	-.023	.045	.886

Note: Sampling adequacy verified by the Kaiser-Meyer-Olkin technique ($KMO = .585$), with Bartlett’s test of sphericity indicating significantly large correlations ($\chi^2(21) = 156.4$, $p < .001$). Inspection of the scree plot suggested a clear inflection point at 3 components, with all components displaying eigenvalues over .989 and combining to explain 63.6% of the variance.

Discussion

This study found that when asked about the importance of kissing at initial stages of a relationship, females in the late follicular phase of their menstrual cycle (i.e. at high risk of conception) rated it as more important than females in the luteal (low conception risk) phase of their cycle. Furthermore, estimated levels of menstrual cycle hormone progesterone were found to be a significant negative predictor for females’ ratings of kissing importance at this relationship stage. When it came to kissing at the more established phases of a relationship, both females in the late follicular and in the luteal phases of the menstrual cycle considered kissing equally

important, and neither estimated estradiol nor estimated progesterone levels were associated with ratings of kissing importance at established relationship stages.

Shifts in Attitudes toward Kissing in Early Relationship Stages

Previous research indicates that females in late follicular phases of their menstrual cycle, who are at the highest risk of conception, show an increased preference for males possessing cues signalling underlying genetic superiority or compatibility, including masculinised faces, facial symmetry, social dominance and MHC compatibility (Gangestad & Thornhill, 1998; Havlicek et al., 2005; Penton-Voak et al., 1999; Wedekind et al., 1995). It has also previously been found that romantic kissing is utilised in the process of assessing a mating partner's desirability (see earlier study in this chapter, and Hughes et al., 2007). The results of the current study offer an original synthesis of these findings by showing that attitudes towards romantic kissing vary across the menstrual cycle and are significantly associated with fluctuations in a biological substrate, namely menstrual cycle hormone progesterone. Since females in the late follicular phase of their cycle are more attracted to, and motivated to find, genetically fit/compatible males it follows that they would place greater value on devices that aid the assessment of genetic qualities – in this case romantic kissing. In the ANOVA analysis comparing only the answers of females in the last 10 days of their cycle to those of females in the five days preceding ovulation, no cycle phase shift was found for ratings of kissing importance at established relationship phases. However, a visual examination of responses across the entire menstrual cycle clearly shows a fascinating pattern of kissing importance ratings, which seem to invert between initial and established relationship phases.

Such a visual examination of the responses of females across the entire menstrual cycle (Figure 10) suggests that while kissing is seen as most important around ovulation in initial relationships stages (where preliminary mate assessment is most likely to take place), it also

appears to be relatively important at established phases of a relationship at all other times of the cycle not associated with high conception risk. Females may place relatively greater value on pair-bonds and traits signalling long-term relationship potential and pair-bond attachments at these other times of the cycle, and may be alternatively using kissing at these other cycle stages with to mediate pair-bond attachments with established partners. These results mirror and corroborate the findings of the previous study in Chapter 3, which found that kissing is useful for two different functions at different stages of a relationship, including assessment of mates at initial stages and as a process contributing to the mediation of mating pair-bonds. It must be noted that although this study design assessed transient cognitive changes associated with variations in menstrual cycle hormone levels, tapping into ‘state’ rather than ‘trait’ effects, these state changes seem to be substantial enough to influence participants’ attitudes towards kissing as imagined at various times in the mating cycle.

The fact that progesterone was significantly negatively associated with ratings of kissing importance at initial relationship stages insinuates that it may be acting as a biological mediator of this observed behavioural cycle shift. Progesterone is one of the candidate mechanisms thought to be responsible for numerous menstrual cycle related behavioural changes (Haselton & Gangestad, 2006), and has previously been implicated in cyclic shifts in mate preference for healthy faces (Jones, Perrett, et al., 2005), self-resemblance (DeBruine et al., 2005), for feminine faces (Jones, Little, et al., 2005) vocal masculinity (Puts, 2005), emotion recognition (Derntl, Kryspin-Exner, Fernbach, Moser, & Habel, 2008), and levels of social monitoring (Maner & Miller, 2013). Although the mechanism by which progesterone effects attitudes towards kissing cannot be established from these results, it is possible that the negative association between this hormone and kissing importance at initial relationship stages is reflective of progesterone-driven aversions to potential sources of contagion (Conway et al., 2007; Flaxman & Sherman, 2000;

Jones, Perrett, et al., 2005), since mouth-to-mouth kissing carries with it some risk of infection (e.g. Cowan et al., 2002; Schoch-Spana, 1992; Tully et al., 2006).

Menstrual Cycle Effects on Importance of Various Factors Associated with Kissing

These results also hint at the idea that menstrual cycle phase and estimated levels of progesterone across the cycle might be related to ratings of the importance of ‘pleasantness of breath’ as a contributing factor to a ‘good kiss,’ and to a lesser extent ‘scent of body’ and ‘taste of lips’. However, the findings at this stage are only suggestive, as adjustments for multiple comparisons, and the relatively small sample size used in these analyses, meant that these differences did not reach traditional statistical significance levels. If one of the major functions of kissing is to assist individuals in assessing the quality of a mate (see also results section of previous study ‘If the mate assessment hypothesis is true, then females and high mate value participants would value kissing more at early relationship stages, since all these individuals are known to be more selective when it comes to assessing genetic quality (see also Chapter 1, Mate Selection p 14). Additionally, unrestricted sociosexuality males should also value kissing more at early stages – such males have been shown to place greater value on, and show improved sensitivity to, easily assessable signs of genetic quality in potential mates (e.g. Sacco et al., 2009; D. S. Smith et al., 2013), and are generally uninterested in pursuing the establishment of relationships. Furthermore, if these three types of individuals rely on kissing as an initial mate assessment device, then they are also more likely to have had their attraction affected by an initial kiss. Conversely, if the bonding hypothesis is true then individuals who are known to value the creation and maintenance of mating pair-bonds, which again included females and high mate-value participants as well as restricted sociosexuality individuals, are likely to value kissing more – particularly at later relationship stages. The bonding hypothesis would also be supported by findings showing that kissing is valued most with long-term partners at times not related to sex, (particularly for females), where it would mediating pair-bonds, and by findings suggesting that kissing frequency is positively related to

pair-bond attachments. The arousal hypothesis would suggest that kissing is most important immediately before sexual intercourse, particularly within short-term (casual sex) romantic partners, with males placing greater value on kissing before sex aid in initiating sexual relations.

The critical tests comparison found that the data generally supported the predictions made by the mate assessment hypothesis (Hypothesis 1) and bonding hypothesis (Hypothesis 3), while showing very little support for the arousal hypothesis (Hypothesis 2).

Kissing and Mate Assessment' p. 96, for more on this), potentially via olfactory or gustatory cues, then females at high conception risk should place greater value on components of kissing which might usefully aid them in assessing the genetic suitability of potential mates. Since one suggestion as to the mechanism by which kissing might convey this information relates to semiochemicals and pheromones found in auxiliary sweat, saliva and skin oils which might convey information about underlying health, as well as genetic quality or compatibility (i.e. Durham et al., 1993; Nicholson, 1984; Roberts et al., 2011; Wedekind et al., 1995; Wobst et al., 1999), females at high risk of conception should be particularly interested in utilising odour and taste cues found in the breath, body and lips to assess mate quality. It is interesting to note than females in the late follicular phases of their cycle have been previously found to show increased sensitivity to odours and to display faster odour processing times (i.e. Doty et al., 1981; Pause et al., 1996; Roberts et al., 2011; Wedekind et al., 1995). Furthermore, other studies suggest that females rate olfaction as the single most important sensory input when selecting a mate and in sexual arousal, whereas men rated visual and olfactory cues equally important (Herz & Cahill, 1997). Such increased sensitivity, and a general reliance on, olfactory cues would be particularly useful in assessing subtle mate olfactory cues, particularly at the most critical time of the menstrual cycle in terms of reproductive fitness outcomes (i.e. when a single act of sexual intercourse is most likely to lead to conception).

When responses to question about factors associated with good kissing were analysed using Principal Components Analysis, the three factors that were extracted coincided rather neatly with several previously proposed theories on the possible functions of romantic kissing (see hypotheses of Chapter 3, p. 81). The first component, relating to ‘sensory factors’, implies that sensations involving smell and taste contribute in a similar way towards making someone a ‘good’ kisser, possibly because these cues can be used to make inferences about the underlying mate quality or genetic suitability using pheromonal cues or on signals of general health (i.e. Durham et al., 1993; Nicholson, 1984; Roberts et al., 2011; Wedekind et al., 1995; Wobst et al., 1999). Interestingly, regression analyses showed a trend towards progesterone levels predicting answers to this sensory factor component of kissing as being an important component, however this result was outside traditional significance levels ($p = .075$). The second PCA component revolved around contact/arousal themes, which have been proposed as another possible function of kissing promoting partner arousal and the initiation of sexual relations. The final PCA factor appears to be related to ‘kissing technique,’ which may also be indicative of mate quality in certain situations, as research in related fields suggests that the quality of execution of complicated behavioural rituals (such as dancing) may be a cue to underlying genetic quality (Hugill et al., 2010).

Study Summary and Outlook

This research study expands on our current understanding of the functions of kissing in human mating by demonstrating that attitudes towards kissing vary across the menstrual cycle and with the fluctuation of menstrual hormones. Specifically, these results indicated that females in the late follicular stages of their menstrual cycles place greater value on kissing in the early stages of a relationship, where it might be used for mate assessment, and that this behavioural shift is related to fluctuations in levels of the hormone progesterone. Furthermore, the data was suggestive of the fact that kissing factors related to smell and taste may be most significant when

it comes to assessing a potential mate's suitability. The findings presented here also suggest that kissing helps assess potential mates at early relationship stages, while also potentially mediating attachment pair-bonds at established relationship stages. These findings extend previous research into shifts in mating partner preferences across the mating cycle, while also corroborating the findings of the previous study in this chapter that romantic kissing is useful for determining mate suitability, as well for processes involved in pair-bonding.

While self-report studies can provide us with some information regarding attitudes towards romantic kissing in different situations, they are limited by recall and desirability biases. The following study was designed to try and examine, using an experimental design, the effects of information conveyed by romantic kissing on the desirability of potential mating partners across various mating situations and among different individuals. Furthermore, although it is known that information from various senses is utilised in mate assessment, the role of vision in mate assessment decisions seems to predominate in most human interactions with the world. A second follow-up study set out to examine relative importance of mate cues associated with kissing, versus the kinds of visual cues that often predominate the assessment of potential mating partners.

4.3 Study 2a – The Influence of Kissing on Mate Choice³

Introduction

As the two previous studies on kissing have demonstrated, the ubiquitous custom of kissing seems to play a functional role in both the initial assessment of mates, and in the maintenance of

³ The results of this study have been published as the following peer-reviewed journal article: Wlodarski, R., & Dunbar, R. I. M. (2014). What's in a Kiss? The Effect of Romantic Kissing on Mate Desirability. *Evolutionary Psychology*, 12(1), 178-199.

pair-bonds in established relationships. While the exact mechanisms by which kissing functions are at this point still unclear, it is almost certain that, like our other mate assessment competencies, it works primarily at a sub-conscious level (Buss & Schmitt, 1993). Just as individuals may decide that someone is attractive without being aware that their appraisal is based on the fluctuating asymmetry that signals basal genetic fitness, for example, it is likely that romantic partners evaluate a kissing situation, sensing that a potential partner is a 'good' kisser, without being cognisant that this assessment results from some kind of sub-conscious appraisal of some variant of their genetic suitability or of the strength of an attachment pair-bond. Indeed, research into mate choice in humans seems to confirm that individuals sometimes have a surprising lack of self-awareness when it comes to understanding the factors that actually influence their attributions of attractiveness and mate choice behaviours, or indeed many other 'conscious' decisions (Eastwick & Finkel, 2008; Nisbett & Wilson, 1977).

While the previous two studies on kissing in this thesis used self-report measures in an attempt to assess participant's attitudes towards kissing in various mating situations, such methodology relies on clear self-knowledge of one's attitudes and on memories relating to kissing experiences, and is therefore highly prone to recall biases (Haefffel & Howard, 2010), with the added issue of sensitive subjects like sex being particularly prone to social desirability effects (T. D. Fisher, 2009). The current study was designed to minimise some of these limitation by examining the direct influence of information relating to romantic kissing on the desirability of a potential mating partner. By presenting various forms of information about a potential romantic partner, including their purported 'kissing abilities,' it may be possible to isolate the influence of information conveyed by romantic kissing on mate desirability in both long-term and short-term mating situations. While the definition of a 'good kisser' is obviously a subjective description which holds potentially unique meanings for each individual, if kissing conveys mate quality information it is reasonable to assume that experiencing a 'good kiss' is likely to be the proximate conscious

manifestations of more complicated underlying mechanisms that are being used to assess a potential mate or mediate levels of attachment.

Aims

The aim of the present study, therefore, was to determine whether romantic-related mate information could affect the desirability of a hypothetical mating partner. It is predicted that participants led to believe that a potential mating partner is a 'good kisser,' a manifest cue potentially signalling a mate's underlying genetic quality/suitability, will find them more attractive, will be more interested in pursuing further courtship (i.e. a date) with them, will be more interested in pursuing non-committal sex with them and be more interested in pursuing a long-term relationship with them. It was further hypothesised that kissing abilities will have a greater influence on female partner preferences than on male partner preferences, as females have been found to be both more discerning when it comes to selecting mates, and more sensitive to cues of genetic fitness, and more interested in the creation and maintenance of pair-bond attachments. It is also predicted that individuals who are higher in 'mate value,' as well as female participants, will generally be more discerning in their appraisals of potential romantic partners, less likely to find potential partners desirable, and will place a greater premium on kissing abilities.

Methods

Participant Recruitment

An online questionnaire was distributed to international online survey and testing repositories and to members of the University of Oxford. Participants were required to be over 18 years of age to complete the survey. No identifying personal data were collected and participants were informed that their responses were voluntary and anonymous. Participants provided informed

consent, and were offered the chance to enter a prize draw for an online shopping voucher. This study was approved by Oxford University's Research Ethics Committee.

In total, 724 participants took the survey to completion, of whom 244 were male and 480 were female, ranging in age from 18 to 63 with a mean age of 24.9 ± 8.1 SD. The majority of the participants self-identified as being ethnically Caucasian/white (77.5%); 4.8% were Latino and 2.8% South Asian. The sample was mostly made up of North American (39.1%), British (35.8%), and Western European (6.8%) nationals. High school education was completed by 99.3% of participants, with 47.6% having attained a Diploma or some college experience. Roughly half of the participants (54.6%) stated that they were in a relationship at the time of the survey.

Questionnaire Design

Participants were presented with descriptive vignettes of four different target individuals of the sex they stated they were most attracted to, and were asked to answer several questions about each. The vignettes were developed to represent descriptions of various personality and relationship-history traits describing each hypothetical target individual, who was also assigned a common English first name. Aspects of target individual 'personalities' were described using 6-7 positive as well as 2-3 negative adjectives made up of positive/negative antonyms (such as trustworthy/untrustworthy, warm/cold, intelligent/unintelligent), which previous research had found were consistently rated as desirable/undesirable personality attributes (Anderson, 1968) and which have been used successfully in past research to create descriptive vignettes (e.g. Fisak, Tantleff-Dunn, & Peterson, 2007). Negative descriptions were included because early pilot testing indicated that purely positive descriptions were less 'realistic' than mixed positive and negative descriptions. Several neutral descriptions of pastimes and casual hobbies (such as singing or cooking) were also included to improve authenticity. The second half of each vignette consisted of a 'third-hand' account describing the target individual's relationship and sexual

competences and experience, e.g. a description of how good their previous partner thought they were in bed, or whether they ‘enjoyed physical intimacy.’ One of the competencies described in all the vignettes was the target individual’s kissing abilities, which acted as the primary independent variable. The exact same four vignettes were presented to every participant, with half of the participants randomly assigned to see vignette 1 and 4 altered to say the target individual was a ‘good kisser’ and vignettes 2 and 3 altered to say the individual was a ‘bad kisser’, and the other half of the participants presented with the same vignettes stating the opposite about their kissing abilities, with vignettes 1 and 4 describing the target individual’s kissing skills negatively and vignettes 2 and 3 describing them positively. The comparison of responses between participants seeing the same vignettes describe a target individual as either a ‘bad’ or ‘good’ kisser formed the variable of interest, i.e. the kissing condition. Examples of all the vignettes used (for the male sex) are included in Appendix C (p. 262).

Upon being presented with a vignette, each participant was asked four questions about the person described in the vignette (the target individual), including: *‘How ‘attractive’ do you find this person?’*; *‘How interested would you be in going on a date with this person?’*; *‘How interested would you be in having a casual, one-off sexual encounter with this person?’*; and *‘How interested would you be in pursuing a committed, long-term relationship with this person?’* Responses were collected using 5-point Likert-type scales ranging from 1 = ‘Not at all,’ to 5 = ‘Extremely’. Participants in relationships were asked to imagine they were single for the purposes of answering these questions⁴.

The second half of the questionnaire asked various demographic questions (about sex, age, education, ethnicity and nationality), as well as questions asking individuals to rate their own attractiveness. Because self-ratings of attractiveness have previously been found to correlate highly with both other-rated judgements of attractiveness and with behaviours related to mating

⁴ Multivariate analysis confirmed that there were no significant differences in mean answers to these four questions between single participants and participants in a relationship ($F(4, 719) = 1.87, p = .114$).

aspirations (Kavanagh et al., 2010; Roberts & Little, 2008), self-rated attractiveness was used as a proxy measure for real-world mate value. All questions used in this survey are included in Appendix C (p. 262).

Statistical Analyses

The study involved asking every participant four questions about each of the four vignettes they read, with the effects of purported kissing quality analysed using multilevel modelling techniques. Multilevel modelling was most appropriate in this context because it allowed interpretable aggregate ratings of attractiveness/mate-desirability despite multiple measures being taken for each participant and the non-independence of these ratings within each participant. Furthermore, multilevel models are also robust to the presence of missing data, allowing for greater utilisation of the data in each analysis. Mixed Linear Models (MLM) were created to run these analyses, with participant ratings of the different vignettes treated as random factors (with random slopes and intercepts) in each model. Each MLM model also had two predictor variables included as fixed factors – kissing condition and participant sex. The predictor variable of participants mate value (as estimated by their self-rated attractiveness) was included in each model as a fixed covariate. Each MLM included tests for main fixed effects of every predictor variable, as well as two-way and three-way interactions between the main predictor variable of interest (kissing condition) and all other fixed factors. In these models, answers to the rating questions for each target vignette were the Level 1 units of analysis, with participants acting as the Level 2 units of analysis. All analyses were carried out in SPSS (version 22.0, SPSS Inc., 2013).

Mate value scores were attained in this study by averaging responses to the questions *'How do you think other people would rate you on physical attractiveness?'* and *'How do you think other people would rate you on sexual attractiveness?'*, with this mean score then further grand mean centred for inclusion in the MLM analyses as a covariate of interest.

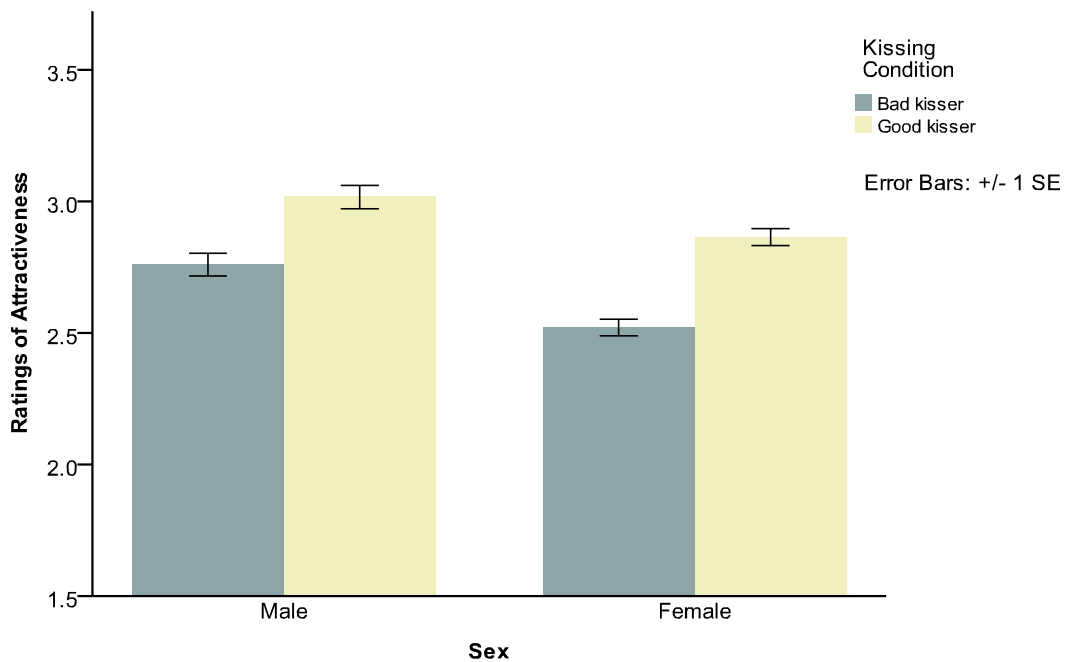
Results

Effects of Purported Kissing Quality on Ratings of Attractiveness

For the question *'How attractive do you find this person?'* significant main effects were found for kissing condition, $F(1, 2159) = 69.34, p < .001$, sex, $F(1, 720) = 15.44, p < .001$, with no main effect for mate value, $F(1, 720) = 2.41, p = .121$, and with no significant two-way or three-way interaction effects present between kissing condition and other predictors (all $F_s < 1.49, p_s > .226$).

This analysis indicated that participants who were informed that someone who was described as good at kissing rated them as more attractive ($M = 2.94, SE = 0.03$) than someone bad at kissing ($M = 2.64, SE = 0.03$), and that males generally rated all target individuals more attractive ($M = 2.64, SE = 0.03$), and that males generally rated all target individuals more attractive ($M = 2.88, SE = 0.04$) than females ($M = 2.70, SE = 0.03$) (see Figure 13).

Figure 13. Effect of sex and kissing condition on ratings of partner attractiveness

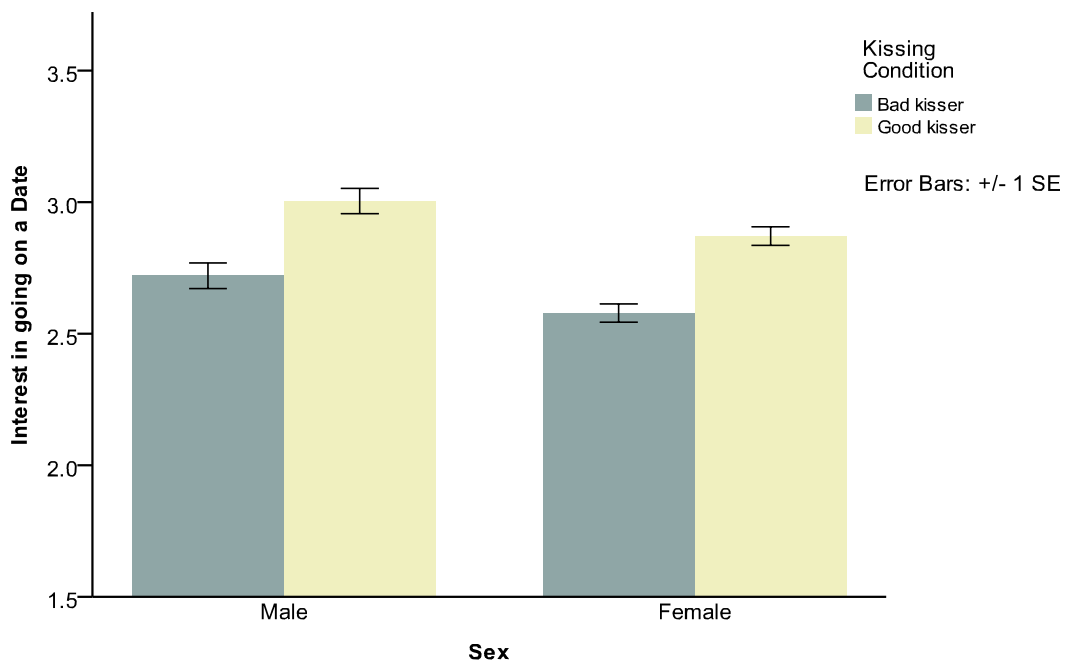


Effects of Purported Kissing Quality on Interest in Going on a Date

For the question *'How interested would you be in going on a date with this person?'*, significant main effects were found for kissing condition, $F(1, 2153) = 57.70, p < .001$, and sex, $F(1, 720) = 5.14, p = .024$, with no main effect found for mate value, $F(1, 719) = 2.34, p = .135$, and with no significant two-way or three-way interaction effects present between kissing condition and other predictors (all $F_s < 1.49, p_s > .222$).

This analysis indicated that participants who were informed that someone was good at kissing were more likely to want to go on a date with them ($M = 2.94, SE = 0.03$) than someone bad at kissing ($M = 2.65, SE = 0.03$), and that males were generally more likely to want to go on a date with all target individuals ($M = 2.85, SE = 0.05$) than females ($M = 2.73, SE = 0.03$) (see Figure 14).

Figure 14. Effect of sex and kissing condition on interest in going on a date

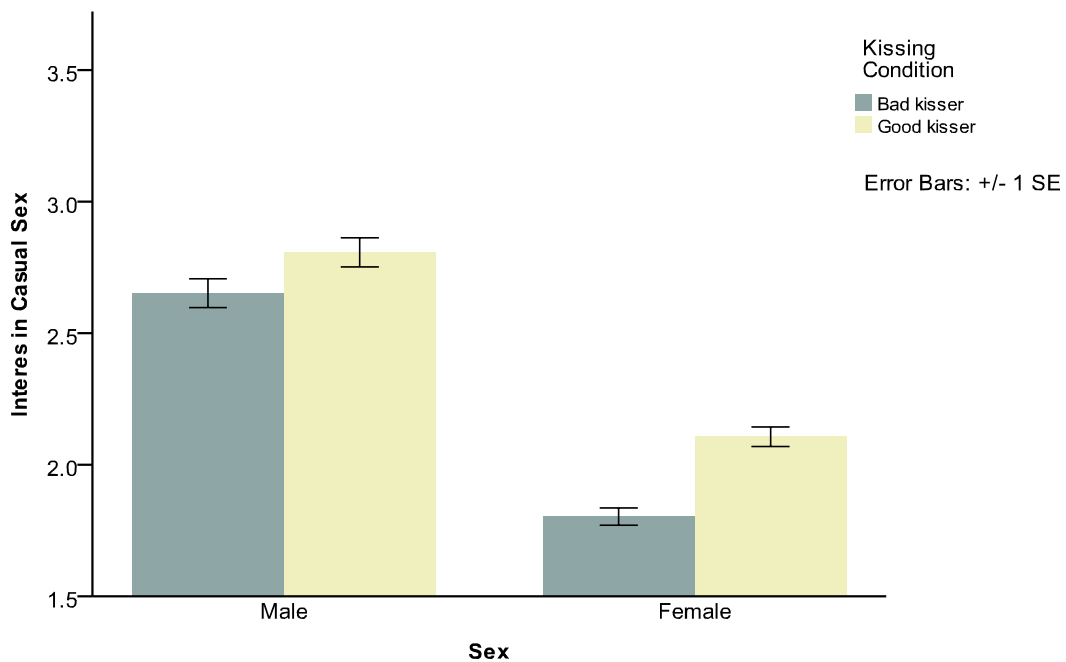


Effects of Purported Kissing Quality on Interest in Engaging in Casual Sex

For the question *'How interested would you be in having a casual, one-off sexual encounter with this person?'* main effects were found for kissing condition, $F(1, 2155) = 36.46, p < .001$, sex, $F(1, 720) = 152.32, p < .001$, and mate value, $F(1, 720) = 9.60, p = .002$, with a significant interaction effect found between kissing condition and sex, $F(1, 2154) = 4.26, p = .039$, with no other interaction effects found to be significant (all F s $< 1.53, p$ s $> .216$).

When asked about interest in casual sex, these results indicated that: participants told a target individual was a good kisser were more interested in having a casual sexual encounter ($M = 2.45, SE = 0.04$) than when a target individual was described as a bad kisser ($M = 2.34, SE = 0.04$); males were more willing to have casual sex ($M = 2.75, SE = 0.05$) with target individuals than females ($M = 1.94, SE = 0.04$); and that the higher the mate value of participants the more interested they were in pursuing casual sex (*slope parameter* $\beta = 0.11, SE = 0.04$). Post-hoc MLM analyses of the two-way interaction effect suggested that while kissing had a significant effect on interest in casual sex amongst males (bad kisser $M = 2.65, SE = 0.07$, good kisser $M = 2.81, SE = 0.07, F(1, 728) = 7.05, p = .008$), among females this effect was more pronounced (bad kisser $M = 1.80, SE = 0.04$, good kisser $M = 2.11, SE = 0.04, F(1, 1436) = 56.32, p < .001$) (see Figure 15).

Figure 15. Effect of sex and kissing condition on interest in casual sex

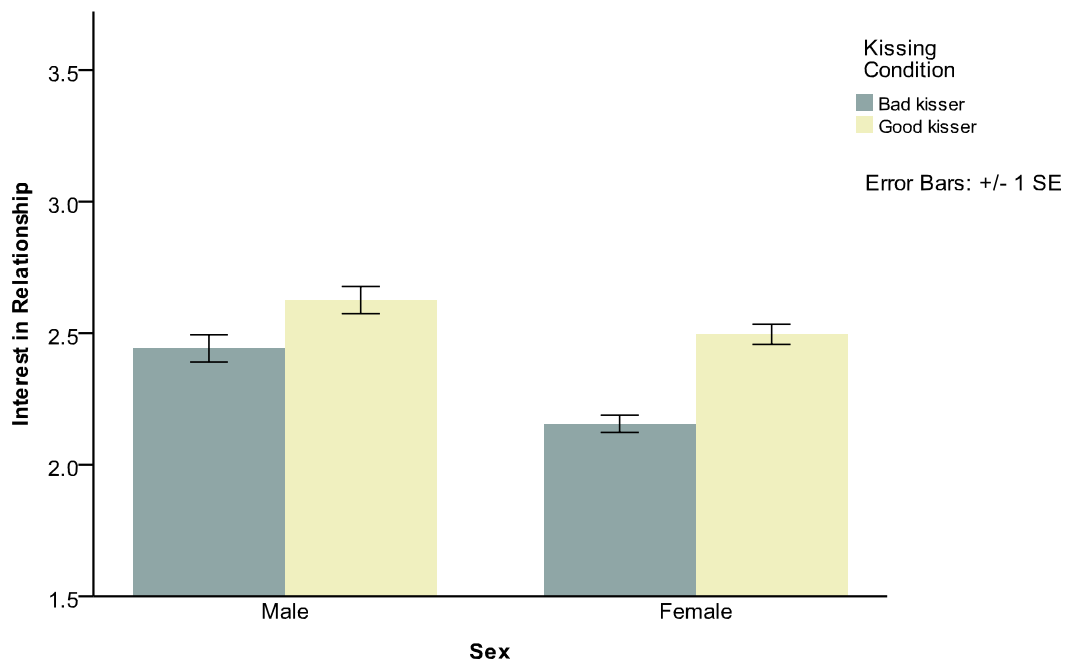


Effects of Purported Kissing Quality on Willingness to Pursue a Long-term Relationship

For the question 'How interested would you be in pursuing a committed, long-term relationship with this person?' main effects were found for kissing condition, $F(1, 2153) = 41.93, p < .001$, sex, $F(1, 722) = 10.76, p = .001$, and mate value, $F(1, 722) = 6.24, p = .013$, with no significant interaction effects found (all F s $< 3.38, p$ s $> .066$).

When answering questions relating to willingness to pursue a long-term relationship, it was found that: participants informed that a target individual was a good kisser were more interested in having a long-term relationship with them ($M = 2.55, SE = 0.03$) than with target individuals described as a bad kissers ($M = 2.91, SE = 0.03$); males were generally more willing to pursue a relationship with all target individuals ($M = 2.51, SE = 0.05$) than females ($M = 2.33, SE = 0.03$) (see Figure 16); and that the higher the mate value of a participant the less likely they were to wish to pursue a relationship (*slope parameter* $\beta = -0.05, SE = 0.03$).

Figure 16. Effect of kissing condition and sex on interest in pursuing a relationship



Discussion

This results of this study suggest that participants led to believe that a target individual was a ‘good kisser’ rated them as more attractive, and were more willing to go on a date with them, to have casual sex with them and to pursue a committed relationship with them than if they were led to believe that the same individual was a ‘bad kisser’. The effect of kissing ability on mate desirability was significantly more pronounced among females than among males, but only when rating willingness to pursue a casual sex encounter. It was also found that participants high in mate value were less interested in a romantic relationship, but more interested in casual sex, with a target individual.

These findings support those of the previous studies in this thesis, which showed that kissing seems to play a role in mate assessment, with purported kissing abilities of a potential partner affecting their attractiveness and desirability for different mating situations, including for

courtship (dating), casual sex, and long-term relationship contexts. On its own, this result may merely reflect the fact that any domain-general trait rated as 'good' might positively affect overall mate desirability. However, once this result is examined in light of its interaction with sex, the unique role of kissing becomes clearer. It was found that the positive impact of purported 'kissing quality' on a participant's willingness to have casual sex with a target individual was significantly greater for females than it was for males – suggesting that females are particularly influenced by kissing-related informational cues. When examined in light of previous findings that females are the more selective sex during the mate assessment process, and are particularly attuned to and discriminating about, cues signalling genetic fitness (Candolin, 2003; Grammer et al., 2000; Kenrick et al., 1990), this result is highly suggestive of the conclusion that kissing conveys pertinent mate suitability information.

These findings also provide some support for research on attitudes towards romantic kissing that suggests it is involved in the process of pair-bonding. The previous experiments in this thesis suggest that females generally place greater importance on romantic kissing across most romantic partner interactions, where it can either convey information regarding mate suitability, as well as in the mediation of established long-term attachment bonds. Similar suggestions are made by the interaction effect trend in the current data when it came to assessing mates for long-term relationship contexts, where kissing quality seemed to have a greater effect on females than males – suggesting that kissing is also be useful in long-term relationship situations. However this trend did not reach statistical significance levels (interaction effect $p = .066$), and therefore is only suggestive at this point. These trends were not seen when merely judging general mate attractiveness or showing interest in pursuing a 'date', situations which have less immediate fitness consequences than casual sex or a long-term relationship (either in the form of pregnancy resulting from casual sex, or the significant time/effort investments of a relationship). This suggests that kissing information may be particularly pertinent for mating situations with

immediate fitness outcomes, perhaps due to the fact that engaging in romantic kissing is not without risks – it can expose relative strangers to numerous potential infection hazards (e.g. Cowan et al., 2002; Schoch-Spana, 1992; Tully et al., 2006).

The current study also found that males were more likely across the board to find descriptions of target individuals more attractive, were more willing to date them, much more willing to have casual sex with them, and more willing to pursue a relationship with them. This result is in line with previous observations that the smaller minimal parental investment burden shouldered by males favours short-term mating strategies involving the pursuit of a much broader range of potential mating partners (Buss & Schmitt, 1993; Candolin, 2003; Grammer et al., 2000; Schmitt, 2003). That females are the more discerning sex when it comes to partner choice was most clearly highlighted by their much lower willingness to pursue casual sexual encounters as compared to males, the one situation which carries the highest immediate risk of incurring parental burden, a burden which might be considerably more onerous if choice of mating partner is poor.

Mate value also plays a role in the evaluation of potential romantic partners. Participants of higher mate value, i.e. those who rated themselves as more attractive, were found to be less interested in pursuing a romantic relationship with a potential partner, although they were more interested in pursuing casual sex. This variation in mate desirability among participants with differing mate values may be explained by the theory that mate choice exists in the context of a wider 'biological marketplace,' where individuals who are in high demand, and are cognisant of the fact that they are in high demand, can generally afford to be more selective when choosing potential mates (Noe & Hammerstein, 1994; Pawlowski & Dunbar, 1999). In this case, high mate value individuals were less likely to wish to pursue long-term relationships with any of the target individuals described in the vignettes, perhaps because they can afford to be selective about with whom they wish make such significant mating investments. Furthermore, attractive males and females have been previously found to be more promiscuous in their mating strategies (e.g. Little

et al., 2001; Perilloux et al., 2013; Rammsayer & Troche, 2013), preferring casual sexual encounters to long-term relationship situations – these differences explain why higher mate value participants displayed greater interest in pursuing casual sex with target individuals. This study did not find that high mate value participants were differentially influenced by purported partner kissing abilities as compared to low mate value participants.

It must be noted, however, that one potential limitation of this study is the lack of a true control condition. It is still possible that any ‘positive’ descriptive trait might have influenced participant ratings of mate desirability, with kissing abilities having no unique effect. While attempts were made to overcome this limitation with the use and analysis of various interaction effects, it remains a possible confounding factor. Future research may attempt to overcome this limitation by exploring the unique contributions that kissing abilities might make to mate desirability, over and above other desirable traits such as ‘cooking ability,’ or as compared to other kissing-related and functionally relevant cues such as body odour.

The primary findings of this study suggest that purported kissing abilities influence a potential mate’s attractiveness and general desirability as a mating partner, particularly for females when rating willingness to pursue a short-term (or potentially long-term) partner interaction. While previous research on attitudes towards romantic kissing has been conducted using self-report measures (i.e. the previous studies in this chapter, and Hughes et al., 2007), this study is the first to use an experimental design in an attempt to measure whether romantic kissing might convey salient information which can be utilised in the process of assessing mates.

4.4 Study 2b – The Influence of Kissing on Mate Choice in the Presence of Visual Information⁵

Introduction

Because kissing is just one of many cues that are used when assessing the value of potential mates, it is likely that the effects of kissing may be influenced by the presence of other mate cue information. Humans are a primarily visual species (Levin, 1993), and although past research suggests that there is multi-modal interplay between the senses when it comes to mate assessment, it is visual cues which are oftentimes prioritised over other senses (Foster, 2008; Kovacs et al., 2004; Saxton et al., 2008). Because of this, it seems likely that in the presence of both kissing-related informational cues and traditional visual cues, visual cues may take precedence when it comes to making assessments about a potential mate. Furthermore, as research shows that males are neurologically more responsive to visual sexual stimuli than females (Hamann, Herman, Nolan, & Wallen, 2004), sex differences are likely to exist in the relative value placed on visual cues of attractiveness as compared to other cues, such as mate cue-information inherent in romantic kissing.

Aims

Because kissing is just one of many cues used in the complex assessment of potential mate suitability, this study aimed to examine whether the effects of kissing-based mate quality information might be mediated by the presence of visual cues of mate quality. In this follow-up study, a smaller sample of participants were presented with the same kissing vignettes as in Study 2a, although this time accompanied by visual mate information (i.e. a profile picture).

⁵ The results of this study have been published as the following peer-reviewed journal article: Wlodarski, R., & Dunbar, R. I. M. (2014). What's in a Kiss? The Effect of Romantic Kissing on Mate Desirability. *Evolutionary Psychology*, 12(1), 178-199.

It was predicted that kissing information would generally be less effective at influencing mate assessments when placed alongside visual mate information, which is the dominant sensory modality in humans. Furthermore, it was predicted that males would be more influenced by the presence of visual mate cues than females, due to their greater levels of responsivity to visual mate information.

Methods

Participant recruitment was the same as for Study 2a, and was approved by Oxford University's Research Ethics Committee. A total of 178 participants completed the survey, including 64 males and 114 females (aged 18 to 63, $M = 23.9$, $SD = 7.4$). Participants predominantly self-identified as Caucasian/white (80.3%), with 4.5% identifying as South Asian and 3.4% as Latino. The sample was mostly made up of British (51.7%), North American (26.4%), and Western European (5.6%) nationals. High school education was completed by 98.9% of participants, with 44.4% having attained a Diploma or some college experience. Slightly more than half of the participants (57.9%) stated that they were in a relationship at the time of the survey⁶.

Questionnaire Design

The design of the questionnaire in this study was identical to that Study 2a, with the exception that participants were also shown four different 'headshot' images of hypothetical mating partners (target individuals), one image paired with each of the four vignettes. The images consisted of life-like composite photos (corrected to appear 'realistic') of faces that had been previously rated as either highly attractive (two photos) or unattractive (two photos) (used with permission from: Braun, Gründl, Marberger, & Scherber, 2001; Jones et al., 2010). The design ensured that each participant viewed two vignettes with partners described as bad kissers, one

⁶ Multivariate tests showed that there were no significant differences between single participants and participants in a relationship on answers to questions about partner desirability ($F(4, 173) = 2.78, p = .063$).

vignette partnered with an attractive photo and one with an unattractive photo, and two vignettes rating partners as good kissers, one with an attractive photo, and one with an unattractive photo.

Participants were again asked four questions about the target individuals based on both their vignette description and photo, including *'How "attractive" do you find this person?'* *'How interested would you be in going on a date with this person?'* *'How interested would you be in having a casual, one-off sexual encounter with this person?'* and *'How interested would you be in pursuing a committed, long-term relationship with this person?'* Responses were collected using a 5-point Likert-type scale ranging from 1 = 'not at all,' to 5 = 'extremely'.

Statistical Analyses

The same Mixed Linear Model analyses were carried out as in Study 2a, with the addition of 'partner attractiveness' as a fixed factor, both as a main effect and as an interaction effect with the other predictor variables in each model.

Results

Effects of Purported Kissing Quality on Ratings of Attractiveness

For the question *'How attractive do you find this person?'* significant main effects were found for attractiveness of picture presented only, $F(1, 534) = 230.37, p < .001$, with no main effects for kissing condition, $F(1, 534) = 1.18, p = .279$, sex, $F(1, 178) = 0.90, p = .345$, or mate value, $F(1, 178) = 2.76, p = .098$. Significant two-way interactions were found between kissing condition and mate value $F(1, 534) = 6.24, p = .013$, and between sex and picture attractiveness $F(1, 534) = 39.73, p < .001$, with no other two- or three- way interactions (all F s $< 2.16, p$ s $> .143$).

This analysis indicated, not surprisingly, that target individuals with more attractive pictures were rated as generally much more attractive (attractive picture $M = 2.89, SE = 0.06$, unattractive

picture $M = 1.90$, $SE = 0.06$). Post-hoc analyses on the first interaction effect suggested that for target individuals described in vignettes as bad kissers, higher mate value participants were less likely to find them attractive (*slope parameter* $\beta = -.13$, $SE = .04$, $t(356) = -3.01$, $p = .003$), whereas for target individuals with vignettes describing them as good kissers mate value had no effect on attractiveness ratings (*slope parameter* $\beta < -.01$, $SE = .05$, $t(356) = 0.06$, $p = .950$). Post-hoc analyses of the second interaction suggests that while males rated target individuals with the attractive picture as much more attractive ($M = 3.16$, $SE = 0.09$) than target individuals with the unattractive picture ($M = 1.77$, $SE = 0.09$), $F(1, 191) = 203.34$, $p < .001$, among females this difference was smaller (attractive picture $M = 2.64$, $SE = 0.07$, unattractive picture $M = 2.05$, $SE = 0.07$, $F(1, 341) = 52.09$, $p < .001$) (see Figure 17a).

Effects of Purported Kissing Quality on Willingness to go on a Date

For the question *'How interested would you be in going on a date with this person?'* significant main effects were found for attractiveness of picture only, $F(1, 533) = 61.43$, $p < .001$, with no main effects for kissing condition, $F(1, 534) = 2.55$, $p = .111$, sex, $F(1, 178) = 0.91$, $p = .342$, or mate value, $F(1, 178) = 3.38$, $p = .068$. Significant two-way interactions were found between sex and picture attractiveness $F(1, 533) = 26.46$, $p < .001$, with no other two-way or three-way interactions present (all F s < 3.54 , p s $> .061$).

This analysis again indicated that when presented with descriptions of target individuals alongside attractive pictures participants were generally more willing to go on a date with those individuals (attractive picture $M = 2.68$, $SE = 0.06$, unattractive picture $M = 2.11$, $SE = 0.06$). Post-hoc analyses of the interaction effect showed that while males were more willing to go on a date with target individuals represented by attractive pictures ($M = 2.93$, $SE = 0.10$) than unattractive pictures ($M = 2.01$, $SE = 0.10$), $F(1, 191) = 60.71$, $p < .001$, among females this difference was

much smaller (attractive picture $M = 2.44$, $SE = 0.07$, unattractive picture $M = 2.23$, $SE = 0.07$, $F(1, 340) = 5.68$, $p = .018$) (see Figure 17b).

Effects of Purported Kissing Quality on Willingness to Engage in Casual Sex

For the question *'How interested would you be in having a casual, one-off sexual encounter with this person?'* main effects were found for kissing condition, $F(1, 532) = 4.55$, $p = .033$, sex, $F(1, 178) = 32.90$, $p < 0.001$, and picture attractiveness, $F(1, 532) = 137.22$, $p < .001$, with no main effect of mate value, $F(1, 178) = 1.83$, $p = .178$. A significant interaction was found between sex and picture attractiveness, $F(1, 532) = 44.97$, $p < .001$, with no other interactions reaching statistical significance (all F s < 2.89 , p s $> .149$).

These results indicate that when asked about casual sex: participants informed that a target individual was a good kisser were more interested in having a casual sexual encounter with them ($M = 2.06$, $SE = 0.07$) than when a target individual was described as a bad kisser ($M = 1.92$, $SE = 0.07$); males were generally much more willing to have casual sex with all target individuals ($M = 2.32$, $SE = 0.09$) than females ($M = 1.63$, $SE = 0.07$); and all participants were more likely to wish to pursue casual sex with a target individual represented by an attractive picture than an unattractive picture (attractive picture $M = 2.36$, $SE = 0.07$, unattractive picture $M = 1.62$, $SE = 0.07$). Post-hoc analyses of the interaction suggests that while males were more willing to have sex with a target partner represented by an attractive picture ($M = 2.91$, $SE = 0.12$) than an unattractive picture ($M = 1.75$, $SE = 0.12$), $F(1, 191) = 107.19$, $p < .001$, among females this difference was much smaller (attractive picture $M = 1.80$, $SE = 0.07$, unattractive picture $M = 1.50$, $SE = 0.07$, $F(1, 340) = 18.11$, $p = .001$) (see Figure 17c).

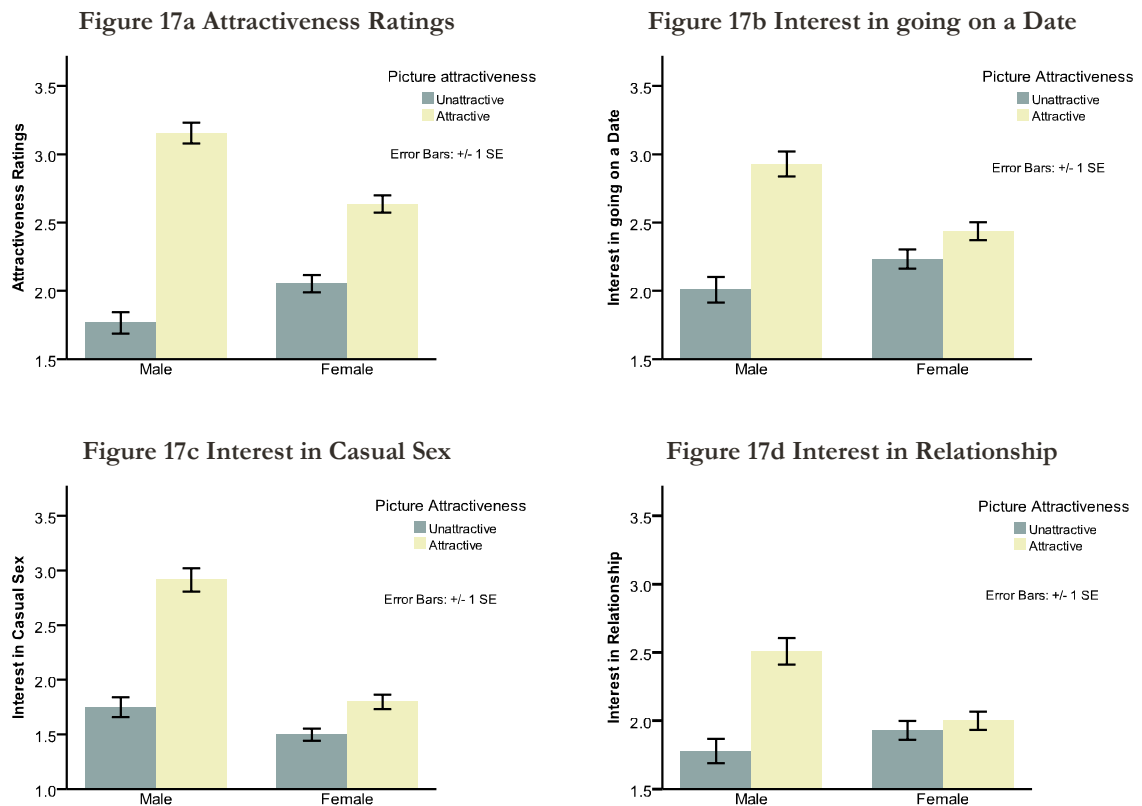
Effects of Purported Kissing Quality on Willingness to Pursue a Long-term Relationship

For the question *'How interested would you be in pursuing a committed, long-term relationship with this person?'* main effects were found for kissing condition, $F(1, 530) = 6.65$, $p = .010$, picture

attractiveness, $F(1, 179) = 30.28, p < .001$, and mate value, $F(1, 178) = 9.14, p = .003$, with no main effect for sex, $F(1, 178) = 1.26, p = .264$. A significant interaction was found between sex and picture attractiveness, $F(1, 530) = 20.33, p < .001$, no other interaction effects were present (all F s $< 2.68, p$ s $> .102$).

When answering questions relating to willingness to pursue a long-term relationship, it was found that: participants informed that a target individual was a good kisser were more interested in having a long-term relationship with them ($M = 2.14, SE = 0.06$) than with target individuals described as a bad kisser ($M = 1.96, SE = 0.06$); participants were more likely to wish to pursue a relationship with a target individual described using attractive pictures ($M = 2.25, SE = 0.06$) than unattractive pictures ($M = 1.85, SE = 0.06$); and that the higher the mate value of participants the less likely they were to wish to pursue a relationship (*slope parameter* $\beta = -0.10, SE = 0.08$). Post-hoc analyses of the interaction effect suggested that males were more willing to pursue a relationship with target individuals with attractive pictures ($M = 2.51, SE = 0.10$) than with unattractive pictures ($M = 1.78, SE = 0.10$), $F(1, 190) = 39.31, p < .001$, while among females there was no significant difference in willingness to pursue a relationship between attractive and unattractive photo target individuals (attractive picture $M = 2.00, SE = 0.08$, unattractive picture $M = 1.93, SE = 0.08, F(1, 340) = 0.77, p = .380$) (see Figure 17d).

Figure 17. Interaction effects of sex and picture attractiveness on ratings of partner attractiveness, willingness to go on a date, interest in casual sex, and interest in relationship



Discussion

The results from Study 2b show that while the presence of visual information alongside a descriptive vignette eliminated the effect of kissing-related mate information on ratings of partner attractiveness and interest in going on a date with that partner, the presence of visual cues did not alter the positive effect of kissing quality information on partner desirability for casual sexual encounters or long-term relationships. Not surprisingly, participants presented with attractive pictures of hypothetical target individuals rated them as more attractive and were more willing to go on a date, pursue casual sex or a committed relationship with them. In all cases, however, this

effect was mediated by sex – with attractive visual information having a much greater effect on male ratings of partner desirability than on female ratings.

These findings highlight the conflicting roles that different mate cues might play in the process of selecting a mate. That the presence of visual information interferes with kissing-related mate information, though only in certain mate selection situations, suggests that a nuanced interplay exists between these two cues. When it came to assessing target individuals on relatively noncommittal mate assessment criteria, such as rating their attractiveness or stating willingness to go on a ‘date,’ participants seemed to rely exclusively on visual information. However, when target individuals were assessed in light of potentially more ‘costly’ mating situations of pursuing casual sex or a relationship, where the consequences of poor mate choice can be more immediate and severe, then kissing-related information managed to significantly affect partner assessment even in the presence of typically dominant visual cues. This suggests that kissing might convey salient information about a potential mate, about either their genetic fitness/compatibility, or their long-term relationship potential, which is at least as important as information that can be garnered from visual cues. This finding mirrors past research suggesting a complex multi-modal cue interplay whereby people take into account, and prioritise, certain cues depending on the mating context that they find themselves in (Foster, 2008; Kovacs et al., 2004; Saxton et al., 2008).

Another explanation for these finding revolves around the series of stages which seem to make up mating and pair-bonding processes, which increase in ‘intimacy’ from initial attraction, to mating, and finally the formation of pair-bond attachments (Grammer, 1989). As less intimate stages of the process are likely to be more highly dependent on visual cues than those of other modalities (which require more physical proximity), individuals may be more reliant on such cues in early pair-bonding process stages (such as rating attractiveness or merely expressing interest in ‘dating’). As pair-bonding processes advance to becoming more intimate, involving sexual intercourse or relationship formation, other mate cues utilising modalities that depend on these

greater levels of physical proximity and intimacy become more salient in making further mate appraisals and informing mating decisions. It is only at these later stages of the process that kissing becomes practical as a mate assessment and bond-mediation tool.

Results from Study 2b also suggest that males and females react differently to picture attractiveness, with males rating potential partners much more positively on all criteria in the presence of an attractive picture than females, clearly showing that males are more influenced by picture attractiveness than females. This finding is in line with a large body of past research, which finds that males in general tend to prioritise cues of physical attractiveness and fecundity in potential partners more than females (Buss, 1989; Townsend & Wassermann, 1998; Waynforth & Dunbar, 1995). Furthermore, males also show higher physiological responses to visual sexual stimuli than females (Hamann et al., 2004), thus further explaining the greater influence of visual cues on mate decisions found in this study. It is interesting to note that while visual cues still had some effect on female ratings of attractiveness and willingness to pursue a date or casual sex, they did not affect female ratings of interest in pursuing a relationship. This is may be because females place greater value than males on mate cues signalling long-term parental investment potential (Bjorklund & Shackelford, 1999; Buss, 1989; Shackelford et al., 2005), which might be more difficult, though not impossible (e.g. Waynforth, Delwadia, & Camm, 2005), to assess from basic morphological visual information alone.

Lastly, while mate value did not have any significant main effects in the presence of partner pictures (although a main effect for interest in dating came close to significance), it was found that high mate value participants rated potential partners as less attractive if they were also rated as a bad kisser. As mentioned previously, this result may demonstrate the increased levels of selectivity displayed by high mate value participants, who can afford to be more selective and discount potential mates who are less desirable as assessed on kissing-related criteria.

4.5 General Discussion

Research to date on romantic kissing has relied solely on self-report attitudinal data when examining this subject, and suffers from a lack of theory or evidence linking any biological substrates that might be affecting its expression and use. The aim of the three studies presented in this chapter was to address these limitations, to extend our knowledge of the exact role played by kissing plays in the process of mate assessment, and to establish a link between the use of kissing in romantic relationships and potential biological mediators, namely menstrual cycle hormones.

Although the mechanism by which romantic kissing aids the assessment of potential mates can only be alluded to as this stage (see also ‘General Discussion’ section of the previous chapter, p. 100), the first study in this chapter on menstrual cycle effects provides further support for the idea that olfactory process may be the key. The results of this study are suggestive of the idea that ‘smell of breath,’ and to a lesser extent ‘scent of body’ and ‘taste of lips,’ are important factors in romantic kissing, varying in importance across the menstrual cycle alongside kissing importance. Regression analyses on a PCA component combining these three factors showed trends towards their contribution to kissing quality and towards being related to fluctuations in levels of progesterone. It has been hypothesised that information relating to mate suitability and health may be conveyed by human breath – research has found that halitosis, or ‘bad breath,’ can signal ill-health or disease in another individual and semiochemicals in saliva and may convey genetic information regarding MHC compatibility (Durham et al., 1993; Nicholson, 1984; Wobst et al., 1999). Furthermore, it is known that various forms of mate quality and compatibility information can also be garnered from auxiliary pheromonal cues (see also ‘Olfaction in Mate Assessment’ p. 22 for more details). These results suggest that further research into the role of pheromonal cues exchanged during romantic kissing encounters may prove to be a fruitful avenue for further research.

The primary findings of the second two studies was that purported kissing abilities influence a potential mate's attractiveness and general desirability, particularly for females in casual sex situations. While the original study presented in Chapter 3 examined attitudes towards romantic kissing using self-report measures, this study is the first time that an experimental design was used in an attempt to measure whether romantic kissing conveys salient information that is then utilised in the process of mate assessment. It was also found that while the presentation of visual information alongside kissing information negated the effect of kissing on relatively innocuous commitments to 'dating' a potential partner or merely finding them attractive, information gleaned from purported kissing ability affected partner desirability for more reproductively important decisions such as casual sex or pursuing a long-term relationship. These results suggest that non-visual mate cues, such as the kinds of olfactory cues that might be assessed during romantic kissing, play an important role in this involved process – particularly at more intimate stages of the pair-bonding process. As olfaction is an important and evolutionarily conserved mode of mate assessment across mammal taxa (Clutton-Brock & McAuliffe, 2009), the possibility also exists that this sense may also be a reliable form of mate assessment in humans, providing additional mate information to that which can be gleaned from visual cues alone. This the first time that the relative roles of kissing-based and classical visual mate information have been examined in the literature, and contribute to our understanding of the interplay between these two modalities. These results highlight the need to take into account the type of mate assessment being made by an individual, i.e. merely rating attractiveness versus rating desirability for long-term relationships, as these differing mating interactions seem to rely differentially on different mate cues.

Regardless of the mechanism by which kissing works, it seems to form an important part of the human reproductive repertoire. The assumption that kissing serves an adaptive purpose in the process of human mating implies that it is likely to have an association to some kind of biological

underpinnings. This research demonstrated a link to such a potential biological mediator, namely the menstrual cycle related hormone progesterone. This novel finding suggests that kissing behaviours are in turn vulnerable to the pressures and processes of evolution and natural selection, which act on the biological underpinnings of behaviour with a hereditary component. This result is an important step in establishing the potentially adaptive role kissing plays in the process of human mating.

Lastly, these results also add to our understanding of the interplay between mate value and sociosexuality. While individuals with unrestricted sociosexuality preferentially pursue multiple short-term mating situations (see also ‘The Construct of Sociosexuality,’ p. 43), it was found here that unrestricted individuals who also have higher mate value, and are known to be more selective (see also ‘Within-sex Variation in Sociosexual Orientations’ p. 46), are less likely to pursue relationship involving some kind of longer-term investment (i.e. dating or long-term relationships). This suggests that low mate value participants, who cannot afford to be highly selective, are more likely to pursue long-term mating situations, perhaps to improve their chances of overall mating success in spite of their lower levels of mate desirability. This insight into the relationship between mate value and mating strategies highlights a more complex interplay between these variables than is sometimes acknowledged in the literature (as discussed in Chapter 2).

4.6 Chapter Summary and Outlook

This chapter built upon the initial findings of Chapter 3 on the role of romantic kissing in processes of pair-bonding by looking at this custom in the context of mate assessment and pair-bond attachments. It was shown here that the use of romantic kissing may be related to a biological substrate, namely menstrual cycle hormone progesterone, and that olfactory cues seem to play an important role in kissing interactions. It was also found that kissing abilities influence a potential mate’s attractiveness and general desirability as a mating partner, particularly for

females when rating willingness to pursue a short- or long-term partner interaction, and that assessments based on kissing quality can affect mate desirability even in the presence of typically dominant visual cues when making certain mate assessment decisions. While previous research on attitudes towards romantic kissing has been conducted using self-report measures (i.e. the previous studies in this chapter, and Hughes et al., 2007), the two studies presented in this chapter are the first to use an experimental design in an attempt to measure whether romantic kissing conveys any salient information which is then utilised in the process of mate assessment.

The following chapter focuses on the direct process of forming and maintaining pair-bonded attachments with a long-term partner. The aim that chapter is to examine the ways in which pair-bonding associated cognitions might function to initiate and maintain attachment between individuals within the context of an established pair-bonded relationship. In particular, a purported link between love-induced neuronal inhibitions and apparently adaptive cognitive outcomes is explored in an attempt to shed light on some of cognitive processes mediating human pair-bonding.

Chapter 5 – The Effects of ‘Romantic Love’ on Cognition

5.1 Introduction

Once a mating strategy has been established, and selection criteria preferentially exercised to select an appropriate partner, the final processes of establishing pair-bond attachments can be initiated. The creation and maintenance of pair-bonds is not necessarily desired and pursued by all mating individuals, but can be preferentially pursued by those practicing long-term mating strategies or in situations where such pair-bond formation enhances reproductive success. Mating pair-bonds, sometimes commonly referred to ‘romantic love’ in humans, are thought to form a motivational system which directs mating interest towards one specific partner, creating intense emotional attachment bonds between two individuals (H. E. Fisher, 1989; Mellen, 1981). Such bonds facilitate the co-ordination of interests and behaviours of mating individuals long enough to successfully rear offspring under the auspices of bi-parental investment and care (*ibid.*). This motivational and attachment system, in turn, is thought to be driven by unique underlying substrates which share biological roots with other mammals who also display pair-bonding behaviour as part of their mating process (H. E. Fisher, 1998). Research into pair-bonding in humans has implicated a role for various neurotransmitters, peptides and hormones, including dopamine, serotonin, oxytocin and vasopressin as well as testosterone, and the involvement of numerous brain centres, including dopaminergic reward-mediating and emotion regulating regions (Esch & Stefano, 2005; L. J. Young et al., 2005).

This final chapter of the thesis examines one specific aspect of established human pair-bonds – namely their purported effects on cognition. As was found in previous chapters of this thesis looking at early processes leading up the establishment of pair-bonds, various mating behaviours seem to play an adaptive role throughout this process, behaviours often mediated by various biological substrates. Pair-bonding is also thought to be related to a unique set of physiological

drivers, which mediate these intense bonds, affecting behaviours that directly further affect the process of bond formation. This chapter sets out to examine how some of the neurological processes which have been previously associated with pair-bonding might affect cognitions, cognitions which, as has been previously hypothesised, might explain commonly observed behaviours associated with individuals who are in a state of romantic love (Zeki, 2007).

The chapter begins by reviewing the current body of literature examining the neural correlates of romantic love using contemporary neuroimaging techniques. Using fMRI to examine Blood-Oxygen-Level Dependent (BOLD) signals, a proxy measure for underlying neuronal activity, past research looking at human pair-bonding has found a consistent set of activations among participants who are ‘in love’ in dopaminergic and reward and emotion processing centres of the brain, including the various parts of the caudate, the ventral tegmental area (VTA), putamen, insula, and the anterior cingulate cortex (e.g. Bartels & Zeki, 2000; H. E. Fisher, Aron, & Brown, 2005). Such activations have been found in some instances to also correlate with the ‘intensity’ of love felt by a participant for their partner, have been found to be present during implicit presentation of love stimuli, have considerable overlap with activations seen in mother-infant attachments, and appear to be present to varying degrees throughout the life of pair-bonded relationships (e.g. Acevedo, Aron, Fisher, & Brown, 2012; Aron et al., 2005; Bartels & Zeki, 2004). Most interestingly, several studies have also reported consistent instances of brain ‘deactivations,’ or a reduction in BOLD signals, in specific brain areas among individuals who are in love. These reductions in brain activity have been typically found to occur in regions such as the amygdala, dorsolateral and medial prefrontal cortex, parietal and middle temporal cortex, the temporal pole, temporoparietal junction and the posterior cingulate gyrus (e.g. Bartels & Zeki, 2000; Xu et al., 2011). It has been hypothesized that such deactivations represent an inhibition of neuronal activity in these particular areas, and that such inhibitions in individuals who are in love may affect cognitions which rely on the activation of these deactivated areas (namely

mentalizing, processing of negative emotions and cognitive self-control) (Zeki, 2007). It is believed that if observed deactivations can adversely affect cognition in this way, then various stereotypical love-related behaviours might be explained by this process, including observations that ‘love is blind’ or irrational, it can reduce levels of fear, and can involve obsessive, uncontrollable thoughts about a loved one (ibid.).

As the predictions arising from this research have never been empirically tested, in this chapter a study was designed to determine whether such brain deactivations actually have any adverse effects on cognitions that rely on these deactivated regions. A controlled experimental study was carried out, following as closely as possible the methodology of previous fMRI studies where these brain deactivations were first observed to take place. Ninety-one participants who were ‘truly, madly, deeply in love’ with their current romantic partner were presented with either a love stimulus or a neutral stimulus (a picture of their partner or a match-controlled friend) and were asked to complete two short cognitive tasks immediately following the presentation of each prime. The cognitive tasks included: assessing the emotional states of others, a component mechanism of theory of mind associated with the temporal poles, temporoparietal junction and medial prefrontal cortex; the attribution of negative emotional states to others, associated with the amygdala; and cognitive self-control, as measured by an incongruent word/color Stroop task and previously associated with the dorsolateral prefrontal cortex region. The consequences of this study’s findings are discussed in terms of their impact on our understanding of the nature of BOLD signal ‘deactivations,’ the use of control/baseline comparison tasks during fMRI, and both neurological and behavioural sex differences in human pair-bonding.

5.2 Literature Review – Neuroimaging the Brain in Love

The intense emotions and cognitions associated with pair-bonding, or the state of ‘romantic love,’ are considered to be a human universal (Dunbar, 2012; Gottschall & Nordlund, 2006; Jankowiak

& Fischer, 1992), with a distinct set of biological substrates thought to underlie these processes in humans. Furthermore, as discussed in Chapter 1 (see 'Pair-bonding in Humans' p. 31), this set of cognitions and motivations most likely exists to serve an important function in the context of human mating, namely the facilitation of long-term attachments which aid the successful rearing to maturity of altricial human offspring (H. E. Fisher, 1989; Fraley, Brumbaugh, & Marks, 2005; Gangestad & Simpson, 2000; Kleiman, 1977).

Love in an fMRI Scanner

In order to try and determine whether a set of common neural correlates might underlie processes of pair-bonding, commonly referred to as 'romantic love', researchers have recently turned to in-vivo brain imaging of individuals who are already in established pair-bonds and who profess to be 'deeply' in love with their mating partner. It is thought that by examining patterns of brain activations which are related to love cognitions, insights might be gained not only into the underlying physiological substrates associated with this phenomenon, but also into the nature of the motivations and cognitions which are uniquely associated with human pair-bonding, as opposed to other kinds of social attachments.

The most common technique used in research on romantic love thus far utilises fMRI technology to approximate regional brain activations by examining Blood-Oxygen-Level Dependent (BOLD) responses in the brain that occur while an individual is presented with a stimuli of their love interest. While the BOLD signal detected during fMRI does not directly show the activations of neurons in a given area, it is thought to approximate neuronal activity by showing changes in blood oxygen flow as it acts to replenish oxygen depleted by the firing of nearby neurons, in a process known as the hemodynamic response. Although it is generally agreed that the BOLD signal is representative of many aspects of nearby neuronal activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001), it is still an imperfect surrogate signal, which can also be affected

by several extraneous physiological variables not directly related to local neuronal activity (for an overview see Arthurs & Boniface, 2002).

Brain Region Activations in Individuals who are 'Deeply in Love'

Numerous fMRI studies carried out over the past 14 years have revealed what appears to be a unique pattern of brain activations among individuals who profess to be in various stages of 'love' with their mating partners (for reviews see Diamond & Dickenson, 2012; Ortigue, Bianchi-Demicheli, Patel, Frum, & Lewis, 2010). The typical methodology of such studies involves recruiting participants who self-identify as being in love with their romantic partner, assessing the 'intensity' of their love using either interviews or questionnaires, and examining the patterns of brain responses within these individuals when they are presented with a stimulus of their love one (either pictures, names or video of their love interest) as compared to activations to a baseline/neutral stimulus condition. The baseline or neutral stimulus comprise of stimuli which are as closely matched to the love stimuli as possible, often involving another individual who is of the same sex, age, and has been known for the same amount of time as the love interest.

The first neuroimaging study to look at this phenomenon selectively recruited 17 participants (six male) who self-identified as being 'truly, deeply, and madly in love' with their partner, assessed their levels of love using the Passionate Love Scale (PLS, Hatfield & Sprecher, 1986), and compared fMRI responses when looking at a colour picture of their loved one to when looking at pictures of control-matched friends (Bartels & Zeki, 2000). This study found that over the time participants were looking at pictures of a loved one (~17 sec) as compared to a friend, activity was greater in the dopaminergic regions of the brain such as the caudate nucleus and putamen, as well as in regions related to reward processing, emotion regulation, and sensory integration, areas which included the insula and anterior cingulate cortex.

Since this original attempt to examine neural activations associated with romantic love, many successive imaging studies have since explored various different aspects of the same topic. A study conducted a few years later, using very similar methodology but looking at pre-determined regions of the brain (using ROI rather than whole brain analyses) found similar activations in sub-cortical dopaminergic brain regions, particularly the ventral tegmental area (VTA), dorsal caudate body, and caudate tail. (Aron et al., 2005; H. E. Fisher et al., 2005). This study additionally looked for, but did not find, sex differences in love-stimuli induced brain activations, while also utilising participants' scores on the Passionate Love Scale (PLS) to show that some of these activations (such as in the caudate) correlated with the self-reported answers on this scale – suggesting a dose-response relationship between 'intensity' of love and love-induced activations in some brain regions.

Another study on 36 female participants, this time using an implicit love stimulus (the subliminal presentation of the partner's name), again implicated subcortical dopaminergic reward areas, as well as emotion and mental association area (caudate nucleus, insula, VTA, thalamus, anterior cingulate gyrus) (Ortigue, Bianchi-Demicheli, Hamilton, & Grafton, 2007). This study also found that such implicit passionate love stimuli uniquely activated regions associated with social cognition, self-representation, and implicit mental representations. Meanwhile, follow-up research to the original Bartels and Zeki (2000) imaging study looking at differences at brain activation between heterosexual and homosexual participants who were in love found the same love-typical activations patterns as before, with no significant differences between individuals of different sexual orientations, while also not finding any differences in activations between the sexes (Zeki & Romaya, 2010).

Change in Love-related Activations over the Length of a Pair-bonded Relationship

In an attempt to look at temporal changes in love-related brain activations over the duration of a pair-bonded relationship, researchers have looked at how fMRI activations and self-report ratings of love intensity (again using a PLS scale) changed over the course of six months within participants who had initially been in love for less than three months (Kim et al., 2009). This research found that while self-ratings of love had decreased only slightly over a six-month period, initial brain activations in the caudate were significantly reduced over this time and activations in cortical regions, such as the cingulate gyrus, increased – suggesting that the nature of romantic love pair-bonds might change over time as relationships develop. Similarly, another experiment which also compared activations at initial stages of romantic love (Xu et al., 2011) to activations 40 months later (Xu et al., 2012) in a Chinese sample, again found the typical pattern of reward-centre activations in early stages of love, but also showed that reduced levels of initial activations in certain forebrain reward areas were predictive of lower relationship satisfaction and of relationship dissolution at the 40-month follow-up period. Research looking exclusively into the relationships of individuals who have been in long-term romantic love pair-bonds (average marriage length 21.4 years) has found similar activations as those of early-stage romantic love in the dopamine-rich reward areas and the basal ganglia system, as well as in areas previously associated with maternal love (Acevedo et al., 2012).

It must be noted, however, that fMRI imaging can have surprisingly poor temporal reliability (Bennett & Miller, 2014). Because of this, any observed within-subject activation changes over time may be in part reflective of limitations in image acquisition and analysis of neuroimaging data.

Scanning other Types of Love

In order to determine whether romantic pair-bonds are unique in their neurological underpinnings or may be related to other forms of close interpersonal attachments, several studies have also examined neural activations associated with other types of 'love.' Bartels and Zeki (2004) compared their original study on romantic love to a follow-up experiment they conducted on maternal love, i.e. the love of a mother for her infant child. Looking at 20 mothers and repeating the methodology of their earlier study (using pictures of the love object, i.e. the child, as a stimulus), they found that much of the maternal love related brain activity overlapped with romantic love, with the exception of extra activation found in the periaqueductal (central) grey matter (PAG) among mothers. A similar study on maternal love, using video stimuli of the love object this time, found corroborating evidence for the unique role of the PAG in maternal love, as well as observing the typical love-related activations in emotion and reward-related areas of the brain (Noriuchi, Kikuchi, & Senoo, 2008). The PAG has high levels of oxytocin and vasopressin receptor sites, has been previously associated with pain suppression (particularly during intense physical and emotional experiences such as child-birth), and is strongly associated with maternal behaviour in rats (Lonstein & Stern, 1998).

The Rewards of Love

Many of the regions found to be active in these studies on love lie in dopaminergic areas that form the brain's reward system, particularly the ventral tegmentum (VTA), dorsal caudate body, and caudate tail. The actions of the neurotransmitter dopamine in these regions have been linked to the motivational state of 'wanting,' with these brain areas further associated with the expectation of rewards, desire, addiction, euphoria and goal-directed behaviours (McClure, York, & Montague, 2004; O'Doherty, 2004; Schultz, 2002). This research suggests that, rather than being a distinct 'emotional' trait, romantic love is in fact based on neural systems associated with motivation to pursue a rewarding experience, which in this case may be the company and physical

intimacy of a romantic partner. Areas such as the VTA also happen to be rich in both oxytocin and vasopressin receptors, neuropeptides which have been linked to monogamous mating behaviour in prairie voles (Carter, 1992; Insel, 1992) and which are thought to mediate both mother-infant and romantic pair-bonds (Diamond, 2004; Donaldson & Young, 2008; Kendrick, 2004; E. E. Nelson & Panksepp, 1998; Porges, 1998; L. J. Young & Wang, 2004) (see also ‘The Biological Roots of ‘Romantic Love’, p. 32).

Limitations of Comparing fMRI Research on Love

Although the studies carried out thus far on romantic love and related neural activations show considerable overlap in their findings, some differences in results do exist. Such differences likely arise from the difficulties inherent in attempting to make general cross-study comparisons when it comes to research of this nature. The first major issue arises with differences in methodologies used across studies. The studies discussed above all used varying types of ‘love’ stimuli (still pictures, videos, subliminal presentation of names, thinking thoughts about the loved one, etc.) presented at varying exposure lengths, some studies used different comparison conditions for assessing BOLD activations (control-matched friend, stranger, blank screen), and only a few studies used distractor tasks between stimuli presentations in an effort to reduce carryover cognition effects. Furthermore, the most obvious difficulty in comparing these studies lies in the nature of the different subject populations recruited. As subjects were asked to decide their own suitability for partaking in this research, based on whether they considered themselves to be ‘in love,’ there was likely considerable self-selection bias and wide variation between participants in each of the studies, bias which makes it difficult to be able to make true cross-study comparisons. While several studies attempted to account for some of these biases, for example by assessing intensity of love felt by participants using self-report measures, or taking into account relationship length, and then seeing how these co-varied with observed BOLD signal activations (e.g. Aron

et al., 2005), not all studies managed to a significant dose-response relationship (e.g. Zeki & Romaya, 2010).

Furthermore, seeing as some studies have found that romantic love induced activations change considerably over the course of a relationship (e.g. Kim et al., 2009), the recruitment of subjects with widely varying relationship lengths across the different studies surveyed above, and not taking this into account during analyses, increases the difficulty of making any direct comparisons between them. Again, issues of fMRI result reliability may further complicate attempts at direct cross-study comparison (Bennett & Miller, 2014). However, considering the fact that even with all these limitations a large amount of overlap in activations induced by a love stimulus between many of these studies was still found, it appears that that the concept of romantic love comprising of key shared neural correlates warrants some merit.

Brain 'Deactivations' when in Love?

Alongside the many cortical region BOLD signal increases that have been observed in past research among individuals in love, many studies in this area have also observed some interesting BOLD signal decreases. Such decreases in signal during the presentation of a love stimulus, as compared to during the presentation of either a neutral or a baseline stimulus, have been referred to as cortical 'deactivations.' The very first study in this area of research was also the first to describe widespread deactivations in distinct brain regions when viewing a picture of a loved one, particularly in the areas of right prefrontal, parietal, and middle temporal cortex, as well as the posterior cingulate gyrus, medial pre-frontal (including dorsolateral) cortex and posterior amygdaloid region (Bartels & Zeki, 2000). The same researchers found remarkably similar deactivations in their follow-up study looking at maternal love (middle and medial [dorsolateral] prefrontal cortices, the parietotemporal junction, the temporal poles and the posterior cingulate

gyrus and the amygdaloid region) (Bartels & Zeki, 2004), and almost the same deactivations again in heterosexual and homosexual participants (Zeki & Romaya, 2010).

Other studies have also found patterns of deactivation during love stimulus presentations similar to these initial observations, though not always as extensive in nature. Research has variously found significant deactivation in the right amygdala and medial prefrontal cortex (Aron et al., 2005; Xu et al., 2011), in bilateral amygdala regions and the right accumbens and medial prefrontal cortex (Xu et al., 2011), and in the right accumbens and middle prefrontal cortex (Acevedo et al., 2012). One study looking at temporal changes in activation patterns among individuals in love even found that greater levels of deactivation in the right accumbens and medial prefrontal cortex at earlier stages of a relationship were predictive of relationship survival and happiness at later stages (Xu et al., 2012).

Some of the regions that have been found to show decreased BOLD signal have previously been found to be responsible for various forms of cognition that may be relevant to the creation and maintenance of pair-bond attachments. The amygdala, for example, is typically more active during recognition of faces, in response to novel stimuli, and when mediating a variety of emotion (Gobbini & Haxby, 2007; Kosaka et al., 2003; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Shin & Liberzon, 2010; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008). The amygdala has also consistently been found to activate in studies of social judgement, and has been found to be closely related to assessing negative emotions such as fear and anxiety (Adolphs, Tranel, & Damasio, 1998; J. S. Morris et al., 1996).

Meanwhile, the set of regions comprising of the temporal pole, temporoparietal junction and the medial prefrontal cortex has been frequently associated with cognitive processes involved in 'mentalizing' (Apperly, 2012; Critchley et al., 2000; Frith & Frith, 2003; H. L. Gallagher & Frith, 2003; Saxe, 2006). Mentalizing, or 'theory of mind', is the ability to attribute mental states to others, and is considered essential to the formation and maintenance of complex social

relationships (Apperly, 2012; Kovács, Téglás, & Endress, 2010). These regions are responsible for various mentalizing-related cognitive tasks, including the assessment of emotional states and social trustworthiness of others (Critchley et al., 2000).

Finally, the medial and middle regions of the prefrontal cortex, which are also deactivated in individuals in love, have been associated with various types of executive functioning, including moral judgment, critical assessment and regulation of intellectual functions such as self-control, inhibition of instinctual responses, and deception and lying (Kartan & Bachmann, 2011; MacDonald, Cohen, Stenger, & Carter, 2000; Zeki, 2007). More specifically, within this region the dorsolateral prefrontal cortex is often associated with the implementation of cognitive control, and has been found to be active during activities such as the incongruent word/colour Stroop task, where individuals are asked to state the colour a word is presented in while ignoring the incongruent colour that the word spells out and is instinctively processed first (MacDonald et al., 2000; Stroop, 1935).

What do these Deactivations Mean?

It has been hypothesized that if deactivation of these regions represents an actual decrease in underlying regional neuronal activity, then cognitions relying on these same regions might be adversely affected in individuals who are in love when presented with a love stimulus (Bartels & Zeki, 2000; Esch & Stefano, 2005; Zeki & Romaya, 2010; Zeki, 2007). It has even been suggested that various casually observed love-typical behaviours, such as suspension of critical judgement, or a reduced ability to critically assess a lover's intentions or character (i.e. the perception that 'love is blind' or irrational), reduced levels of fear when in love, and intrusive thoughts about a love-interest that are difficult to control, might actually be the result of such brain deactivations (ibid.). These behaviours, in turn, while not necessarily adaptive under normal circumstances,

may exist to aid the initial establishment of mating pair-bonds, reducing inhibitions, and increasing motivations to pursue contact with new mating partners.

It is important to note, however, that the true nature of ‘deactivations’, or negative BOLD responses, and their relationship to neuronal activity remain poorly understood. It is generally believed, and some evidence supports the notion, that deactivations likely represent the direct inhibition of neuronal activity in the affected area, in non-task-relevant brain areas for example (Saad, Ropella, Cox, & DeYoe, 2001; Shmuel et al., 2002; Shmuel, Augath, Oeltermann, & Logothetis, 2006). However, other explanations for these observed decreases in BOLD signal have also been proposed. It has been suggested, and supported by some experimental evidence, that these decreases may be merely a hemodynamic response to the increases in cerebral blood flow of adjacent areas (‘vascular steal’), and thus may have little correspondence with actual inhibitions of local neuronal activity (Becerra et al., 2011; Devor et al., 2005; Harel, Lee, Nagaoka, Kim, & Kim, 2002; Kannurpatti & Biswal, 2004; Tomasi, Ernst, Caparelli, & Chang, 2006; Wade, 2002). It remains to be seen, therefore, whether deactivations induced by exposure to a love prime can affect any actual cognitions and behaviours that might rely on the function of such deactivated brain areas.

5.3 Aims

The discovery of deactivations in specific brain regions among individuals who are ‘in love’ as a result of being presented with a love stimulus has led to some interesting speculation. It has been proposed that if such deactivations are related to decreases in underlying neuronal activity in these areas, then these activity decreases may affect an individual’s ability to carry out cognitive functions and behaviours relying on these areas. The brain regions that have been found to show deactivation have been previously associated with cognitive tasks such as mentalizing, assessing emotional (particularly negative) stimuli, and executive function tasks including exerting cognitive

control. However, to date such conjectures remain untested. If we are to understand the relationship between these observed pair-bonding-related neuronal patterns and cognitive/behaviour outcomes, it is imperative that the proposed link between this biological activity and actual real-world cognition is clarified. Such clarification would help us understand the nature of pair-bond formation in humans, and the cognitive processes involved in the mediation of pair-bond creation and maintenance.

This study was motivated by this gap in our understanding of the effects of love-induced BOLD signal reductions on related cognitive processes. The aim of this study, therefore, was to examine the effect of a love stimulus (a love prime) on cognitions associated with the very same brain regions which have previously been found to deactivate in individuals who are ‘in love.’ The cognitions and brain areas explored here include: the attribution of emotional states to others (a component mechanism of theory of mind), associated with the temporal poles, temporoparietal junction and medial prefrontal cortex; the attribution of *negative* emotional states to others, also associated closely with the amygdala; and cognitive self-control as measured by an incongruent word/color Stroop task, previously associated with the dorsolateral prefrontal cortex. Although past research had not found any sex differences in love induced activations (Zeki & Romaya, 2010), the fact that females display enhanced performance on mentalizing tasks and the attribution of emotions states (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Stiller & Dunbar, 2007) suggests that the role of sex must be taken into account. It was predicted that if previously observed deactivations arise from regional neuronal inhibitions which can adversely affect cognitions relying on the same regions, then individuals would perform worse on region-related cognitive tasks following a love prime than following a neutral prime.

5.4 Methods

Participants

Participants were recruited from students and staff of the University of Oxford using posters and e-mail mailing lists. The recruitment materials advertised for participants who considered themselves ‘truly, madly, deeply in love’ with their current romantic partner (as per Bartels & Zeki, 2000) for an experiment on love and cognition, for which they were remunerated for their time. The research was approved by the University of Oxford Ethics Committee, with all participants providing informed consent to participate in the research. All data provided was completely confidential and results were anonymized.

In total, 102 participants completed the study; however, 11 participants were excluded from the analysis because their self-appraised English skill level and understanding was below ‘very good’.

⁷ Of the remaining 91 participants, 23 were male and 63 were female, aged 18 to 51 ($M = 23.4$, $SD = 4.5$), with 49.5% being British Nationals, 17.6% North American, 9.9% Western European, and 8.8% Eastern European. Seven participants identified themselves as primarily homosexual and provided pictures of their same-sex partners for the love prime condition. These data were included in analysis since previous fMRI research had found no difference in brain region activations between heterosexual and homosexual individuals in love (Zeki & Romaya, 2010).

Procedure

Before arriving at the laboratory participants were asked to provide a digital colour photograph of their partner, as well as of a friend who was the same sex and age as their partner, and whom they have known for roughly the same amount of time.

⁷ It was observed that many of these participants had to consult the emotion word definition list throughout the RTM task, and are likely to have experienced reduced English word-color interference during the Stroop task.

Cognitive Tasks

All experimental instructions and materials were presented on a PC, with two computer-based measures of cognitive function used in this study: Reading the Mind in the Eyes task (RTM, Baron-Cohen et al., 2001) and the Stroop task (Stroop, 1935) (samples of each are included in Appendix D, p. 267). In the RTM task, participants observed a series of black and white photographs of cropped male and female eyes displaying a wide variety of emotions (36 total), including some negative emotions, and were asked to ascertain which emotion was being felt by each target set of eyes (choosing from among four possible options). The ability to attribute emotions and mental states to other individuals is a fundamental component of theory of mind (mentalizing), which is in turn associated with regions found to be previously deactivated during a love prime, namely the temporal poles, temporoparietal junction and the medial prefrontal cortex (for a review see Apperly, 2012). Furthermore, a sub-score of the RTM was also calculated for attributing emotions to ‘negative’ stimulus faces, since previous love-prime deactivations have also been observed in the amygdala – a region implicated in the judgement and recognition of fearful/negative emotions (e.g. J. S. Morris et al., 1996). The Stroop task involved a visual stimulus comprising of series of 20 words presented in a 5 x 4 table spelling out various colour names, but presented in non-matching colours (incongruent Stroop Task). Participants were tasked with saying the colour of each word aloud (rather than what the word spelled) as quickly as possible. Performing the word/colour Stroop task involves inhibiting the interference created by each word’s lexical content, and performance on this task has been strongly associated with one of the regions previously found to be deactivated during a love prime, namely the dorsolateral prefrontal cortex (MacDonald et al., 2000). The RTM and Stroop tasks were chosen for this study partly because of their association with the brain regions of interest, but also because they could each be completed relatively quickly following the presentation of a prime (i.e. within 60 seconds), falling in the relatively small 45-60 second post-prime window within which a love prime is thought to affect brain activity (Mashek, Aron, & Fisher, 2000).

Participants were previously provided with a list of definitions of all the emotion words that were to be used during the RTM task and were asked to familiarize themselves with them. Upon arrival at the laboratory, participants were given a short practice run of the tasks they were to perform (one RTM photograph and five words of the Stroop task) to ensure task understanding.

Love Prime and Neutral Prime

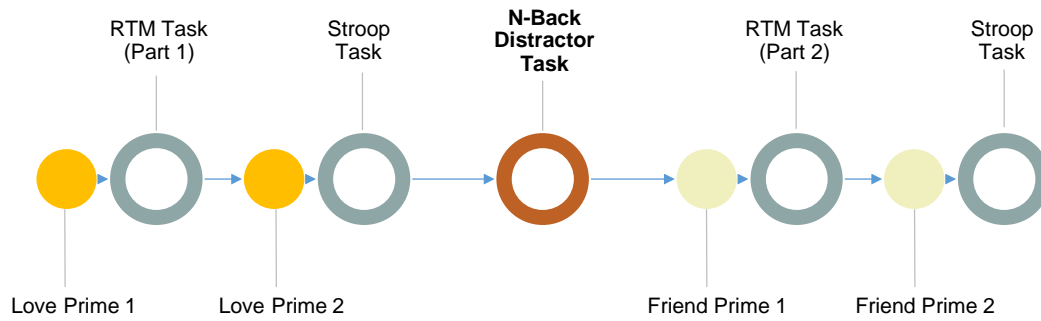
The love prime condition involved presenting participants with the picture and the name of their loved one for 45 seconds, while asking them to either ‘think about one of the very first times you met’ (prime 1) or to ‘think about the last pleasant (non-sexual) activity that you did together’ (prime 2) for 45 seconds. The neutral prime condition was the same as the love prime, except that the picture and name presented was that of the participant’s friend.

Experimental Procedure

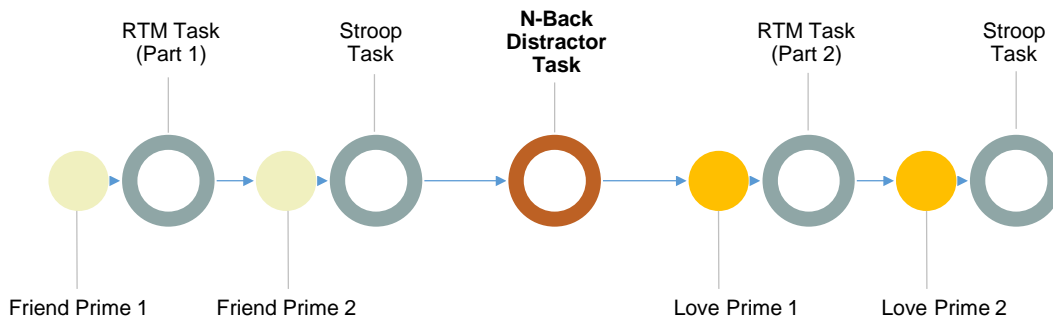
Each experimental session consisted of the two love primes, the first prime followed by half of the RTM task and the second prime by a 20-word incongruent Stroop task. Participants were then asked to complete a 2-3 minute cognitive distractor task consisting of a visual and auditory 2-back N-back task (Owen, McMillan, Laird, & Bullmore, 2005), after which time the two neutral primes were presented, the first prime followed by the second half of the RTM task and the second prime followed by a 20-word incongruent Stroop task. The order of love and neutral priming conditions was counterbalanced between participants (see Figure 18 for graphical depiction of experimental procedure).

Figure 18. Graphical depiction of experimental procedure

Procedure



Procedure (Counterbalanced)



Scoring of Dependent Variables

The first dependent variable, the RTM task, was scored as the proportion of emotions attributed correctly to each set of eyes following either a love prime or a neutral prime. Correct attribution of negative emotions only (i.e. despondent, distrustful) was used to create a separate negative emotion RTM sub-score, with correct attribution of the remainder of the emotions making up a neutral/positive RTM sub-score.

The second dependent variable, the incongruent Stroop task, was assessed by the total time taken to state aloud the colour of all 20 words, ignoring the incongruent colour that each of the words

spelt out. The total reaction time (RT) was automatically recorded using the PC-based presentation software. An experimenter was present in the room to confirm that each participant completed the task correctly by naming colours aloud.

Other Predictor Variables

To confirm that participant feelings towards their partner and their friend differed significantly, and to determine if love ‘intensity’ had an effect on the cognitive tasks assessed, participants rated both their romantic relationship and their friendship on both the Passionate Love Scale (PLS, Hatfield & Sprecher, 1986) and on the Other in Self scale (OIS, Aron & Aron, 1992), copies of which are included in Appendix D, p. 269. All analyses were carried out in SPSS (version 22.0, SPSS Inc., 2013).

5.5 Results

Partner versus Friend PLS and OIS Scores

Two separate 2 x 2 mixed-design ANOVAs were carried out on PLS and OIS scores, each ANOVA treating partner/friend PLS/OIS ratings as within-subject factors and sex as between-subject factors. All participants had significantly higher PLS score for partners ($M = 105.8$, $SD = 12.9$) than for friends ($M = 31.1$, $SD = 10.1$) ($F(1, 88) = 1951.12$, $p < .001$, partial $\eta^2 = .957$), with no sex effects ($F(1, 88) = 0.01$, $p = .947$, partial $\eta^2 < .001$) or interactions ($F(1, 88) = 0.02$, $p = .896$, partial $\eta^2 < .001$). Similarly, participants had significantly higher OIS scores for partners ($M = 5.3$, $SD = 1.3$) than for friends ($M = 2.1$, $SD = 1.3$) ($F(1, 89) = 374.64$, $p < .001$, partial $\eta^2 = .808$), with no sex ($F(1, 89) = 0.01$, $p = .949$, partial $\eta^2 < .001$) or interaction effects ($F(1, 89) = 0.14$, $p = .714$, partial $\eta^2 = .002$).

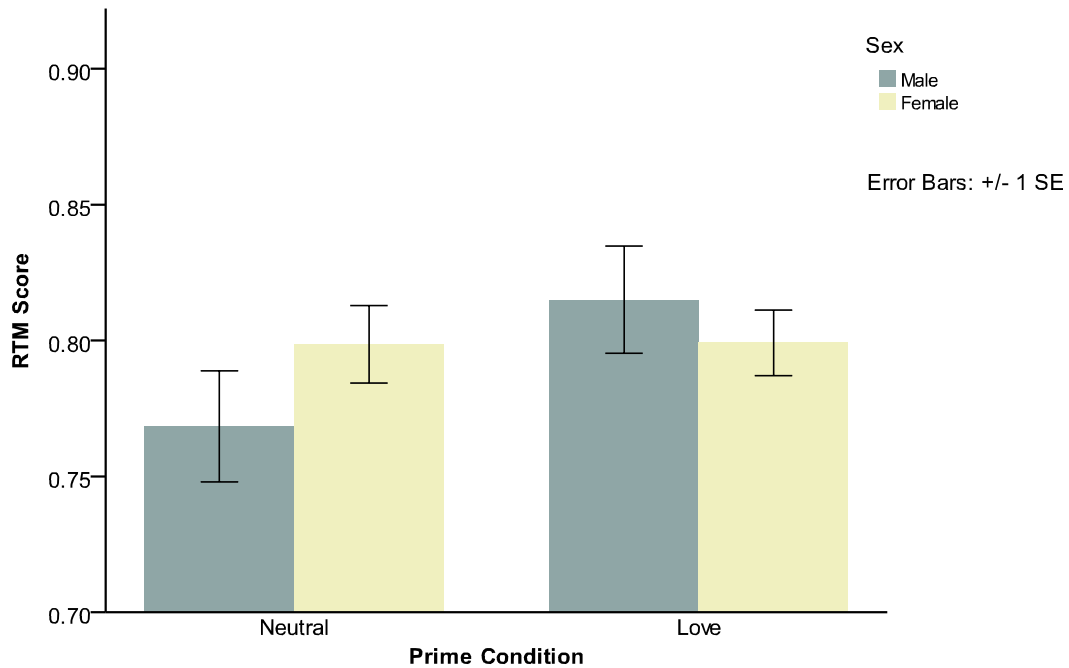
When male and female participants’ partner scores on the PLS and OIS were correlated with each participant’s RTM score differences following either a love prime or neutral prime, negative

emotion and positive/neutral emotion RTM subset scores differences, and their performance differences on the Stroop task following either a love or neutral prime, no significant correlations were found either before or after Bonferroni correction for multiple comparisons (all *Pearson's r*s < 0.13, all *p*s > .216).

Reading the Mind in the Eyes Task Scores following a Neutral and Love Prime

To determine whether performance on the Reading the Mind in the Eyes task differed following a love prime versus following a neutral prime, a 2 x 2 mixed design ANOVA was carried out with RTM score as the dependent variable, love/neutral prime condition as a within-subject factor, and sex as a between-subject factor. Overall, RTM scores were significantly higher after a love prime than after a neutral prime ($F(1, 89) = 4.46, p = .037, \text{partial } \eta^2 = .048$), and while there were no overall sex differences in RTM scores ($F(1, 89) = 0.087, p = .769, \text{partial } \eta^2 = .001$), there was a significant interaction between sex and prime condition ($F(1, 89) = 5.43, p = .022, \text{partial } \eta^2 = .057$). This interaction suggests that while female participants' RTM scores did not change following the love ($M = 0.81, SD = 0.10$) and following the neutral ($M = 0.81, SD = 0.11$) prime conditions, male participants' RTM scores were significantly higher following a love prime ($M = 0.83, SD = 0.09$) than following a neutral prime ($M = 0.77, SD = 0.11$) (Figure 19).

Figure 19. Mean RTM scores for male and female participants after neutral and love prime

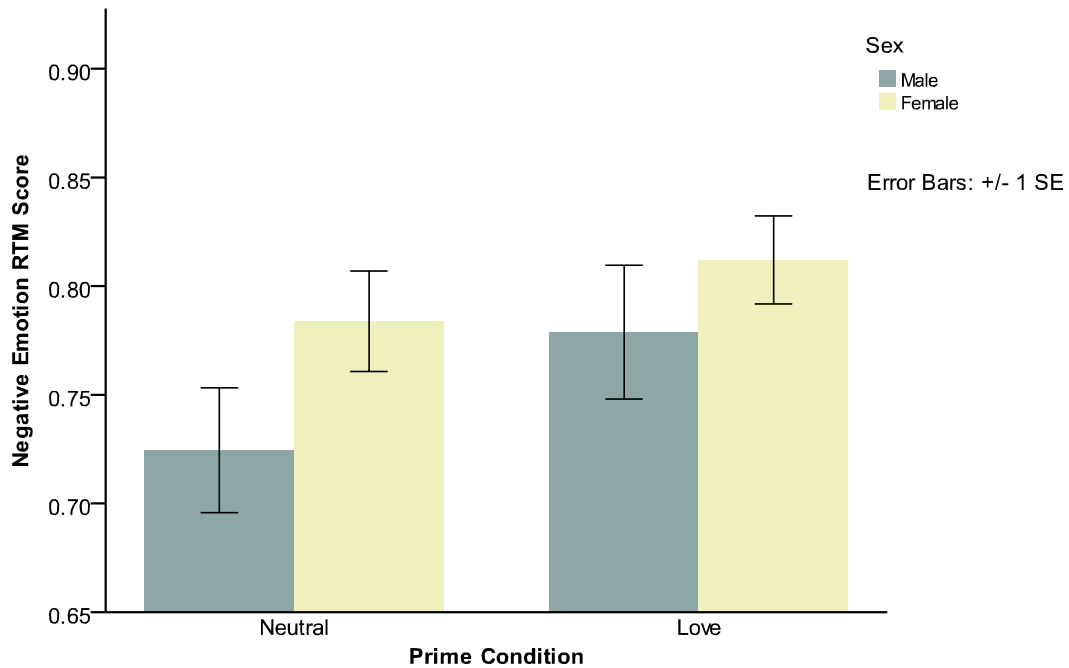


Reading the Mind in the Eyes Task Scores for Negative Emotions following a Neutral and Love

Prime

Analyses were also carried out on the sub-score of participants' RTM results which involved attributing emotion to faces displaying negative emotions only. A similar 2 x 2 mixed design ANOVA was carried out, with negative RTM sub-score as the dependent measure, love/neutral prime condition as a within-subject factor, and sex a between-subject factor. A significant main effect of prime condition ($F(1, 89) = 5.19, p = .025, \text{partial } \eta^2 = .055$) suggested that negative emotion RTM scores were higher overall after a love prime ($M = 0.82, SD = 0.17$) than after a neutral prime ($M = 0.77, SD = 0.19$), and a significant main effect for sex ($F(1, 89) = 4.24, p = .042, \text{partial } \eta^2 = .045$) found that female participants ($M = 0.81, SD = 0.13$) had higher overall negative emotion RTM scores than male participants ($M = 0.75, SD = 0.13$). No significant interaction effect was found ($F(1, 89) = 0.77, p = .383, \text{partial } \eta^2 = .009$) (Figure 20).

Figure 20. Mean negative emotion RTM scores for male and female participants after neutral and love prime

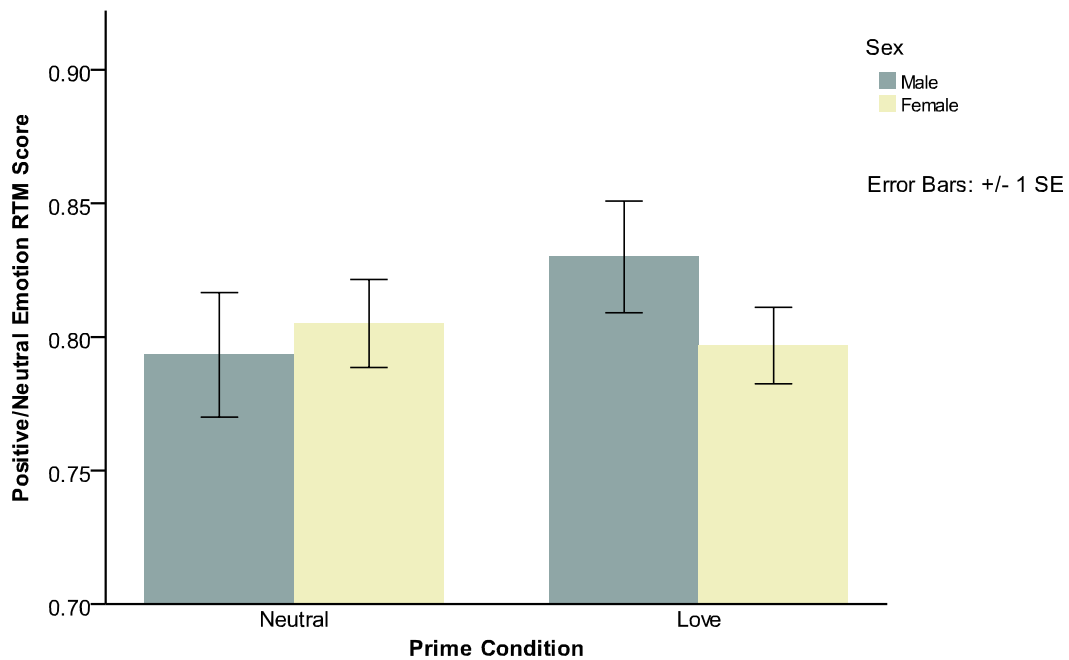


Reading the Mind in the Eyes Task Scores for Positive/Neutral Emotions following a Neutral and Love Prime

Analyses on a sub-score of participants' RTM scores involving attributing emotion to positive/neutral emotion faces only were run using the same 2 x 2 mixed ANOVA design, with positive/neutral RTM sub-score as the dependent measure, love/neutral prime condition as a within-subject factor, and sex a between-subject factor. No significant main effect for prime condition was found ($F(1, 89) = 0.63, p = .429, \text{partial } \eta^2 = .007$), or for sex ($F(1, 89) = 0.56, p = .455, \text{partial } \eta^2 = .006$), with the interaction effect just failing to reach significance ($F(1, 89) = 3.20, p = .077, \text{partial } \eta^2 = .035$). The trend behind the interaction effect suggested that while female scores on positive/neutral RTM task did not differ after a neutral prime ($M = 0.81, SD = 0.14$) or a love prime ($M = 0.80, SD = 0.13$), male scores may have improved somewhat following

a love prime ($M = 0.84, SD = 0.10$) compared to following a neutral prime ($M = 0.80, SD = 0.13$) (Figure 21).

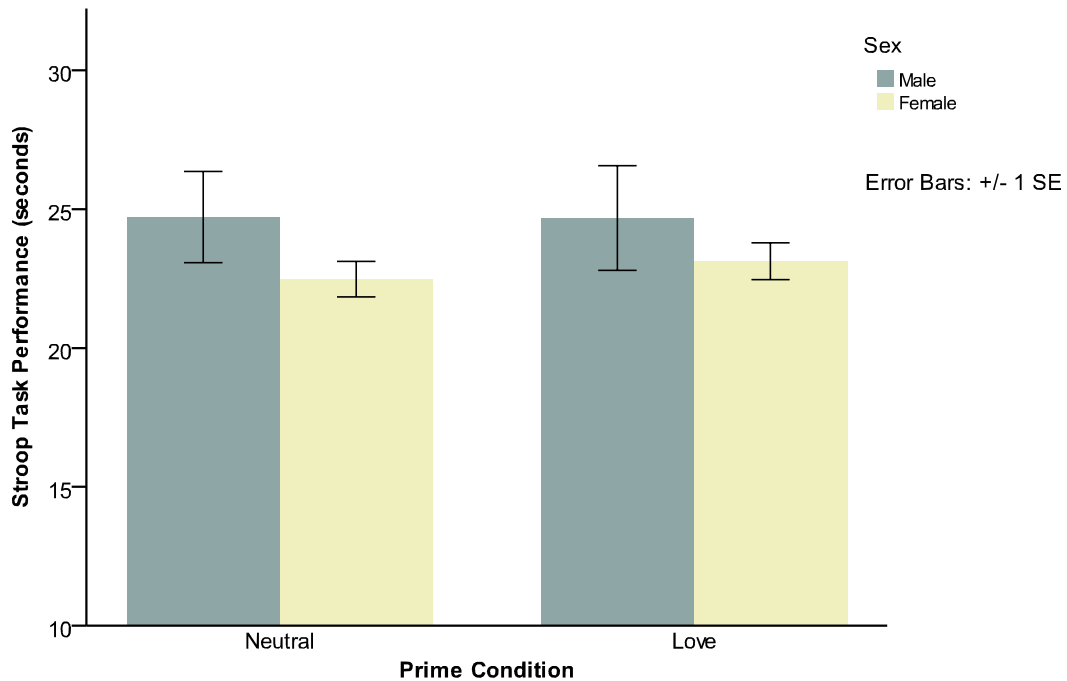
Figure 21. Mean positive/neutral emotion RTM scores for male and female participants after neutral and love prime



Performance on the Stroop Task following a Neutral and Love Prime

Performance on the Stroop task, as measured by the time taken to read aloud the colours of all 20 words presented (in seconds), was analysed using a 2 x 2 mixed design ANOVA, with Stroop performance as the dependent variable, love/neutral prime condition as a within-subject factor, and sex as a between-subject factor. No significant main effect of prime condition ($F(1, 89) = 0.29, p = .594, \text{partial } \eta^2 = .003$) or sex ($F(1, 89) = 1.81, p = .182, \text{partial } \eta^2 = .020$) was found, and there was no interaction effect ($F(1, 89) = 0.36, p = .552, \text{partial } \eta^2 = .004$). These results can be seen in Figure 22.

Figure 22. Mean Stroop Task performance scores for male and female participants after neutral and love prime



5.6 Discussion

This study found that when individuals in love were primed with a picture of their loved one, performance on a subsequent mentalizing task was improved, but performance on a task requiring self-control (the inhibition of an impulsive response) was not affected. Furthermore, analyses showed that when it came to assessing negative emotions, male participants, but not female participants, were significantly better at interpreting negative emotions in others (RTM task) following a love prime than following a neutral prime. There were no observed differences in performance on a Stroop task following either a love or neutral prime for either sex. There were no significant correlations between the difference in participants' performance following a love or neutral prime and self-reported levels of intimacy with a pair-bonded partner (as assessed by the Passionate Love Scale and the Other in Self Scale).

No Decrease in Cognitive Performance Following a Love Prime

These findings suggest that deactivations observed during previous fMRI research on love and brain activity, which were found in the temporal poles, temporoparietal junction, medial prefrontal cortex, amygdala and dorsolateral prefrontal cortex amongst other areas, do not have a detrimental effect on subsequent cognitions relying on those same areas, including assessing emotions (negative or otherwise) or on exerting cognitive control. This finding implies that such deactivations may merely be indicating a hemodynamic response to activity in adjacent areas, with cerebral blood flow immediately redirected back to deactivated areas as soon as their neuronal resources are required again (Shmuel et al., 2002; Tomasi et al., 2006). Alternatively, if observed deactivations relate to local neuronal inhibition, it is possible that they may only have an effect on cognitions which relate directly to a love-stimulus in question, and may not expand to influence cognitions about other, non-love related stimuli (such as the assessment of the emotions of strangers) or to the inhibition of control over non-love relevant cognitions, such as lexical tasks (Zeki, 2007).

The lack of a relationship between performance change on the experimental tasks examined following either a love prime or a neutral prime and several measures of love intensity (as approximated by the PLS and OIS) also undermines the idea that love-prime induced deactivations might affect subsequent cognitions. Since several fMRI studies have previously found a significant between-subject dose-response effect of PLS score on BOLD activations during the presentation of a love prime (Acevedo et al., 2012; Aron et al., 2005; Ortigue et al., 2007), one would expect to see a similar relationship in the current study if deactivation intensity affected cognitive performance. However, this relationship was not found. It must be noted, however, that studies looking at PLS scores and brain activity did not examine whether PLS correlated directly with any deactivations as such. Furthermore, at least one other study was unable to replicate this relationship between the same measure of love intensity and fMRI

observed activity (Zeki & Romaya, 2010), so the lack of such a relationship in this particular experiment study might also be attributable to slight differences in methodology.

The Role of Conceptual Priming

The finding that a love prime *improved* the ability of participants to attribute emotions to others, while not predicted by previously research on brain deactivations, might be explained by the phenomenon of conceptual priming (Fazio, Sanbonmatsu, Poweu, & Kardes, 1986; Keane, Gabrieli, Fennema, Growdon, & Corkin, 1991; Tulving, Schacter, & Stark, 1982). This body of research finds that the presentation of a stimulus may activate schema and memories relevant to that stimulus, which in the case of a love prime are likely to include thinking about the beliefs of the other individual (i.e. mentalizing) (Hatfield & Sprecher, 1986). This priming of related concepts is thought to enhance the accessibility of such schemas, thus resulting in improved performance on a subsequent task which requires the use of similar schemas (Tulving et al., 1982). Since it is known that participants in love devote more cognitive resources to thinking about various aspects of a love interest than about other individuals (H. E. Fisher, 1998; Hatfield & Sprecher, 1986; O'Leary, Acevedo, Aron, Huddy, & Mashek, 2011; Zeki, 2007), sometimes to the point of mirroring traditional obsessive-compulsive type behaviors (Feygin et al., 2006), it is feasible that the love stimulus in this instance would be a more effective prime for concepts related to mentalizing than a neutral stimulus. Previous research in related areas has found that participants are actually faster in identifying the intentions of a romantic partner than of a friend or a stranger (particularly if they were 'passionately in love' with that partner) (Ortigue, Patel, Bianchi-Demicheli, & Grafton, 2010), and that even the subliminal presentation of a romantic partner's name can facilitate cognitive performance on some decision tasks (Bianchi-Demicheli, Grafton, & Ortigue, 2006; Cacioppo, Grafton, & Bianchi-Demicheli, 2012). Furthermore, the presentation of a love prime, alongside instructions to think about the love interest, is less likely

to have primed schemas related to the exercising of self-control, potentially explaining the lack of improved performance on the Stroop task following a love prime.

Sex Effects

When examining the effect of sex on the results of this experiment, it appears that while a love prime had little effect on overall female RTM scores, it significantly improved the RTM scores of males (to the point where they matched those of females). While past research suggests that females typically display superior mentalizing abilities in general (Stiller & Dunbar, 2007) and outperform males on the RTM task (Baron-Cohen et al., 2001), these results showed that this sex difference in mentalizing ability can be eliminated following a love prime. This is a fascinating finding, suggesting that while a mentalizing prime seems to have a limited effect on females, perhaps because females are already near an upper limit of mentalizing ability to begin with, a love prime can significantly improve the mentalizing abilities of males, who typically show poorer baseline mentalizing performance. This improvement in mentalizing ability varied with the valence of the emotions being assessed, with male participant's poor performance in discerning negative emotions following a love prime driving this effect. Past research has found that females are particularly adept at encoding emotionally negative stimuli and assessing negative emotions (Canli, Desmond, Zhao, & Gabrieli, 2002; Rotter & Rotter, 1988), which might explain the particularly large sex discrepancy in baseline (i.e. neutral prime) assessment of negative emotions observed in the current study.

5.7 General Discussion

The goal of this chapter was to examine in detail one aspect of the underlying biological mechanisms thought to mediate mating behaviours associated with pair-bonded relationships. This tested a proposed link between previously observed neurological activity in pair-bonded individuals and its effects on cognitions underlying 'romantic love' behaviour. Specifically, it had

previously been proposed that BOLD signal ‘deactivations’ seen among individuals in love in brain regions responsible for theorising, assessing fearful emotions and exercising cognitive control may be responsible for various casually observed ‘love-typical’ behaviours such as an inability to accurately assess a lover’s character (‘love is blind’), fearlessness, and obsessive thoughts and behaviours. Using a methodological paradigm closely matched to one where these deactivations were previously observed, it was found that the predictions of these past neuroimaging studies did not hold up under examination.

These results highlight a major issue concerning how decreases in BOLD signal activations have sometimes been interpreted. Regional BOLD signals observed during fMRI research are often meaningless in their own right, and only lend themselves to interpretation once they are contrasted with a BOLD signal acquired under different conditions. This is typically done by comparing BOLD signal activation changes in a given brain region between two conditions, an experimental condition of interest and a baseline or control condition. Ideally, good experimental design allows for brain activity observed during the experimental condition to differ from brain activity during the control condition solely due to the effects of the unique properties of the experimental condition – this lets researchers ascribe any observed BOLD signal differences to the influence of the variable under scrutiny. Because of this, the selection of a control in fMRI research is actually of utmost importance, and sometimes overlooked as a possible confounding factor during the interpretation of results.

Early fMRI research sometimes used ‘rest’ periods, where individuals were presented with a blank screen or no stimuli at all and asked to ‘rest,’ as a control or baseline which was used as a comparison to an experimental condition of interest. As it turns out, during such rest baseline conditions the brain is actually still involved in a significant amount of neural activity (Stark & Squire, 2001), with large, interconnected swathes of the brain, now referred to as the default mode network, consistently found to be highly active during these rest periods (Greicius,

Krasnow, Reiss, & Menon, 2003). When activations during experimental conditions are compared to these supposed resting states, it is impossible to interpret any observed differences in activity as attributable solely to the experimental condition. In some instances, a lack of activity difference between conditions means that no neuronal activation was happening during either the experimental or control condition, but it could alternatively mean that the same level of 'high' activity was actually present in both the experimental and the rest condition. Because of this, task-relevant 'control' conditions are typically selected to act as a brain activity point of reference.

In romantic love research, a typical control condition involves looking at a picture of an individual who is not the object of love interest, but who is the same sex, age, and has been known for roughly the same amount of time. In theory, therefore, any difference in activation observed during the experimental (love) condition can be attributed to the fact participants are 'in love' with one individual and not the other, all other things remaining equal (such as activations arising due to face processing, recall of memories associated with that individual, etc.). In reality, however, it is impossible to ensure that pair-bond related cognitions are truly the sole difference between these two conditions. The 'deactivations' which have been observed in past research on love are instances where localised activation are *lower* in the experimental condition than the control condition. However, since the control condition does not entail a complete lack of activity, these activation differences could equally be interpreted as instances where localised activations are *higher* during the control condition. Looking at the deactivations found in past studies on love, therefore, it could be argued that when presented with a friend prime, individuals show *greater* activity in regions associated with mentalizing and control of inhibition when presented with a friend prime than when presented with a love prime. To explain such observations one could further argue, for example, that as individuals are better at interpreting the intentions of love interests than of others (Ortigue, Patel, et al., 2010), and thus may be more efficient at mentalizing when it comes to a love interest, they may have to expend more cognitive

effort in order to wonder about the intentions of a friend (hence higher the activations in related regions during the supposed control condition). While the experimental design of the current study did not lend itself to verifying such interpretations, it is nonetheless important to note that decreases in BOLD activity seen during fMRI are only decreases relative to a control condition, and could equally be interpreted as increases in activity that are occurring during the control condition.

The findings from this study also affect our understanding of the potential of romantic love to have sex differentiated cognitive consequences. Although past research on the topic of love and brain activity had not found any sex differences in activations when presented with love stimuli (e.g. Zeki & Romaya, 2010), it was discovered here that romantic love may nonetheless affect cognitions of the two sexes in differing ways. In particular, a love prime seemed to have a significant positive effect on the mentalizing abilities of males who are in love when assessing negative stimuli, while having little effect on females. This is a very interesting finding which begs further explanation. As mentioned earlier, a love prime may be affecting both sexes' ability to assess emotions, but as females are typically better than males at assessing emotions in others (Baron-Cohen et al., 2001), they may already be working at an upper limit of capability on this task, allowing little room for improvement following a prime. Alternatively, one can speculate that the improvement of males on this particular task may signify some adaptive advantage in the process of pair-bonding.

As forming pair-bonded attachments involves a considerable investment and opportunity cost on a males' part, as they must oftentimes sacrifice potentially beneficial alternate mating opportunities to do so (Buss & Schmitt, 1993), this effect may be beneficial to males in protecting their relationship investments. An improved ability to detect negative/threatening emotion in non-pair others may improve a male's ability to carry out certain male-typical mate 'guarding behaviours', which are sometimes used to assess and rebuff either physical threats from others,

or mate-poaching attempts (Buss, 1986, 2002a; Hughes, Harrison, & Gallup, 2004). Such past research suggests that males have a suite of behavioural proclivities that serve to protect such intense parental investments as those established by long-term pair-bonds. Alternatively, since forming and maintaining pair-bonds involves co-ordinating behaviours and intentions with another individual, and as males are typically worse at the kinds of empathising abilities which aid pair-bond formation and mediation, a state of romantic love may act to improve male empathy so as to assist in the maintenance of a pair-bonded relationship long enough to successfully raise offspring. Being more adept at recognising negative feelings and emotions in a pair-bonded partner could assist males in addressing these negative feelings and safeguarding the health of their pair-bond.

5.8 Chapter Summary and Outlook

This study found that the presentation of a love prime to individuals in love improved performance on a subsequent mentalizing task, particularly for males when it came to assessing negative emotion, but not on a task requiring self-control. These results suggest that previously observed brain region deactivations in subjects looking at stimuli of a love object may not correspond to a reduction in cognitive abilities associated with these regions. It appears, rather, that a love stimulus may conceptually prime mentalizing concepts and motivations and act to enhance subsequent performance on assessing the emotional states of others. This improvement is particularly obvious in males, who otherwise fare worse at assessing negative emotions in others than females. This is the first time that such hypotheses regarding love-induced brain deactivations and their relationship to love-relevant cognitions have been empirically tested, with this experiment enhancing our understanding of the relationship between fMRI observed brain activity and real-world cognitions. It is possible that the cognitive effects observed in this study may aid in the process of forming and maintaining pair-bonded attachments, particularly for males who typically demonstrate inferior empathising abilities.

The next, final discussion chapter summarises the results from all the research carried out in this thesis on various processes involved in human pair-bonding. An attempt is made to expand on the implications of these results for our understanding of human mating and the formation and mediation of pair-bonding attachments, and hypothesise in general on the nature and evolution of pair-bond attachments in humans. The implications that the findings presented herein have for future research in this field are also further explored.

Chapter 6 – Discussion

Thesis Overview

This thesis presented a series of studies looking at the various processes involved in, and leading up to, the creation and maintenance of pair-bonded mating attachments in humans. Though each study was logically independent of the others, they nevertheless offer a composite picture of crucial aspects of the pair-bonding process. Throughout, the emphasis fell on critically interrogating existing work, leveraging diverse methodological tools, and extending the current boundaries of our understanding in this field. The specific processes examined included the distribution of alternate mating strategies within the sexes and their bio-psychological underpinnings; the role of a common courtship custom (namely romantic kissing) in the selection of suitable mates with whom pair-bonds might be formed; and the consequences of pair-bond formation on cognitive processes.

Chapter 2 of this thesis used a novel statistical approach to establish that both males and females exhibit two distinct mating strategy phenotypes, both at the behavioural level and at the physiological level. These splits in strategy seem to underlie some within-sex differences in mating strategies, which direct mating effort towards either the pursuit of short-term mating encounters or long-term mating relationships. The establishment of these strategies, in turn, affects the likelihood that any future mating encounter may result in the formation of pair-bonded attachments. These bio-psychologically driven strategies also determine the nature of mate choice criteria against which potential mating partners will be assessed, as each individual engages in the search for mates whose attributes complement their mating strategy in an attempt to maximise overall reproductive fitness outcomes.

The subsequent two chapters examined the role of the common courtship custom of romantic kissing in human mating, and how this custom might contribute to various stages of the pair-

bonding process. The data presented in Chapter 3 of this thesis provided evidence that kissing in the context of romantic relationships serves two main functions: that of initial mate assessment and the creation/mediation of pair-bond attachments. Chapter 4 of this thesis extended these initial findings to suggest that the use of romantic kissing in females is linked to a biological substrate, namely the menstrual cycle hormone progesterone, and to show that olfactory cues seem to play a pivotal role in the use of kissing in mating interactions. Furthermore, it was also found across two additional studies in this chapter that kissing-related information can directly affect mate desirability, even in the presence of typically dominant visual cues.

The final data chapter in this thesis, Chapter 5, examined the cognitive repercussions of established pair-bonded relationships. This chapter found that pair-bonded attachments, or being in a state of romantic 'love,' seem to improve aspects of theory of mind (mentalizing), particularly for males when it comes to assessing negative emotions in other individuals. These results suggest that the establishment of pair-bonded mating relationships has significant cognitive effects in certain domains among individuals in who are 'in love', cognitive effects which may potentially be adaptive to the continued maintenance of such interpersonal mating attachments.

The Implications of two Phenotypes for Research on Human Mating

Chapter 2, as mentioned, examined within-sex distributions of mating strategy in two homogenous populations. Up until this point, the literature on mating strategies has primarily focused either on aggregate sex differences in strategy (e.g. Schmitt, 2005b), or on conditional mating strategies as drivers of within-sex mating strategy variation (e.g. Gangestad & Simpson, 2000). As the possibility that within-sex strategy in humans may also be reflective of different underlying polymorphisms has until now not been addressed (Gross, 1996), the results presented in Chapter 2 have significant implications for our understanding of the nature of these strategies. The novel finding that within-sex mating strategy differences in males and females may be driven

by two phenotypes suggests that some groups of individuals within each sex are more predisposed to form pair-bonded attachments than others, adding a layer of complexity to the study of within-sex strategy decisions that must be taken into account when conducting future research in this field.

This finding does not negate the value of looking at conditional mating strategies – each of these two within-sex phenotypes still contain considerable (continuously distributed) variation with them, and it is this *within-phenotype* variation which could still be driven by conditional mating strategies based on various environmental cues (i.e. individuals of the more restricted sociosexuality phenotype could still vary considerably in their level of restrictedness based on environmental conditions). However, if the structure of two within-sex phenotypes is not considered when examining mating strategies, then it may be erroneously anticipated that all (assumedly monomorphic) individuals within a sex have equal potential to pursue a long-term mating strategy, rather than being physiologically predisposed towards the preferential pursuit of one type of strategy over another. Such an omission could lead to incorrect inferences about the actual impact of environmental factors on observed strategy distributions, as the same factors may lead to differential responses in the two phenotypes present within each sex.

If assessments of within-sex phenotypic differences are not considered when examining aggregate population-wide sex differences in mating strategy (i.e. sociosexuality), then the resulting aggregate sociosexuality means will not be representative of true underlying mating strategy variation. If the sample size is small, it could be that, by chance, the within-sex strategy distribution may be comprised of a large proportion of restricted sociosexuality individuals and few unrestricted individuals, or alternatively of few restricted and many unrestricted individuals. While both of these possibilities could be described by the same aggregate sociosexuality score, the underlying distribution differences may tell a very different story. When examining the impact of environmental factors on differences in mating strategy between the sexes, for example,

variation in underlying within-sex phenotype proportions may be as, if not more, informative when it comes to assessing the actual impact of external factors on strategy choices than aggregate scores alone.

It was also proposed in this thesis that a major driver of mating strategy, and in turn the phenotypic diversity, is the hormone testosterone. Although past research attempting to show direct links between testosterone and sociosexuality has come up with equivocal results, testosterone does seem to be related to some fundamental components of mating strategy, such as mating drive and sexual desire (Bribiescas, 2001; A. P. Clark, 2004; Ellison, 2001; Regan & Berscheid, 1999; Wingfield et al., 1990). The fact that prenatal exposure to testosterone, as indexed by 2D:4D ratio, shows a similar bimodal within-sex distribution to sociosexuality in a homogenous British population corroborates the existence of a link between this purported biological substrate and observed behavioural mating strategy outcomes. It is possible that males with high prenatal/baseline testosterone levels preferentially pursue unrestricted mating strategies as high testosterone is related to sexually dimorphic traits acting as purported signals of 'genetic quality,' and such high quality males can afford to pursue such strategies as they are seen as more attractive and are likely to have greater access to potential mates. However, while a direct link between testosterone and underlying genetic quality (based on immunocompetence) has proved to be elusive (see Chapter 1, 'The Role of Attractiveness', p. 18, for more on this debate), this is not the only possible pathway by which testosterone might affect mating strategy. Testosterone could, and most likely does, work to drive mating strategy by increasing mating effort, sexual desire and intra-sexual competition. Since variation in these factors may constitute the key determinants of sociosexuality, and as testosterone has been most clearly linked to both mating effort and desire (see above), this seems the most likely pathway by which testosterone influences mating strategy outcomes.

Several lines of research have also found that fluctuating testosterone levels, as assessed by serum or salivary testosterone, are related to current relationship status – where males, and to a lesser extent females, in relationships show reduced levels of fluctuating testosterone as compared to single males and females (Booth & Dabbs, 1993; Burnham et al., 2003; van Anders & Watson, 2006). However, this relationship seems to be mediated by sociosexual orientation – whereby only individuals with restricted sociosexual orientations show lower testosterone levels when in relationships, with unrestricted individuals having the same levels of testosterone regardless of relationship status (Edelstein et al., 2011). This suggests that even though contextual factors (such as relationship status) may affect fluctuating testosterone levels and mating effort (and therefore mating strategy), long-term dispositional factors (such as prenatal testosterone exposure and phenotypic diversity) can, and do, still affect long-term mating strategy decisions across the lifetime of any one individual.

Furthermore, the future study of pair-bonded mating attachments in humans may need to take into account the possibility that there are two distinct classes of individuals within each sex who display marked bio-psychological differences in their desire, and perhaps even ability, to form such long-term bonds. As some research has already suggested that individuals pursuing short-term mating strategies show sensitivity and memory adaptations which aid them in the process of pursuing strategy-relevant mates (Sacco et al., 2009; D. S. Smith et al., 2013), it is likely that individuals pursuing long-term pair-bonded attachments may also differ significantly in their aptitudes for forming such attachments. Phenotypes with low testosterone levels are likely to be more adept in the formation and maintenance of pair-bonded attachments since lower levels of fluctuating testosterone have already been linked to lower levels of relationship infidelity, fewer life-time sexual partners and lower chances of divorce (Booth & Dabbs, 1993; Manning et al., 2000; Pollet et al., 2011). Lower levels of this hormone seem to also be adaptive for the rearing of offspring under the auspices of bi-parental care, one of the primary drivers for the formation

of pair-bonded relationships, as low testosterone levels are variously associated with increased parental efforts and higher biological sympathy responses to crying infants (Fleming et al., 2002; Muller et al., 2009). These initial findings imply that future study of pair-bonded attachments must consider taking gross phenotypic differences, such as the ones exposed in this thesis, into account when examining the formation and maintenance of these bonds.

Evolutionary Stable Strategies?

An interesting question arising from the results of this thesis lies in the nature of the relative distributions of mating strategy phenotypes within each sex. The phenotype proportions, as estimated by statistical analyses in Chapter 2, suggest that in males the proportional split favours an unrestricted mating strategy, while in females this split is slightly in favour of a restricted strategy. The fact that these two distinct strategies co-exist suggests that they both must have desirable fitness payoffs, and if those fitness payoffs vary in proportion with their relative frequency, then these phenotypes might form part of an evolutionary stable strategy (ESS) (Maynard Smith, 1984). While there is little data on the fitness outcomes of the two main strategies pursued by individuals in these two particular populations, similar data, which included proxy measures of mating strategy decisions, have been previously collected on males in a Québécoise population (Perusse, 1993). In that case, it was found that a larger proportion of males (~75%) were pursuing a restricted mating strategy, with the relative fitness payoffs of restricted versus unrestricted strategies potentially held in balance by risk-discounted fitness payoffs (reproductive success, as estimated from reported copulation frequencies) (Dunbar, 1993). This proportional split seems to be the reverse of what was found in this thesis. However, it must be noted that all married males were identified as pursuing a ‘restricted mating strategy.’ As that study was carried out in a population with strong monogamy norms, the use of marital involvement as a proxy for restricted strategies is inherently flawed – socially enforced monogamy is likely to lead artificially high marriage outcomes, even among males who might otherwise be

inclined to pursue strategies that are more unrestricted. The preliminary findings of this thesis highlight the need for further research into the idea that the two phenotypes might form evolutionary stable strategies, with reliable estimates of reproductive fitness outcomes established within a given population and compared directly to phenotypic proportional splits to see whether these two mating strategies are being held in evolutionary balance.

Implications for the Evolution of Human Pair-bonding

The possibility also exists that these two mating strategy distributions do not reflect equal respective payoffs, suggesting that they are not in fact in evolutionary balance and may still be changing in response to selection pressures. The mating systems of extinct hominids, as estimated from digit ratios of fossil remains, suggests that the social systems of Late Pleistocene *Homo* were more polygynous, and most likely promiscuous, as compared to most contemporary human populations (E. Nelson et al., 2011). Data suggest that evolutionary drivers for pair-bonding in primates, which include the need for mate guarding or infanticide risk and lead to increased parental care, may have been responsible for shifting mating systems towards pair-bonded attachments (Fuentes, 2002; Lukas & Clutton-Brock, 2013; Opie et al., 2013; Quinlan, 2008), with some form of pair-bonding now found among all contemporary human populations (H. E. Fisher, 1989; White et al., 1988). However, the question remains as to when exactly the transition from promiscuous mating to bonded mating occurred. Though it is likely to have been a relatively recent shift, exactly how recent is still under debate (E. Nelson et al., 2011; Opie et al., 2012). The data presented in this thesis add weight to proposals that pair-bonding in humans is a relatively recent phenomenon, with the presence of two distinct bio-social drivers within the sexes signalling that the transition to pair-bonding in humans is far from a complete one.

This phenotypic split in males and females, both in digit ratios and expressed behavioural inclinations, supports previous findings that humans are not solely monogamous (see 'Mating

Systems' p. 7 for more on this debate). These two phenotypes may also potentially allow for the greatest flexibility in mating strategy outcomes in response to environmental variables – with a biological phenotypic division (based on baseline testosterone) shaped by long-term evolutionary forces acting as a starting point, which is then further fine-tuned by local environmental conditions to create appropriate behavioural mating strategy outcomes (sociosexuality) which best maximise fitness outcomes in a particular local conditions. In other words, it is possible that while testosterone levels in early development differentiate males and females into two sociosexuality phenotypes, it is various local cues, such as sex ratio, gender equality or environmental stress (see also 'Sex Differences in Sociosexual Orientation' p. 44), which also mediate final sociosexual expression adaptively to these conditions. These adaptive effects may explain not only some of the aggregate differences observed in sociosexualities between cultures, but may also be responsible for differences in the relative within-sex phenotype proportions in any given culture. Research repeatedly finds that humans display incredible flexibility when it comes to solving mating dilemmas, as signalled by the fact they invariably fall midway between monogamous and promiscuous species on various mammalian mating system indices, such as sexual dimorphism, testes size, and direct mate competition (Clutton-Brock, 1989; e.g. Harcourt et al., 1981; Mealey, 2000; E. Nelson et al., 2011). It may be that this multi-level flexibility, in both the phenotypic bio-psychological biological drivers of mating strategy as well as in the final strategy behavioural outcomes within each sex, is responsible for such flexibility – allowing for an adaptive response to both sustained evolutionary pressures and more temporally variable, localised pressures across multiple ecological niches.

The Role of Courtship Customs in Human Mating

Findings from this thesis relating to the use of the courtship custom of romantic kissing in the pair-bonding process also suggest that individuals following these two different mating strategies use kissing in divergent ways to attain their respective mating goals. Sociosexually unrestricted

individuals seem to use kissing at initial relationship stages to assess the suitability of potential mates, while sociosexually restricted individuals utilise this custom at established stages of a relationship to mediate long-term pair-bond attachments. Past research finds that individuals of different sociosexualities seem to show adaptations in various domains when it comes to assessing strategy-relevant mate cues. For example, it has been found that unrestricted individuals display increased sensitivity to, and memory recall of, signs of genetic quality in a potential mate (Sacco et al., 2009; D. S. Smith et al., 2013). The findings of this thesis may be indicative of similar differences in sensitivity to, and use of, kissing as a mate assessment tool among individuals following divergent mating strategies. In other words, the two mating phenotypes, driven by testosterone, may show adaptive use of the same courtship custom to their individual advantage.

These findings have implications for research into other forms of mate assessment and courtship rituals, which should always take into account the presence of these distinct phenotypes when examining how individuals employ mate selection criteria to further their mating goals and maximise individual fitness outcomes. Though research into mate assessment and choice already typically differentiates between decisions based on short-term or long-term mate desirability, the differing sociosexual orientations of individuals making these assessments is not always taken into consideration. Furthermore, these findings impact our understanding of courtship behaviours and their use in the mating process, suggesting that heretofore treatments of some other courtship behaviours as idiosyncratic socio-cultural constructs may be overlooking their important functional roles. Many such behaviours may in fact not only be serving functional purposes in mate assessment and retention process, but may also be utilised in different ways by individuals following divergent mating strategies. It may be that human courtship behaviours, such as mirroring gestures, may be preferentially used by individuals pursuing long-term relationships to establish and mediate attachment, while lekking behaviours among males competing for potential mates may be preferred by individuals pursuing short-term mating

strategies to further their respective aims (e.g. Grammer, Kruck, & Magnusson, 1998; Lycett & Dunbar, 2000).

Adaptive Cognitions related to Pair-bonded Attachments

It had been previously hypothesised that those individuals preferentially pursuing a long-term mating strategy, involving the creation and maintenance of long-term pair-bonds, might exhibit cognitive processes that help create and maintain such bonds. These adaptations had been assumed, based on previous fMRI findings, to assist individuals in forming bonds by limiting their ability to assess another's intentions accurately (making love 'blind') and reducing their ability to exercise control over instinctual behaviours (leading to obsessive love-typical behaviours). What was found was in fact the opposite. It appears that the state of being in a pair-bond may actually improve an individual's ability for reading emotion in others, particularly for males and particularly when it comes to negative emotions. This might be adaptive in its own way, allowing individuals to improve their understanding of the emotions and intentions of a mating partner, and thus helping them better coordinate mating efforts and investments. This improvement would be particularly beneficial for males of the phenotype that is motivated to establish long-term bonds, since males typically fare worse than females on various empathy and mentalizing tasks (Baron-Cohen et al., 2001; Stiller & Dunbar, 2007). Whether this improvement in emotional empathy applies to all individuals, or is preferentially and adaptively experienced among individuals following restricted (long-term) mating strategies, could not be answered within the scope of this thesis, though it is an interesting question which begs following up in future research.

In particular, these findings raise the issue of whether capacities like theory of mind are the product of cultural contrivance or innate ability. This debate has become particularly pressing in recent years with the emergence of 'enactivism' – the view that theory of mind does not exist as

a mental construct, but is instead largely mediated by cultural prostheses such as narrative (S. Gallagher, 2001, 2011; Hutto & Myin, 2013; Hutto, 2012). Here, it is shown that experimental stimuli conditions can impact theory of mind, thereby suggesting that the capacity is open to environmental manipulation – even if not to the extent suggested by enactivists.

Wider Implications

More generally, the findings from this research have implications for policy making and social planning. The existence of within-sex behavioural repertoire differences implies that environmental cues have a major impact on sexual behaviour, as well as vice versa. Given that issues of social cohesion, family breakdown, single parenthood and inter-generational poverty can be linked (in very different ways) to sexual behaviours, there is a clear social value in developing a ‘map’ of how genetic, hormonal, and environmental causes enter into human sexuality. Mating strategies and their sexual behavioural outcomes also have direct effects on sexual health, including the transmission of sexually transmitted infections, including outbreaks and prevalence of diseases such as HIV (A. M. Johnson et al., 2001). A clearer understanding of human sexual behaviour, and its drivers and mediators within various physical and cultural environments, is likely to be useful in the planning and implementation of sex education, policy and sexual health interventions programmes attempting to mitigate the negative health outcomes of various sexual behaviours.

Future Research

Some of the unique findings and contributions of this research open up interesting possibilities for future work, which might probe these initial findings in more detail and possibly address some of the new questions that have been thrown up these results. The findings on the phenotypic divide in sociosexuality and testosterone, and potential differences in phenotypic ratio splits, invite exploration of how these phenotypes might vary in distribution across different

cultures facing different environmental pressures. Since general sociosexuality has been found to vary with external pressures such as environmental stress and sex ratios (Lippa, 2009; Schmitt, 2005b), it is highly likely that these relative phenotypic proportions would also vary as relative fitness payoffs of these different mating strategies change in different environments. By examining such differences in light of quantifiable environmental variance, it may be possible to establish scalar relationships between environmental factors and such phenotypic distributions.

In any population where two behavioural phenotypes are present, the question arises as to whether they form an Evolutionary Stable Strategy (ESS), with the proportions of each phenotype within each sex held in balance by their relative payoff ratios and the probabilities of assortative or disassortative mating (Maynard Smith, 1984). To determine whether these sociosexuality phenotypes form such a balanced strategy, it may be possible in future to test their fitness outcomes using game-theoretical modelling approaches (e.g. Härdling & Kokko, 2005; S. E. Hill & Reeve, 2004; Simão & Todd, 2003). Alternatively, the nature of the relationship between phenotypic distribution and their relative fitness outcomes could be established by utilising direct measures of potential fitness outcomes that might accrue to individuals in different populations pursuing these divergent mating strategies (e.g. Perusse, 1993).

In this thesis 2D:4D ratios were used as indices of testosterone exposure, since it has been suggested that they are an accurate proxy measure of prenatal testosterone and lend themselves to easy assessment (Manning et al., 1998; Manning, 2002). Prenatal testosterone seemed appropriate in this case since it drives the development of much of the early morphological and behavioural differences between the sexes (Hunter & Garn, 1972; Wells, 2007), and is also likely to play a role in driving the kinds of behavioural phenotypic divisions observed here. However, measurements of 2D:4D ratios have shown some inconsistencies between different methodologies (e.g. Manning et al., 2010; Xi et al., 2014). A natural follow up experiment to what was presented here would involve using other measures of testosterone differences in a given

population, such as adult baseline serum testosterone levels, to see whether the same bi-modal phenotypic splits persist into adulthood.

The role of romantic kissing in mating relationships also begs more detailed examination, as the mechanisms by which it allows us to assess mates or mediate bonds could not be fully resolved within the scope of this thesis. It would be interesting to expand on these initial findings and examine whether the attitudes to kissing discovered here extend to individuals from pre-industrialised cultures, with less exposure to the kinds of Western cultural practices that are pervasive across the world. Furthermore, while a link was found here between estimated menstrual cycle hormone progesterone and kissing attitudes, future research could follow up on these initial menstrual cycle effect findings using more methodologically robust techniques to assess menstrual cycle phase and hormonal levels, perhaps using serum hormonal assays and more direct assessments of cycle phase. It may also be possible to pursue more methodologically challenging research in order to clarify the role of olfactory assessment and its relationship to 'kissing quality' and mate desirability, perhaps using experimental designs based on live stranger interactions. In such research strangers could be asked to engage in several forms of kissing interaction (on the mouth, cheek, etc.) and asked to rate the quality of each 'kiss' and the desirability of each potential mating partner, whereupon these ratings would be examined in light of several mate quality/suitability variables, including MHC compatibility, fluctuating asymmetry, sexual dimorphism and so on, to examine the relationship between kissing and mate assessment in more detail. Execution of such methodology would certainly be more difficult, and would have to overcome ethics issues associated with exposing participants to various forms of infection (e.g. flu, influenza) and with post-study psychological carry-over effects associated with such intimate interactions between relative strangers. Furthermore, it may be hard to estimate the ecological validity of results arising from this kind of lab-based research, which would be carried out

between strangers in highly contrived situations, quite disassociated from the typical scenarios under which romantic kissing and the potential for mate assessment may take place.

The purported role of kissing and bonding effects could also be examined in follow-up research that utilises more controlled experimental designs. In order to try and isolate the mechanism by which kissing might function to mediate attachment bonds, it may be possible to look at changes in various biomarkers which occur immediately after a kissing interactions between two individuals, examining several biological variables which have been previously indicated in the mediation of interpersonal bonds (i.e. oxytocin/vasopressin, cortisol, testosterone). Such research could potentially be carried out within established romantic couples, who would have their biomarker samples taken pre- and post-kissing interaction in a laboratory setting, minimising ethical issues associated with tasking strangers to partake in kissing-mediated bonding sessions.

Lastly, when it comes to the neuropsychology of pair-bonding, there is much still left to be explored. While the link between previously observed brain deactivations and subsequent cognitions seems to be non-existent, it remains unclear whether this lack of relationship is due to a misunderstanding of the nature of brain deactivations, or a lack of effect of actual neuronal inhibitions on cognitions that rely on the activations of said neurons. Future research should attempt to elaborate on these relationships using more focused experimental designs which attempt to clarify this specific issue, perhaps using techniques such as Transcranial Magnetic Stimulation (TMS) to see whether neuronal inhibition of theory of mind associated brain regions actually has direct consequences on theory of mind related cognitions, such as empathizing or attribution of emotional states to others.

Furthermore, it would be interesting to examine whether individuals pursuing different mating strategies, such as restricted versus unrestricted strategies, show differing adaptations for pair-bonding. Unrestricted sociosexuality individuals are already known to display higher levels of sex drive and a greater desire for sexual diversity (Penke & Asendorpf, 2008; Simpson et al., 1991),

to show adaptations for limiting emotional engagement (Haselton & Buss, 2001), to have increased sensitivity to short-term mating strategy relevant mate cues (Lewis, Easton, Goetz, & Buss, 2012; Sacco et al., 2009; D. S. Smith et al., 2013), and to be more likely to display the kinds of ‘dark triad’ personality characteristics (narcissism, psychopathy and Machiavellianism) which facilitate short-term mating (Jonason, Li, Webster, & Schmitt, 2009; Mouilso & Calhoun, 2012). It is therefore not unreasonable to assume that restricted sociosexuality individuals are conversely more adept at behaviours and cognitions related to the formation and maintenance of pair-bond relationships. It would be worthwhile examining whether such individuals show improved mentalizing or empathizing abilities, which may prove useful in helping individuals co-ordinate long-term mating attachments and investments with another individual. Such improved abilities are already found amongst females (Baron-Cohen et al., 2001; Stiller & Dunbar, 2007), who are also generally more likely to pursue long-term mating relationships (e.g. Penke & Asendorpf, 2008).

The key driver of such behavioural and cognitive differences may again be testosterone. Prenatal testosterone exposure has been linked to increased ‘systemizing’ cognitive processes (involving analysis and construction of systematic rules to understand the environment) and decreased ‘empathising’ cognitive abilities (used in identifying thoughts and emotions of others), with autism spectrum disorders potentially arising from cogitations which are over-reliant on systemising processes at the expense of empathising abilities (Auyeung et al., 2006; Baron-Cohen, 2009). While some studies looking at associations between 2D:4D ratio and systemizing/empathizing abilities have not found any relationship (e.g. Voracek & Dressler, 2006), other studies using more rigours 2D:4D ratio measurement methodologies do find that a relationship seems to exist, with higher levels of prenatal testosterone associated with better systemizing abilities and sometimes lower empathizing abilities (Manning et al., 2010; Von Horn, Bäckman, Davidsson, & Hansen, 2010; Wakabayashi & Nakazawa, 2010). The next logical step

in this line of research would be to examine the relationship between mating strategies and empathising abilities to determine if individuals of a restricted sociosexuality phenotype display the improved cognitive abilities in this realm as an adaptation that aids the process of pair-bond formation. This is a fascinating possibility that begs further exploration.

Conclusion

This thesis has made an original contribution to our understanding of several different mating behaviours that contribute to the formation and maintenance of mating pair-bonds. It was shown that mating strategies within the sexes might be based on two distinct phenotypes, driven by underlying differences in prenatal testosterone exposure. It was found that the courtship custom of romantic kissing is utilised during the mate selection process divergently by individuals pursuing one of these two mating strategies, with those interested in short-term mating using it to assess the quality of potential mates at initial relationship stages, and those interested in long-term mating opportunities using it to mediate long-term pair-bonds. It was also found that the use of kissing varies across the menstrual cycle among females and is related to estimated fluctuations in the hormone progesterone, and that third-party assessments of partner kissing quality can affect mate desirability, even in the presence of typically dominant visual cues. Lastly, it was found that individuals who pursue a long-term mating strategy and establish mating pair-bonds with another individual show improved empathising abilities, particularly males and particularly when it comes to assessing negative emotions in others.

Each chapter contributes to our understanding of these different behaviours, with a wide array of research techniques leveraged in this thesis to address research questions that have as yet not been adequately considered by the literature.

These results have implications for future research into mating strategy and the important role that phenotypic differences might play in strategy decisions, as well as for the study of various

courtship and related mating behaviours. These results also have implications for our understanding of the evolution of human pair-bonding, suggesting that it is a relatively recent phenomenon among humans, and that pair-bonds can adaptive affect cognitions of individuals in established pair-bonded relationships, particularly, males. While the behaviours examined in this thesis are diverse in nature, they are in fact closely related and interdependent on each other, in that they all contribute to the pair-binding process that forms an adaptive response to unique evolutionary pressures. Only when viewed through an evolutionary framework do the complex relationships between the research questions become apparent, with each mating behaviour shaped by evolutionary pressures to address the same problem – that of maximising inclusive fitness in the face of varying local environments.

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Appendix A

Attitudes to Kissing Questions

How important do you think kissing is . . .

	Not at all Important	Slightly Important	Fairly Important	Very Important	Extremely Important
. . . at the very initial stages of a relationship?	()	()	()	()	()
. . . during the established phases of a committed, long-term relationship?	()	()	()	()	()

How important do you think kissing is with a casual, short-term romantic partner (i.e. a one-night stand) in the following situations

	Not at all Important	Slightly Important	Fairly Important	Very Important	Extremely Important
Immediately before sex.	()	()	()	()	()
During sex.	()	()	()	()	()
After sex.	()	()	()	()	()
At all other times (not related to sex).	()	()	()	()	()

How important do you think kissing is with a committed, long-term romantic partner (i.e. someone you are in a relationship with) in the following situations

	Not at all Important	Slightly Important	Fairly Important	Very Important	Extremely Important
Immediately before sex.	()	()	()	()	()
During sex.	()	()	()	()	()
After sex.	()	()	()	()	()
At all other times (not related to sex).	()	()	()	()	()

Have you ever felt attracted to someone, only to find that your attraction to them had changed after an initial kiss?

() Never () Rarely () Sometimes () Often () Always

Kissing Frequency and Satisfaction Questions

How 'good' at kissing would you say your current romantic partner is?

Poor Fair Good Very Good Excellent

On average, how often would you say that you . . .

	Once a month or less	A few times a month	Once a week	A few times a week	Nearly every a day
. . . kiss your romantic partner (either on the lips or open-mouth)?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
. . . have sexual intercourse with your romantic partner?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

How satisfied are you with . . .

	Not at all Satisfied	Slightly Satisfied	Moderately Satisfied	Very Satisfied	Extremely Satisfied
. . . the amount of kissing you and your romantic partner do?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
. . . the amount of sexual intercourse you and your romantic partner have?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Mate Value Estimation Questions

In general, how do you think other people would rate you on . . .

	(Very Low) 1	2	3	(Avera ge) 4	5	6	(Very High) 7
. . physical attractiveness?	()	()	()	()	()	()	()
. . sexual attractiveness?	()	()	()	()	()	()	()

Relationship Assessment Scale (RAS)

Please state how much you agree or disagree with the following statements about your relationship with your current romantic partner.

	Strongly Disagree	Moderately Disagree	Slightly Disagree	Neutral	Slightly Agree	Moderately Agree	Strongly Agree
My partner meets all my needs.	()	()	()	()	()	()	()
I am totally satisfied with my relationship.	()	()	()	()	()	()	()
My relationship is much better than most other relationships.	()	()	()	()	()	()	()
I often wish I hadn't gotten into this relationship.	()	()	()	()	()	()	()
My relationship has met all my original expectations.	()	()	()	()	()	()	()
I am completely in love with my partner.	()	()	()	()	()	()	()
There are many problems in my relationship.	()	()	()	()	()	()	()

Sociosexuality Scale (SOI-R)

The following questions are about your sexual history and your general attitudes towards sex.

With how many different partners have you had sexual intercourse on one and only one occasion?

0 1 2 3 4 5-6 7-9 10-19 20 or more

With how many different partners have you had sexual intercourse without having an interest in a long-term committed relationship with this person?

0 1 2 3 4 5-6 7-9 10-19 20 or more

With how many different partners have you had sex within the past 12 months?

0 1 2 3 4 5-6 7-9 10-19 20 or more

Please rate your agreement with the following statements

	(Strongly Disagree) 1	2	3	4	(Neutral) 5	6	7	8	(Strongly Agree) 9
Sex without love is OK.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
I can imagine myself being comfortable and enjoying "casual" sex with different partners.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
I do not want to have sex with a person until I am sure that we will have a long-term, serious relationship.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

How often do you . . .

	Never	Very seldom	About once every 2-3 months	About once a month	About once every two weeks	About once a week	Several times per week	Nearly every day	At least once a day
. . . have fantasies about having sex with someone you are not in a committed romantic relationship with?	()	()	()	()	()	()	()	()	()
. . . experience sexual arousal when you are in contact with someone you are not in a committed romantic relationship with?	()	()	()	()	()	()	()	()	()
. . . have spontaneous fantasies, in everyday life, about having sex with someone you have just met?	()	()	()	()	()	()	()	()	()

Appendix B

Menstrual Cycle Study – Kissing Importance Questions

How important do you think kissing is . . .

	Not at all Important	Slightly Important	Fairly Important	Very Important	Extremely Important
. . . at the very initial stages of a relationship?	()	()	()	()	()
. . . during the established phases of a committed, long-term relationship?	()	()	()	()	()

Menstrual Cycle Study – Kissing Factor Questions

In deciding whether someone is a 'good kisser', how important are the following factors

	Not at all Important	Slightly Important	Fairly Important	Very Important	Extremely Important
How pleasant their breath is.	()	()	()	()	()
The scent of their body.	()	()	()	()	()
The taste of their lips/skin.	()	()	()	()	()
How 'wet' the kiss is.	()	()	()	()	()
How much touching/physical-contact/caressing is involved.	()	()	()	()	()
How physically aroused it makes you.	()	()	()	()	()
Whether their kissing style is the same as yours.	()	()	()	()	()

Menstrual Cycle Estimation Questions

For female participants - the following questions are about your menstrual cycle and any hormonal methods of contraception you might be taking.

Are you taking any form of hormonal contraception at the moment (i.e. are you 'on the pill' or taking DepoProvera injections)?

Yes No

Do you experience fairly regular menstruation (periods)?

Yes, my periods are fairly regular

No, my periods are highly unpredictable

No, I do not menstruate

What is the typical length of your entire menstrual cycle (the average number of days between the beginning of each period, i.e. 28 days, 30 days etc. . . .)? () days

Using the calendar icon below, please mark the approximate date that your last period began (format: mm-dd-yyyy). ()

Appendix C

Vignettes used in Chapter 4, Study 2a & 2b (Male Versions)

Chris - Good Kisser

Chris is generally a friendly and sociable individual who enjoys hiking and the outdoors. He has been described as warm and kind, though can be unreliable at times. He is known for his conscientiousness, though does not always make wise decisions when it comes to his career path. When it comes to relationship skills, his previous partner said that Chris seemed to really enjoy close physical intimacy, that he was not a particularly good kisser, and that he was a bit dull in the bedroom. He has a cat named Rich and a dog named Ginger.

Chris - Bad Kisser

Chris is generally a friendly and sociable individual who enjoys hiking and the outdoors. He has been described as warm and kind, though can be unreliable at times. He is known for his conscientiousness, though does not always make wise decisions when it comes to his career path. When it comes to relationship skills, his previous partner said that Chris seemed to really enjoy close physical intimacy, that he was a particularly good kisser, and that he was a bit dull in the bedroom. He has a cat named Rich and a dog named Ginger.

Rob - Good Kisser

Rob has been described by friends as pretty trustworthy and honest. One of his favourite pastimes is cooking and staying in at home to read a good book. Though he is not very sociable, and some people see him as downright unfriendly and rude, he is very intelligent and open to trying new experiences. When his personal relationship skills were evaluated by his previous partners, they reported that Rob could be quite romantic at times, that he was a good kisser, and can be a bit adventurous when it comes to love making. He is generally very respectful of others and is warm once you get to know him.

Rob - Bad Kisser

Rob has been described by friends as pretty trustworthy and honest. One of his favourite pastimes is cooking and staying in at home to read a good book. Though he is not very sociable, and some people see him as downright unfriendly and rude, he is very intelligent and open to trying new experiences. When his personal relationship skills were evaluated by his previous partners, they reported that Rob could be quite romantic at times, that he was not a good kisser, and can be a bit adventurous when it comes to love making. He is generally very respectful of others and is warm once you get to know him.

Mat - Good Kisser

Matt has many friends who mostly see him as a sociable person. He has eclectic tastes, and some of his many hobbies include running and going to the movies. He has been known to be a bit selfish and insincere at times and comes across as cold to people who he doesn't really know, but he is generally seen as a trustworthy person, kind and respectful of others. His previous partner commented that he is good in the kissing department, and although he is not particularly fond of physical intimacy, his partner mentioned that he is a good listener and has an open-minded attitude towards sex.

Mat - Bad Kisser

Matt has many friends who mostly see him as a sociable person. He has eclectic tastes, and some of his many hobbies include running and going to the movies. He has been known to be a bit selfish and insincere at times and comes across as cold to people who he doesn't really know, but he is generally seen as a trustworthy person, kind and respectful of others. His previous partner commented that he is not so good in the kissing department, and although he is not particularly fond of physical intimacy, his partner mentioned that he is a good listener and has an open-minded attitude towards sex.

Sam - Good Kisser

Sam is very smart and did particularly well in his school studies. Friendly and outgoing, he has a tight circle of close friends, though he is not always as honest with them as he would like to be and can be critical of others. He is well known for being dependable - when he promises to do something he always follows through. Sam is the indoor type, and prefers intimate get-togethers to large parties. As for Sam's relationship skills, his last partner said that while he was quite affectionate and caring, he was not particularly inspiring in bed. His partner also didn't think he was particularly good at kissing.

Sam – Bad Kisser

Sam is very smart and did particularly well in his school studies. Friendly and outgoing, he has a tight circle of close friends, though he is not always as honest with them as he would like to be and can be critical of others. He is well known for being dependable - when he promises to do something he always follows through. Sam is the indoor type, and prefers intimate get-togethers to large parties. As for Sam's relationship skills, his last partner said that while he was quite affectionate and caring, he was not particularly inspiring in bed. His partner also thought he was particularly good at kissing.

Questions about each Target Individual

Please answer the following questions about this person.

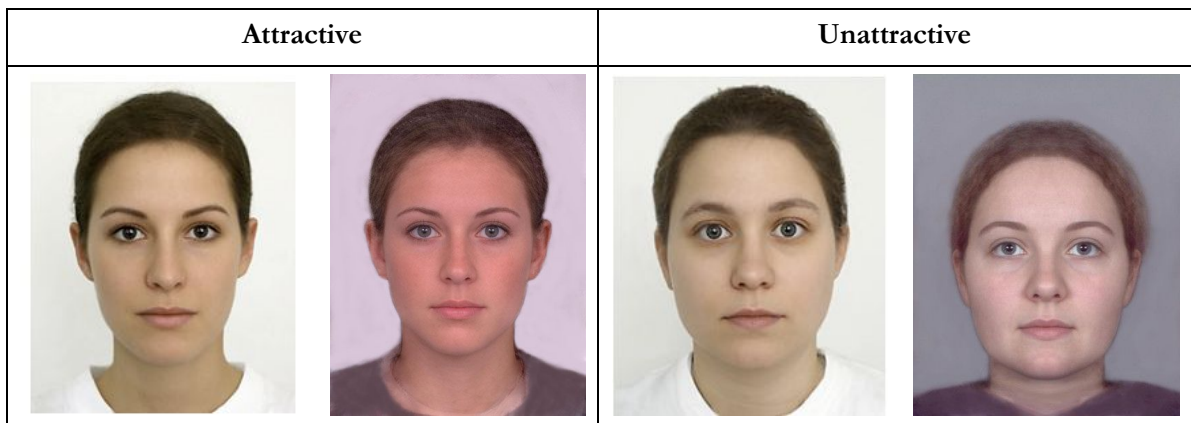
	Not at all	Slightly	Somewhat	Very	Extremely
How 'attractive' do you find this person?	()	()	()	()	()
How interested would you be in going on a date with this person?	()	()	()	()	()
How interested would you be in having a casual, one-off sexual encounter with this person?	()	()	()	()	()
How interested would you be in pursuing a committed, long-term relationship with this person?	()	()	()	()	()

Additional Visual Information used in Chapter 4, Study 2b

Males



Females



Appendix D

Reading the Mind in the Eyes Task (RTM) – Example

The next exercise is the 'Reading Eyes' task. For each of the next 16 sets of eyes, choose which word best describes what the person in the picture is thinking or feeling as quickly and accurately as possible.

jealous

panicked



arrogant

hateful

Stroop Task – Example

The next task is the 'Reading Colours' task.

Remember, for the task on the following page you must NAME THE COLOURS OUT LOUD that each of these words are presented in, do not read what the words say.

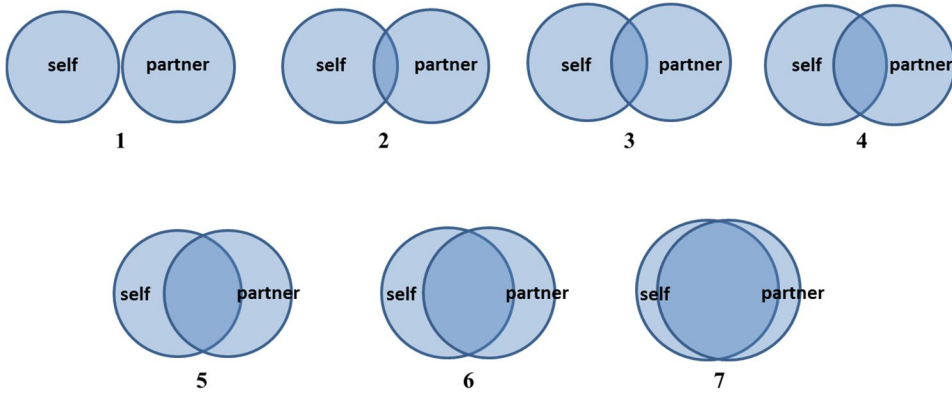
Name all the colours as fast as you can, following the words left to right and top to bottom. Press 'Next' when you are ready to begin, then press 'Next' again when you are finished naming all the colours.



Other in Self Scales (OIS)

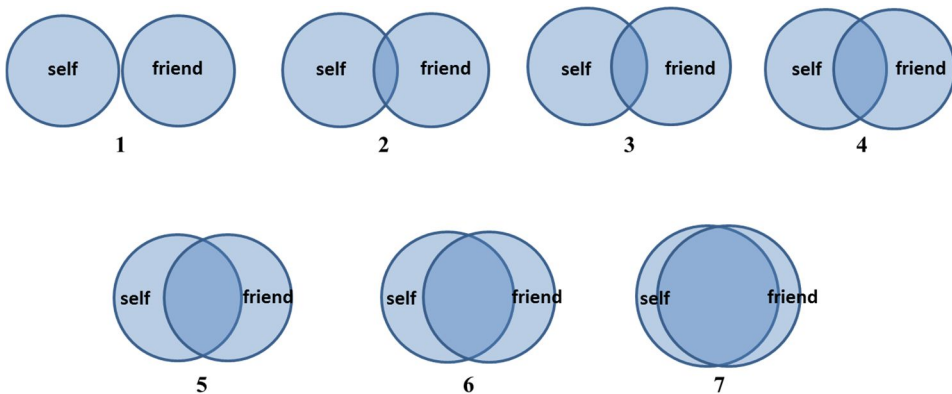
Please indicate which picture best describe your relationship with your partner.

1 2 3 4 5 6 7



Please indicate which picture best describe your relationship with your friend.

1 2 3 4 5 6 7



Passionate Love Scale (PLS)

The following questions are about your feelings towards your [partner / friend].

Note: your answers can range from 'Not at all true' (1) to 'Definitely True' (9)

[Note: two version were presented, one for partner and one for friend]

	1	2	3	4	5	6	7	8	9
I would feel deep despair if my partner / friend left me.	()	()	()	()	()	()	()	()	()
Sometimes I feel I can't control my thoughts; they are obsessively on my partner / friend.	()	()	()	()	()	()	()	()	()
I feel happy when I am doing something to make my partner / friend happy.	()	()	()	()	()	()	()	()	()
I would rather be with my partner / friend than anyone else.	()	()	()	()	()	()	()	()	()
I'd get jealous if I thought my partner / friend was falling in love with someone else.	()	()	()	()	()	()	()	()	()
I yearn to know all about my partner / friend.	()	()	()	()	()	()	()	()	()
I have an endless appetite for affection from my partner / friend.	()	()	()	()	()	()	()	()	()
For me, my partner / friend is the perfect romantic partner.	()	()	()	()	()	()	()	()	()
I sense my body responding when my partner / friend touches me.	()	()	()	()	()	()	()	()	()
My partner / friend always seems to be on my mind.	()	()	()	()	()	()	()	()	()
I want my partner / friend to know me – my thoughts, my fears, and my hopes.	()	()	()	()	()	()	()	()	()
I eagerly look for signs indicating my partner / friend's desire for me.	()	()	()	()	()	()	()	()	()
I possess a powerful attraction for my partner / friend.	()	()	()	()	()	()	()	()	()
I get extremely depressed when things don't go right in my relationship with my partner / friend.	()	()	()	()	()	()	()	()	()