Modality related effects of face and voice information and the perception of human attractiveness

Timothy J. Wells

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ABSTRACT

The process of sexual selection is likely to incorporate multiple sources of information that can be used to identify a suitable mate. Utilising multiple signals for sexual selection could be advantageous since together these might limit the chance of mating with a suboptimal partner (Møller & Pomiankowski, 1993) and thus avoid the cost of unhealthy progeny. However to date, research has focused primarily on unitary signals of attractiveness. Therefore, this thesis aimed to identify the function and relative importance of face and voice signals in human mate attractiveness, with particular reference to Candolin's (2003) framework of signal integration.

The findings suggested that female face and voice signals appear to be related and are likely to constitute back-up signals. Together, female faces and voices interact thus modulating the attractiveness of face-voice compound stimuli and provide a more accurate estimate of fertility. Male voices decreased female response latencies when presented congruently with male faces, which suggests that they are integrated. However, male face-voice integration did not enhance the detection or discrimination of attractive male faces. Rather, females' readiness to rate male faces and voices was delayed when the stimuli were more attractive. Male faces and voices were shown to positively and independently influence the perception of compound stimuli attractiveness and in contrast to female stimuli, male face and voice signals appear to be unrelated; as such, they are likely to constitute multiple messages. While faces are proposed to signal health, male voices have been proposed to communicate information relating to dominance. Together, male faces and voices provide a more accurate estimate of overall mate quality.

In conclusion, taking into account aspects of sensory integration promises to add further insight into the cognitive processes involved in mate attractiveness and person perception. Furthermore, studies investigating the integration of different modalities and in different contexts will be important to understanding their evolution, function and importance in human attractiveness perception.

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CHAPTER 1: LITERATURE REVIEW

1.1 Introduction

Darwin (1871) proposed two fundamental selective criteria that can influence the development and prevalence of evolutionary adaptations; *natural* selection and *sexual* selection. Successful adaptations that evolve via natural and sexual selection pressures can both provide an organism with a reproductive advantage. However, natural selection favours traits that increase an organisms chance of survival in an environment. As such, the pressure to adapt comes largely from ecological conditions. In contrast, traits that evolve through sexual selection arise via pressure from members of the same species. Evolution through sexual selection can increase an organisms attractiveness to a potential mate thus providing a reproductive advantage. It should be noted that natural and sexual selection are not mutually exclusive: traits may favour both survival and promote successful mating. However, adaptations that have evolved through sexual selection can serve to increase the chance of reproducing even at the potential cost of threatening survival.

The presence of multiple signals for sexual selection could be advantageous since together they could limit the chance of mating with a suboptimal partner (Møller & Pomiankowski, 1993), thus avoiding the costs of unhealthy progeny. However, to date, research has mainly focused on single signals of attractiveness. Sexual selection is likely to give rise to multiple sources of information that can be used to identify a suitable mate in multi-sensory organisms, in order to facilitate both sending and receiving of such messages in variable environments. Since it is unlikely that signals of attractiveness are assessed in isolation, particularly in the presence of other potentially useful information, inferences regarding their function and relative importance should be treated as tentative.

The present literature review aims to discuss the nature and function of multiple signals with regard to sexual selection. It begins with an introduction to examples from the attractiveness literature most commonly researched in isolation (c.f. faces and voices). Current literature on face and voice attractiveness will be discussed in an effort to integrate findings within a theoretical framework outlined by Candolin (2003) describing how signals interact. Related to this, the present review will also discuss aspects of perceptual cognition, extending the project to include sensory integration and responding to socially relevant face and voice information. This review will be used to formulate predictions for a series of experiments that aim to increase understanding of evolved attractiveness preferences. Moreover, the present research will consider attractiveness in multimodal domains in an effort to determine how they can together inform mate choice.

1.2 Attractive faces

Human face attractiveness research has concentrated on three major dimensions; averageness, symmetry and sexual dimorphism (see Rhodes 2006; Thornhill & Gangestad, 1999). Preference for facial averageness is purportedly derived from an innate capacity to process prototypical faces (Langlois & Roggman, 1990). For example, the human face is considered to be a special visual object that is processed in a specific area of the brain (Duchaine, Yovel, Butterworth & Nakayama, 2006; Kanwisher, McDermott & Chun, 1997). Furthermore, the brain does process information that is closer to a prototype much more efficiently (Winkielman, Halberstadt, Fazendeiro & Catty, 2006). Averaged birds, fish and even non-living objects are perceived to be more attractive (Halberstadt & Rhodes 2000; Halberstadt & Rhodes, 2003) and elicit positive affect (Winkielman & Cacioppo, 2001). Babies look longer at average faces, which suggests that preference for prototypical faces is innate, although the development of an average is itself based on visual experience (Rubenstein, Kalakanis & Langlois, 1999). Consequently exposure to faces that deviate from a population average can lead to adaptation to a different facial average (Cooper, Geldart, Mondloch & Maurer, 2006; Webster, Kaping, Mizokami & Duhamel, 2004). Such adaptations have been shown to increase both normality and attractiveness attributions (Rhodes, Jeffery, Watson, Clifford & Nakayama, 2003).

Fluctuating asymmetry (FA) is a feature of human faces that refers to deviation from a symmetrical norm believed to reflect inherent developmental stability (Kowner, 2001). That is, some characteristics of the face are genetically predisposed to have bilateral symmetry. However, normal development, can be disrupted owing to factors such as disease that compromise the immune system and stunt growth (Kowner, 2001). Faces with lower FA are, therefore, purported to be more attractive because they indicate greater immunocompetence: the capability to resist disruption of normal symmetrical development. A number of studies have consistently provided confirmatory evidence that faces with low FA are perceived to be more attractive (Grammer & Thornhill, 1994; Jones et al., 2001; Mealey, Bridgstock & Townsend, 1999; Perrett et al., 1999; Rhodes, Proffitt, Grady & Sumich, 1998; Rhodes, Sumich & Byatt, 1999; Rhodes et al., 2001; Thornhill & Gangestad, 1999). Problematically, average faces tend to be symmetrical (Alley & Cunningham, 1991). Grammer and Thornhill (1994) found that symmetrical but not average faces to be attractive. Such research suggests that averageness may not be an important factor in attractiveness perception when symmetry is controlled for (Grammer & Thornhill, 1994).

Rubenstein, Langlois and Roggman (2002) point out however, that stimuli used by Grammer and Thornhill (1994) comprised up to 16 faces and could be deemed less average than the composite stimuli comprising 32 faces used by Langlois and Roggman (1990). Further investigation indicates that averageness and symmetry are exclusive facets (Jones, Debruine & Little, 2007; Rhodes, Sumich & Byatt, 1999). Rhodes, Sumich and Byatt (1999) found that averageness and symmetry correlated in the stimuli used. However, both symmetry and averageness accounted for a significant proportion of the variance in attractiveness when the other was partialled out (Rhodes, Sumich & Byatt, 1999). Changes in averageness also altered the perception of attractiveness when symmetry was held constant (Rhodes, Sumich & Byatt, 1999). Together, these findings show that both averageness and symmetry appear to independently contribute to the perception of attractiveness.

The importance of average, symmetrical faces appears to be at odds with evidence that infants show strong preferences for looking at distinctive stimuli (Fant, 1964; Hunter & Ames, 1988). In one experiment, infants were shown to be sensitive to facial averageness and symmetry although there was no evidence of a preference for looking longer at more average or more symmetric faces (Rhodes, Geddes, Jeffery, Dziurawiec & Clark, 2002). Adults have further been shown to be more accurate and faster at recognising distinct faces (Valentine, 1991; Valentine, 1992). While average faces can be attractive, not all attractive faces are average (Thornhill & Gangestad, 1999). Attractiveness can also be defined in terms of exaggerated sexually dimorphic traits (Alley & Cunningham, 1991; Baudouin & Tiberghien, 2004; Debruine, Jones, Unger, Little & Feinberg, 2007; Perrett, May & Yoshikawa, 1994; Rhodes, 2006).

Sexual dimorphism occurs in human faces because of relative levels of circulating hormones. The development of masculine features appears to be related to higher concentrations of testosterone (Penton-Voak & Chen, 2004), which exert an influence on the exaggeration of features such as strong jaw line, thick eyebrows, and smaller eyes. By contrast, the development of feminine facial features appear to be related to higher concentrations of oestrogen (Law-Smith et al., 2006). As a result, female faces typically have small chins, high cheek bones and large round eyes; features that signal neoteny (Berry & Mcarthur, 1985; Jones et al., 1995), youthfulness and fertility (Jones et al., 1995).

Female preference for indicators of testosterone are likely to be beneficial because testosterone is an immunosuppressant (Folstad & Karter, 1992, Grossman, 1985). That is, high levels of testosterone serve to lower the immune system rendering an organism more susceptible to bacterial and/or parasitic infection. Zahavi (1975) proposed that the expression of such ornaments is an indication of genetic fitness owing to an organism's survival despite bearing this handicap. For example, an attractive male with high testosterone is likely to be genetically superior owing to normal development despite the handicap of a suppressed immune system. There is some suggestion that oestrogen, like testosterone is deemed attractive in female faces because of similar immunosuppressant properties, although the evidence for this claim is much weaker (see Rhodes, Chan, Zebrowitz & Simmons, 2003). Instead there is stronger support for oestrogen as an indicator of fertility status (Law-Smith et al., 1996; Thornhill & Gangestad, 1999). As such, female faces may have evolved to reflect healthy, fecund females (Thornhill & Gangestad, 1999). Hence, males and females should show preferences for traits that indicate high levels of testosterone and oestrogen respectively.

Males do show a preference for feminine features (Perrett, May & Yoshikawa, 1994; Perrett et al., 1998; Rhodes, Hickford & Jefferey, 2000) and females show a preference for masculine features (Johnston, Hagel, Franklin, Fink & Grammer, 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). Such preferences for feminine and masculine features appear to be universal (Cunningham et al., 1995; Perrett, May & Yoshikawa, 1994; Perrett et al., 1998). However, putative benefits of hormone mediated fitness indicators are likely to lead to preferences for increasingly exaggerated traits. However, male faces with extreme masculine features are not preferred by females (Rhodes, Hickford & Jeffery, 2000). Although exaggerated masculine faces are perceived to be more dominant, they are no more attractive to females (Swaddle & Reierson, 2002). Moreover, some studies have shown that females perceive feminised male faces to be more attractive (Perrett et al., 1998; Rhodes, Hickford & Jeffrey, 2000; Little & Hancock, 2002).

Female preference for feminine male faces could reflect strategic sexual selection. Although high testosterone males purportedly provide genetic benefits, dominant males are associated with negative characteristics such as dishonesty and aggression (Perrett et al., 1998), and are less likely to invest in their offspring (Gangestad & Simpson, 2000; Gray, Kahlenberg, Barrett, Lipson & Ellison, **2**002). Evidence suggests (see Jones, et al., 2008) that female preference for masculine features is more pronounced for short-term partners and when the probability of conception is high (Danel & Pawlowski, 2006; Johnston et al., 2001; Little, Jones, Burt & Perrett, 2007; Little, Jones & Debruine, 2008; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). Pronounced sensitivity to indicators of genetic fitness is most likely used by females for selecting mates that increase the chance of producing healthy progeny.

In contrast, there is evidence of female sensitivity to facial signals indicating potential paternal investment (Roney, Hanson, Durante & Maestripieri, 2006). Moreover, female preference for healthy male faces were found to be strongest during the luteal phase of the ovulation cycle (when females are less likely to conceive) and pronounced for pregnant women (Jones et al., 2005). Cyclic preferences are, therefore, likely to be adaptive. Females are able to maximise genetic fitness of their offspring in the short-term and/or select for paternal investment, or increase the likelihood of a successful pregnancy in the long-term (Jones et al., 2008; Jones et al., 2005; Penton-Voak et al., 1999).

Although female preferences for male faces may vary with regard to ovulation phase, there is contrasting research. For example, cyclic preferences have typically been found with stimuli manipulated on a continuum of sexual dimorphism (see Peters, Simmons & Rhodes, 2009). Using non-manipulated faces, Peters, Simmons and Rhodes (2009) found no evidence of increased female attraction to masculinity in male faces during peak ovulation phase. Cyclic preferences for masculine male faces may be a small effect detectable only when stimuli are manipulated on a single dimension (Peters, Simmons & Rhodes, 2009). Experiments using facial caricatures (Rhodes & Tremewan, 1996) and faces manipulated on a continuum of sexual dimorphism (Perrett et al., 1998; Rhodes, Hickford & Jeffrey, 2000; Little & Hancock, 2002) have also typically found that females prefer feminised male faces. However, a meta-analysis of research shows that females do prefer masculine male faces when experiments use non-manipulated faces (Rhodes, 2006). While there may be variation in female preferences for male faces owing to the ovulation cycle, it is therefore likely that a general preference for masculine faces exists.

1.3 Attractive voices

Vocal communication serves a variety of functions in many animals, including advertising for a mate, intimidating a rival and signalling an alarm call in the presence of a predator (Ohala, 1984). Acoustics can be used to assess the characteristics of the sound-producer (Fitch, 1997). Recently, Evolutionary Psychology has witnessed growing interest with the assessment of vocal parameters as a potential signal of genetic fitness in the domain of human mate selection.

Vocalisations in humans occur through the formation and modulation of auditory frequencies as they travel through the vocal apparatus (Fant, 1960). The larynx situated at the top of the trachea contains elastic structures called vocal folds or cords, which vibrate to modulate the flow of air to produce acoustic energy. The sound created by vibrations of the vocal cords is termed pitch. Although this auditory sensation is referred to in terms of a musical scale, pitch is perceptual (Bendor & Wang, 2006). That is, pitch is a subjective attribute that cannot be measured directly. Pitch is the perception of fundamental frequency (F0); the lowest frequency in a period, of which each harmonic component in a spectrum of complex sound is a multiple (Bendor & Wang, 2006). For example, the 3rd harmonic in a spectrum of sound will be 3 times the frequency and 1/3 the amplitude of the F0 . A F0 of 100Hz, therefore, would have a 3rd harmonic of 300Hz at 1/3 the amplitude, and a 5th harmonic of 500Hz at 1/5 the amplitude.

The function of voice pitch in humans is of evolutionary significance. Voice pitch is sexually dimorphic owing to developmental differences in pubertal hormones (Hollien, 1960). In males, the size of the vocal folds increases rapidly in relation to body size under the influence of higher levels of testosterone (Dabbs & Mallinger, 1999; Hollien, 1960). In contrast, female vocal folds develop very slowly over time owing to higher levels of oestrogen (Arbitbol, Abitbol & Abitbol, 1999; Hollien, 1960). It is the larger vocal folds in males relative to females that result in a lower (on average) voice pitch (Titze, 1994), which emerges as a secondary sexual characteristic. Given the hormone mediated development, the evolution of male voice pitch might be a signal driven by selective female pressures to choose healthy male mates. Similarly, female voices are oestrogen dependent and are thus likely to be driven by male pressures to choose fertile mates. A central prediction here is that females should prefer males with a low voice pitch and males should prefer females with a high voice pitch and that these proposed signals of fitness and fertility respectively should at least be honest. That is, voice pitch is a reliable indicator of mate quality that is selected for by opposite sex partners.

Voice pitch is an element of vocal information that is important for the attribution of attractiveness (Zuckerman & Miyake, 1993). Measures of voice quality, including pitch (deepness, squeakiness and throatiness) and impact (monotonous, loudness and resonance) have been shown to be influential in the attribution of attractive voices (Zuckerman & Miyake, 1993). A number of studies have also shown that pitch preferences are directional, such that, males prefer higher pitch female voices (Collins & Missing, 2003; Feinberg et al., 2005; Fraccaro et al., 2008). Females prefer lower pitch male voices (Bruckert et al., 2006; Collins 2000; Feinberg, Jones, Little, Burt & Perrett, 2005; Feinberg et al., 2006; Feinberg et al., 2008; Puts, 2005; Puts, 2006; Riding, Lonsdale & Brown, 2006; Vukovic et al., 2009), Moreover, female preference for masculine voices develop in conjunction with their reproductive capability (Saxton, Caryl & Roberts, 2006) and is also more pronounced when the probability of conception is high (Feinberg et al., 2006; Puts, 2005; Puts, 2006).

While it is clear from studies of vocal attractiveness that there are general sex-specific preferences relating to sexual selection, the role of voice pitch in mate choice is more equivocal. Although voice pitch may be a viable indicator of male fitness and female fertility, to date, there is no direct evidence that males or females actively select mates based on this signal. Unless the presence of a signal (e.g. voice pitch) leads to copulation such signals might only be a social preference rather than a sexually selected trait (see Snowden, 2004). For example, in a study using mice (a comparable social species), Gubernick and Addington (1994) found that given a choice of two potential mates, female mice develop a preference for one male mouse over the other (irrespective of oestrus). However, such preferences translated to actual mating in only 50% of cases. Moreover of those that mated, only 60% mated with their preferred partner. In short, preferences do not necessarily lead to mating, and mating may not occur with the preferred mate.

It is possible that female preferences for male voice pitch may not, therefore, actually reflect a signal that ultimately leads to copulation. For example, research that showed voice pitch can elicit a sexual arousal response in the receiver would provide some evidence of such a causal link. However, evidence showing that men with low voice pitch have more sexual partners (Hughes, Dispenza & Gallup, 2004; Puts, 2005) and sire more children (Apicella, Feinberg & Marlowe, 2007) appears compelling. Nevertheless, voice pitch is one signal amongst many that could be used. It might be that a high testosterone male is attractive because of the hormone mediated influence on face morphology rather than vocal folds. This may particularly be the case since vocalisations are subject to aberrations as a result of relaxed muscle control over the course of a day (Titze, 1994) and emotional/arousal state (Banse & Scherer, 1996; Millot & Brand, 2001; Russell, Bachorowski & Fernandez-Dols, 2003), which could render it a less reliable indicator.

It is possible, however, that male vocalisations serve another function. Male voice pitch purportedly developed through intra-sexual pressures as a symbol of dominance and aggression (Puts, Gaulin & Verdoloni, 2006; Puts, Hodges, Cárdenas

& Gaulin, 2007) as in other animals such as the red deer (*cervus elaphus;* see Clutton-Brock & Albon, 1979). For example, males have been shown to modulate their voice pitch down in the presence of a perceived less dominant male (Puts, Gaulin & Verdolini, 2006). Evidence of reproductive success related to low voice pitch in a tribe of hunter gatherers (Apicella, Feinberg & Marlowe, 2007) could, therefore, reflect selection for dominance and social rank. This may be particularly important in populations where access to resources is paramount. Thus rather than selecting for genetic fitness (indirect genetic benefits), it could be that females are selecting for partners capable of providing food for their offspring (direct benefits).

Female preferences for low voice pitch may be a more important factor in attributing dominance. In one study, voices that were manipulated to be slightly higher in pitch were rated by female participants as more benevolent (Riding et al., 2006). Furthermore, vocal attractiveness (low pitch) was shown to significantly affect judgments of dominance (Zuckerman & Driver, 1989; Zuckerman et al., 1990). Female mate choice based on investment potential would be particularly useful since masculine, dominant men are less likely to invest in and support their offspring (Gangestad & Simpson, 2000; Gray et al., 2002). Indeed, Roney et al. (2006) found that male interest in children predicted female attractiveness ratings of male faces in a long-term mating context. However, attractiveness and pro-social attributes were found to negatively correlate with male participants' ability to engage in child directed speech (determined by higher average voice pitch) when asked to give directions to an imaginary child (Penton-Voak et al., 2007). These results were discussed in terms of a possible halo effect. That is, attractive faces were attributed with positive characteristics (Penton-Voak et al., 2007). As such, voices may not be a reliable or important aspect of attractiveness attribution if they can be influenced by physical appearance.

1.4 A framework for signal integration

The importance and function of mate quality signals expressed in human faces and voices, for example, is limited in that little is known about their combined effect when presented together. Partan and Marler (1999) proposed that multiple signals can be divided into *redundant* and *non-redundant* signals (see Figure 1.1).

Redundant signals transmit the same information and can be equivalent or multiplicative in their effect. In different environmental conditions redundant signals could be useful communicating the signal in the most effective modality. In contrast, non-redundant signals transmit more information and tend not to be related to each other. As such, non-redundant signals are likely to express different aspects of a mate that leads to a variety of responses from the receiver. For example, two signals may have effects that are independent of each other, one signal may predominate, one signal may modulate the perception of another, or the combination of two signals may lead to the emergence of a new response.

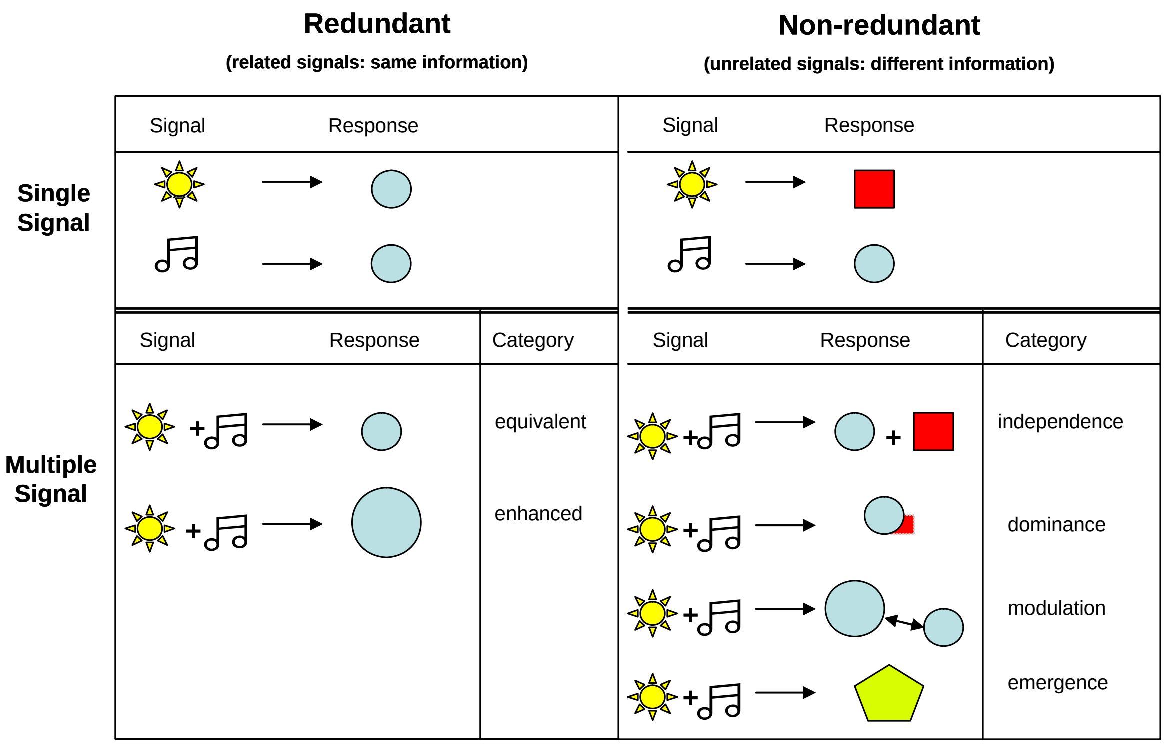

Figure 1.1: *The effect of two signals on the response of a receiver when presented singularly or together as redundant and non-redundant multiple signals, adapted from Partan and Marler (1999)*

The work of Partan and Marler (1999) provides an excellent illustration of the variable effects produced when two signals are presented together. Moreover, they highlight the importance of considering multiple signals together in an effort to elucidate their combined effects. For example, voice pitch could have little or no effect on attractiveness ratings when presented together with a face. However, Rowe (1999a) criticised the work of Partan and Marler (1999) for arguing that each signal, whether redundant or non-redundant, elicits a response on its own. Much of the sexual selection research has focused on identifying the evolutionary benefit of a signal in terms of heritable genetic fitness. It is possible that some signals produce no response on their own but serve to enhance another signal (Rowe, 1999a). For example, vocalisations could serve to enhance the detection of a potential male mate or rival over a greater distance. If a signal is not costly to produce (i.e. no risk to health) and can facilitate the detection of another more salient signal, it is likely to be adaptive (Rowe, 1999b). That is, if a signal elicits no response but rather increases the likelihood of detection it may be adaptive although the signal itself is uninformative. As such, signals can be categorised as being reliable, unreliable or even uninformative with regard to mate quality.

Although Partan and Marler (1999) provided a useful illustration of the combined effects of multiple signals, Candolin (2003) extended the framework to include more categories by which multiple signals can be defined (see Figure 1.1). Multiple signals may be (a) *adaptive*, such that, the presence of more than one signal reduces mate choice costs and errors, (b) *non-adaptive*: having no influence on fitness and are simply remnants of past selection, or (c) *maladaptive*, they appeal to a pre-existing bias that aids sexual selection but they are costly to the receiver. Furthermore, Candolin (2003) proposed that signals can further be categorised depending on their content. Signals may be *informative* (providing information about mate quality) or *uninformative* (providing no indicators about mate quality) although they can still be adaptive, have no influence or be maladaptive. The following section will discuss theories relating to adaptive informative signals and adaptive uninformative signals.

Nature of signal	Information Content	Signal Type Hypotheses	Proximate benefit
Adaptive	Informative →	*Multiple messages*	Assessment of overall quality
	Informative →	*Back-up signals*	More accurate assessment
	Informative →	*Fisherian signals*	Heritable attractiveness
	Uninformative →	*Receiver psychology*	Facilitates mate assessment
Non-adaptive	Uninformative		No effect
Maladaptive	Uninformative		Costly

Figure 1.2: *Categories[1] of multiple signal hypotheses adapted from Candolin (2003)*

1 Hypotheses relating to *species recognition* and *unreliable signals* have been omitted since (a) this review is not concerned with avoiding mating with other species and (b) unreliable signals have no direct benefits, but are proposed to call attention to other signals (Candolin, 2003). As such, unreliable signals could be subsumed by receiver psychology.

1.4.1 Adaptive informative signals

1.4.1.1 *The Multiple messages hypothesis*

Multiple messages occur where two signals communicate independent information about mate quality (Møller and Pomiankowski, 1993). Although unrelated, together they can provide a more accurate estimation of overall quality. Multiple messages that communicate independent qualities could be used differentially depending on their relative importance to the receiver. In human mate choice, females could weight multiple messages differently when considering direct or indirect benefits for example (Candolin, 2003). A female with access to resources need not select for direct benefits if she is already capable of providing for her children and as such might prefer to choose partners with greater fitness indicators. Females are, however, less likely to use signals of fitness where there is little variation between mates or the signals themselves are difficult to detect given perceptual or environmental constraints (Cotton, Small & Pomiankowski, 2006; Roberts & Gosling, 2003). Moreover, there are different costs associated with varying environments: the relative prevalence of disease (risk of disease/infection is high) makes selection for an optimal immune system more important. Females are therefore more likely to use information that allows for the most appropriate signals to be used in a given context.

1.4.1.2 *Back-up signals hypothesis*

Back-up signals occur where two signals communicate information pertaining to a single message. All signals are communicated with a degree of error or dishonesty (Guilford & Dawkins, 1991). The presence of more than one signal pertaining to a single trait makes dishonesty, such as attempts to mimic, less effective. As such, back-up signals allow for a more accurate assessment of a single trait (Møller & Pomiankowski, 1993). The belief here is that all signals reflect the same underlying trait, such as levels of testosterone, albeit with a certain degree of error. As such, back-up signals should correlate with each other. There is a similarity between multiple messages and back-up signals in that traits that correlate with overall fitness are essentially back-up signals (Candolin, 2003). However, signals often do not correlate with each other, rendering back-up signals less common than multiple messages (Candolin, 2003).

1.4.1.3 *Fisherian runaway signals hypothesis*

A final form of informative adaptive signals are those which arise through Fisher's runaway process. Fisher (1930) proposed that attractive traits could grow exponentially through sexual selection, provided that the magnitude of average male traits grew in accordance with female preferences over each successive generation and, that magnitude was not stabilised owing to costs incurred by inheritance. For example, female preferences for the peacock's tail could have adapted to genetic drift causing an increase in average size. As long as the fitness of progeny does not suffer as a result of a larger trait, both preference for and increase in trait size will be inherited. Fisherian traits are informative because they may have once (although possibly no longer) correlated with fitness (Fisher, 1930). Moreover, the heritability of Fisherian traits and their relationship with attractiveness are adaptive since males possessing the trait are likely to mate.

1.4.2 Adaptive uninformative signals

1.4.2.1 *Receiver psychology hypothesis*

Signals related to receiver psychology exploit pre-existing sensory biases in the receiver and can be assessed alongside other more reliable signals (Iwasa & Pomiankowski, 1994; reviewed by Rowe 1999b). Rather than shape a response, signals that develop through receiver psychology hijack a response that already exists (Ryan, 1998). Such signals often do not indicate any indirect genetic benefits and are, therefore, termed unreliable (Møller & Pomiankowski, 1993). However, if signals are relatively cheap to produce and can attract attention to another more informative signal, then they are likely to be adaptive (Rowe, 1999b).

Signals related to receiver psychology are proposed to enhance the detection and discrimination of another signal (Guilford & Dawkins, 1991; Rowe, 1999b). For example, reaction times are faster when two signals are presented together than when separate (Miller, 1982; Rahne, Bockmann, von Specht & Sussman, 2007; Vroomen & de Gelder, 2000). Vocalisations could serve to amplify other more fixed morphological signals where there is impoverished light conditions (Rowe, 1999b). Receiver psychology signals also improve discrimination of other signals (Rowe, 1999b). Speech, for example, is more easily perceived when both visual and auditory information are available (Chen & Rao, 1998). Although acoustic signals may not aid facial recognition *per se*, it is possible that sound is used to make facial discriminations (Kendrick et al., 1995). Some signals may not produce a response by themselves but could have adaptive significance by integrating with more informative signals thus improving transmission.

1.4.3 Summary

Explanations that are not mutually exclusive are a particular challenge for multiple signal research (Hebets & Papaj, 2005). For example, multiple signals may correlate with overall fitness and yet signal different aspects of a potential mate (Candolin, 2003). Thus, careful scrutiny of individual signals is important and in order to elucidate their function, inclusion and analysis of multiple signals is critical (Hebets & Papaj, 2005). The framework outlined by Candolin (2003) defines multiple signals as being informative (provides information) or uninformative (does not provide information) about mate quality, whilst being adaptive, non-adaptive or even maladaptive. When presented together, signals can have several potential effects on the receiver, by producing equivalent or enhanced responses (see Partan & Marler, 1999) or by simply improving transmission of another signal (see Rowe, 1999b). Considering prevailing research on multiple signals with reference to the framework proposed by Candolin (2003) is crucial for hypothesis testing. Moreover, investigating the effects and relative influence of signals presented together may be crucial for understanding their relative function in mate choice.

1.5 Integrating human face and voice attractiveness

In humans, very little research has focused on the interaction between signals of putative genetic quality in sexual selection. Signals such as facial attraction (Rhodes, 2006; Rhodes et al., 1998; Rhodes et al., 2001; Thornhill & Gangestad, 1999) and voice pitch (Evans, Neave & Wakelin, 2006; Hughes, Dispenza & Gallup, 2004; Hughes, Harrison & Gallup, 2002; Hughes, Pistazzo & Gallup, 2008) have been proposed as indicators of fitness selected for by potential partners. This section will consider the prevailing research in an effort to integrate face and voice signals within the multiple signal framework.

Face and voice signals are unlikely to develop under selective pressures akin to Fisher's runaway process. For example, evidence of female cyclic preferences for masculinity (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999; Puts, 2005; Puts, 2006) and evidence that extreme sexually dimorphic features are not preferred (Rhodes et al., 2000), suggests that faces and voices are stabilised. That is, they are not driven by preference for increasing exaggeration. Rather, given the proposed directional selection for hormone dependent traits, it could be that faces and voices are back-up signals. As such, it is expected that females should have a preference for a masculine face and low pitched voice, and that both signals correlate in males. Furthermore, males should prefer a feminine face and high voice pitch, which should correlate in females.

Female faces that express higher oestrogen levels are more attractive (Law-Smith et al., 2006). High voice pitched females also have higher oestrogen than those with low pitched voices (Arbitbol, Abitbol & Abitbol, 1999). Oestrogen may be linked to successful conception (Baird et al., 1997; Baird et al., 1999) and has been shown to correlate with, for example, follicle size and egg quality (Eissa et al., 1986; Woodruff & Mayo, 2005). Female voices are, therefore, likely to also reflect levels of oestrogen and thus fertility. Males prefer more feminine faces (Feinberg et al., 2005; Johnston et al., 2001; Law-Smith et al., 2006; Perrett et al. 1998; Rhodes et al., 2000) and have been shown consistently to find higher voice pitched female voices more attractive than lower voice pitched females (Collins & Missing, 2003; Feinberg et al., 2005; Fraccaro et al., 2008). Moreover, evidence has supported the positive relationship between attractive faces and voices in female stimuli (Collins & Missing, 2003; Feinberg et al., 2005; Lander, 2008; Saxton et al., 2009). The relationship between male preferences for female faces and voices suggests (see Feinberg, 2008) that they are back-up signals transmitting information with regard to a single trait (i.e. fertility).

Since an attractive male face and voice are proposed to signal the same information (i.e., high testosterone), they are also likely to be back-up signals. There is some evidence of a positive relationship between testosterone and attractive male faces (Pento-Voak & Chen, 2004; although see Swaddle & Reierson, 2002). Research has also shown a general female preference for masculine faces (Keating, 1985; Koehler et al., 2004; Penton-Voak et al., 2001; Scheib, Gangestad & Thornhill, 1999; although see Perrett et al., 1998; Penton-Voak, Jacobson & Trivers, 2004). This effect is most apparent at peak ovulation phase when reproductive benefits are paramount (Johnston et al., 2001; Jones et al., 2008; Little et al., 2007; although see Peters, Simmons & Rhodes, 2009). A relationship also exists between testosterone and male voice pitch (Dabbs & Mallinger, 1999) and there is evidence of a general female preference for low male voice pitch (Apicella, Feinberg & Marlowe, 2007; Bruckert et al., 2006; Collins 2000; Feinberg et al., 2006) that is most apparent at peak ovulation phase (Feinberg et al., 2006; Puts, 2005).

A number of studies have shown there to be a relationship between preferences for male faces and voices (Feinberg et al., 2008; Saxton, Caryl & Roberts, 2006; Saxton et al., 2009). However, while there is concordance between findings from the investigation of female signals, the relationship between face and voice attractiveness in males is equivocal. For example, two studies found no relationship between male face and voice attractiveness (Oguchi & Kikuchi, 1997; Lander, 2008). It is important to discuss the discrepancies between these studies in an effort to improve understanding of male face and voice attractiveness.

Feinberg et al. (2008) investigated female preferences for male face and voice stimuli that were manipulated on a continuum of masculinity. While females were shown to prefer a masculine face and voice (Feinberg et al., 2008), the manipulated stimuli were from different sources and so this does not address the question of whether a masculine face and voice occur in an individual (Wells, Dunn, Sergeant & Davies, 2009). Also, both the Feinberg et al.(2008) and the Saxton, Caryl & Roberts (2006) studies found correlated face and voice preferences using a forced-choice paradigm, where participants continually chose the most attractive of two simultaneously presented stimuli (relative judgement) as opposed to rating a single stimulus on a scale (absolute judgement; see Lander 2008).

Humans may often use (either internally or externally) a referent with which to judge the attractiveness of a potential mate. Comparative evaluation may be an important aspect of mate choice although such contexts render decisions to be labile (see Bateson & Healy, 2005). For example, the attractiveness of a target face is influenced by the assimilation of juxtaposed faces (Geiselman, Haight & Kimata, 1984; Wedell, Parducci & Geiselman, 1987). The relationship between findings based on relative and absolute judgments would be an interesting focus of further investigation. Nevertheless, discrepancies between studies applying different methods pose interesting questions regarding the perception of signals. For example, relative judgements have been shown to be more sensitive compared to absolute judgements when detecting small differences between images (Gur et al., 1997). This is evident in judgements of masculine faces which were more pronounced when differences between testosterone indicators were large (Penton-Voak & Chen, 2004). As such, it could be that preferences for male voices are shown to be related to faces only when signals are evaluated in comparison to a referent stimulus. This is compounded by evidence that male face and voice attractiveness ratings were not found to be related when participants provided an absolute judgement for faces and voices separately (Lander, 2008).

Face and voice attractiveness may not be related in males owing to the function of voices and the evolutionary pressure governing vocal development and propagation in sexual selection (see Wells et al., 2009). Voice pitch is likely to have developed in males as a signal of dominance and aggression through intra-sexual selection pressures (Clutton-Brock & Albon, 1979; Puts et al., 2006; Puts et al., 2007). Divergent pressures influencing face and voice selection could mean that the attractiveness of faces and voices are unrelated in an individual. That is, a male with an attractive masculine face may not necessarily have an attractive voice. Rather than back-up signals, the face and voice of males could communicate multiple messages. While the face may provide an indication of indirect genetic benefits related to immunocompetence, male voices could be used to indicate dominance and direct benefits such as access to resources or investment potential. As such, both face and voices could be unrelated in an individual yet contribute independently to the overall attractiveness of a male.

In a recent study, however, Saxton et al. (2009) found that the attractiveness of male faces and voices were related when stimuli were rated separately using a rating scale (although not when analysed by sex of the rater possibly owing to a small sample size; Saxton et al., 2009). Using a regression analysis faces and voices were shown to contribute comparably to the attractiveness of face-voice compound stimuli. Similar effects for the contribution of faces and voices to compound stimuli may appear surprising since humans are visually dominant animals and variation evident in vocalisations may render it a less reliable signal.

One issue with the Saxton et al. (2009) study may be that participants were assumed to be homogeneous in their attractiveness preferences. As such, different groups were used to rate the attractiveness of individual cues and the face-voice compounds. Moreover, participant averages were used to detect the relationship between face and voice attractiveness. Using average ratings could lead to an ecological fallacy (Robinson, 1950). That is, stimuli averages could be erroneously inferred as representative of individual stimuli attractiveness. Importantly, looking only at group or participant averaged data can produce different size or even direction of a relationship between variables compared to correlations between individual observations. Regressing participant averages could therefore produce misleading estimates of face and voice effects on compound stimuli attractiveness.

Although there is some evidence of universal attractiveness (e.g. Cunningham et al., 1995), there is a growing body of evidence as to the heterogeneity of attractiveness judgements owing to a number of factors including, for example, parental influence, sexual history and self-perceived mate value (DeBruine et al., 2006; Jennions & Petrie, 1997; Widemo & Saether, 1999). Individual preferences have also been shown to have an important influence on attractiveness ratings compared to shared preferences (Hönekopp, 2006). Accommodating sources of variance between individuals and stimuli would provide more accurate data with regard to face and voice attractiveness effects. In order to determine face and voice effects on face-voice compound attractiveness, further investigation should therefore incorporate individual participants' ratings of each component. Moreover, investigating the relationship between face and voice attractiveness should incorporate scores for individual stimuli for each participant rather than using participant averages in order to incorporate variance within participants and between stimuli.

1.5.1 Summary

The face and voice of males and females are proposed to signal the same information (i.e. underlying sex related hormone levels) and as such may be back-up signals. Research has supported the relationship between female face and voice attractiveness although evidence of a relationship between male face and voice attractiveness appears equivocal. Male faces and voices could be multiple messages, communicating independent information thus providing females with an estimate of overall mate quality. Further investigation of the relationship between and influence of face and voice signals in males and females would further enhance this suggestion.

1.6 Perceptual cognition

Faces and voices together may not necessarily contribute toward an overall perception of attractiveness. Rather, they may function together by enhancing cognition through sensory integration. The receiver psychology hypothesis, for example, describes signals that evolve alongside more informative signals in order to facilitate detection and discrimination. Rather than elicit any meaningful effect on their own, male voices could simply improve the ability to detect and respond to male attractiveness. There is reason to believe that face and voice together could enhance cognition. Sensory regions within the brain were historically considered to be modular. However, sensory regions have more recently been shown to have enormous plasticity potential (see Shimojo & Shams, 2001). For example, studies have shown that cortical areas typically developing to process visual information are activated by auditory input when subjects are deprived of visual input (e.g. Uhl, Franzen, Lindinger, Lange & Deecke, 1991). Such plasticity evident in cortical organisation allows for integration of multimodal information.

Sensory integration has an important role in perception. For example, visual experience can alter the perception of auditory information; the word ‘da’ is perceived when the sound ‘ba’ is presented with a mouth miming the word ‘ga’ (McGurk & MacDonald, 1976). Auditory signals can also alter visual perception. For example, participants are more accurate making temporal order judgements when a light is both preceded and followed by a tone (Scheier, Nijwahan & Shimojo 1999). The modulatory appropriateness hypothesis (Welch & Warren, 1980) posits that sensory information that is either most relevant or reliable in a given task will predominate. Vision therefore influences spatial tasks owing to higher spatial resolution while audition influences temporal tasks owing to higher temporal resolution (Shimojo & Shams, 2001).

Auditory interactions with visual input are not limited to temporal tasks. Maurer, Pathman and Mondloch (2006) demonstrated that there is a pre-existing bias for visual stimuli with sharp edges to be associated with harsh sounds, whilst stimuli with soft edges are associated with soft sounds. Moreover, it has been shown that such examples of inter-sensory facilitation aid object recognition (Amedi, von Kriegstein, van Atteveldt, Beauchamp & Naumer, 2005; Beauchamp, Lee, Argall & Martin, 2004; Molholm, Ritter, Javitt & Foxe, 2004). Evidence of voice pitch modulation (Millot & Brand, 2001; Puts et al., 2006) could, therefore, serve to either shape or draw attention to fixed morphological features: modulation of a low pitch could enhance a male’s masculinity. Conversely, modulation of a higher pitch could allow the same male face to be perceived as less threatening by a female partner or more feminine in the case of a female face.

Vocal interactions with face perception may be an important aspect of human perception. There is some evidence to suggest that voices may be a special case of auditory perception (Belin, Fecteau & Bedard, 2004). Moreover, functional magnetic resonance imaging (fMRI) has shown that the primary auditory cortex is activated when participants view a face mouthing words without sound (Calvert et al., 1997). The influence of vocal information on face perception may be dependent on aspects such as quality and intensity of the signal. There is evidence that the structure of visual perception can be enhanced or even altered by specific auditory information. A recent study (Smith, Grabowecky & Suzuki, 2007) conducted an experiment where participants rated the masculinity or femininity of androgynous faces. When paired with a low frequency (male) or high frequency (female) pure auditory tone, participants rated an androgynous faces in accordance with the respective male or female tone. However, on their own, the tones were not rated as either male or female. This findings suggest that auditory signals are important for influencing face perception, although auditory signals by themselves serve to facilitate recognition and discrimination of faces.

Multiple signals can increase the probability of detection against background noise (Rowe, 1999b). Reaction times, for example, are faster when responding to two signals that are presented together than when separate (Bernstein, Clark & Edelstein, 1969; Miller, 1982). This is evident when the multiple signals are bimodal (Miller, 1982; Rahne et al., 2007; Vroomen & de Gelder, 2000) owing to inter-sensory facilitation. That is, integration between sensory modalities in the brain serves to enhance perception. Miller’s (1982) race inequality model proposed that inter-sensory facilitation is evident when the probability of detecting a bimodal target is significantly faster than the sum of probabilities for detecting either of the two unimodal targets.

While inter-sensory facilitation occurs for an auditory stimulus accompanying a visual stimulus, the same does not occur when reversed (Miller, 1986). In such instances, multiple signals can actually inhibit performance because of a visual dominance effect (Colavita, 1974). Sinnett, Soto-Faraco and Spence (2008) found both sensory facilitation and sensory competition in a single experiment depending on whether the target modality was either visual or auditory respectively. In a mixed block design, participants were asked to respond as rapidly as possible to a specific visual or auditory target and withhold responses to the non-target in a variation of a go/no-go task. Stimuli were randomly presented in unimodal and bimodal forms. Response latencies showed faster responding to visual compared to auditory targets. While bimodal trials facilitated faster responses to visual targets, bimodal trials impeded responses to auditory targets.

Participants in Sinnett et al.'s (2008) study responded to either the sound of a cat meowing in the auditory target phase, a picture of a stop light in the visual phase or to both when they occurred together in either phase (Sinnett, Soto-Faraco & Spence, 2008). Stimuli used in the experiment were however, unrelated. Target detection occurs more often in an ecological condition when stimuli are related. When detecting human emotional responses, for example, both face and voice arise from the same source. Since face and voice perception appear to be interrelated (see Calvert et al., 1997) it is quite possible that the presence of related bimodal information will facilitate response times rather than impede them, irrespective of target modality. That is, visual dominance may be less likely to occur when the stimuli are faces and voices originating from the same source.

The assumption of unity refers to the commonly held belief that information occurring together is likely to originate from a single source (see Welch & Warren, 1980). Two fundamental sources of information that affect perceptual unity are space and time (Radeau, 1994). For example, integration of speech occurs with synchronous and not asynchronous mouth movements (Calvert et al., 1997). Such evidence suggests that temporal aspects can affect perceptual binding. It therefore follows that spatial incongruency may similarly affect the binding of multiple sources of information into a perceptual whole.

Behaviour toward a visual target may be dependent on the location of an accompanying auditory stimulus. Animals trained to approach a target, for example, were enhanced by auditory stimuli in the same location and impeded by an auditory target in a different location to the visual stimulus (Stein, Meredith, Huneycutt & McDade, 1989). In humans, bimodal stimuli response timing of arm movements (Simon & Craft, 1970) and saccadic eye movements (Lee, Chung, Kim & Park, 1991) toward a visual target are faster when accompanied by auditory stimuli emanating from a congruent location. Moreover, evidence of event related potentials (ERPs) and positron emission tomography (PET) have shown distinctive patterns of brain activation in regions related to bimodal stimuli presented in different compared to same spatial locations (Macaluso, George, Dolan, Spence & Driver, 2004; Teder-Sälejärvi, DiRusso, McDonald & Hillyard, 2005). Such evidence suggests that perceptual binding is related to the spatial/temporal contiguity of stimuli.

There is, however, evidence that performance relating to disrupted spatial contiguity can be unaffected or even enhanced. Response to visual stimuli when accompanied by auditory stimuli showed decreased response latencies irrespective of spatial location (Teder-Sälejärvi et al., 2005). These findings can be explained in terms of the ventriloquism effect. That is, visual location can be biased by auditory stimuli. Audio-visual integration may occur early in the attention process (Colin, Radeau, Soquet, Dachy & Deltenre, 2002) with both auditory and visual spatial information integrated in the superior colliculi of mammals (see Stein & Meredith, 1993). Neural responses in the superior collicului of a cat (analogous to the human superior colliculi) are greater when auditory and visual stimuli are presented at roughly the same time and spatial location (Meredith & Stein, 1986).

Since auditory receptive fields are much larger than visual receptive fields in the superior colliculi (Knudsen, 1982), overlap between them leads to an aggregate in localisation (Knudsen & Brainard, 1995). Higher spatial acuity in the visual fields leads to visual dominance (Shimojo & Shams, 2001), therefore, incongruent audio-visual information biases auditory location toward the visual target. While visual location can be biased by auditory stimuli, however, auditory location is less often biased by visual information (for a review see, de Gelder & Bertelson, 2003). Rather than enhance perception, auditory signals may therefore serve to shift attention to a visual object even when the auditory stimuli is spatially incongruent with the visual stimuli.

1.6.1 Perceptual cognition and attractiveness

Auditory and visual information together may serve to enhance responding to stimuli through sensory integration. An important consideration that has received little attention, however, is how signals of putative mate quality affect the temporal attribution of attractiveness. Face and voices have both independently been shown to influence attractiveness judgements. However, it remains unclear whether the voice, by itself, is a strong selective criterion. Some species of female treefrogs (e.g. family *hylidae*) are attracted to male calling and movement toward the male frog is likely to result in mating (Gerhardt, 1991). As such, there is a direct relationship between the signal, signal quality and sexual selection. In humans, low voice pitch males have more sexual partners (Hughes, Dispenza & Gallup, 2004; Puts, 2005) and sire more children (Apicella, Feinberg & Marlowe, 2007). However, there is little evidence of causation; that the voice itself was the motivation for mating behaviour. Human voices do influence attractiveness judgements but they could also serve another function; the receiver psychology hypothesis describes signals that evolve alongside more informative signals in order to facilitate detection and discrimination. Rather than elicit any meaningful effect on their own, male voices could simply improve the ability to detect and respond to male face attractiveness.

The potential cost associated with making the wrong decision is likely to affect mate choice (Chittka, Skorupski & Raine, 2009). In a study of romantic first-time encounters, for example, female professed interest in a male was concealed for between 4-10 minutes following initiation (Grammer, Kruck, Juette & Fink, 2000). During this time, females attempt to ascertain male intention by initially concealing theirs because males are more prone to seeking short term partners and may attempt deception (Grammer et al., 2000). This delay tactic may be a strategic attempt to gather or process more information about the potential partner. Nevertheless, research indicates that initiation often begins with female non-verbal communication (e.g. coy smile, short glance; see Grammer, 1990; Grammer et al., 2000). Such initiation is likely to be based on impressions of attractiveness from auditory and visual signals initially available.

Zuckerman, Miyake and Hodgins (1991) found that faces influenced attractive voice judgements (and visa versa) irrespective of whether participants were asked to ignore one of the modalities. However, research has not investigated whether attractiveness judgements take longer when both signals are present. Face attractiveness can be assessed in as little as 100 milliseconds (Willis & Todorov, 2006). However, humans tend to stare longer at attractive faces (Kampe, Frith, Nolan & Frith, 2001; Shimojo, Simion, Shimojo & Scheier, 2003) possibly because fMRI studies have shown attractive faces to be rewarding (Aharon et al., 2001; Kranz & Ishai, 2006; O'Doherty et al., 2003). There is also evidence that humans more readily attribute negative characteristics to unattractive faces (Griffin & Langlois, 2006). Such evidence supports a negative bias. That is, humans find it easy to reject stimuli that have negative characteristics and take more time over decisions to determine positive ones.

There is a relationship between the difficulties of a decision and the speed and accuracy with which the decision can be made (see Chittka et al., 2009). This may be particularly important for female decisions given evidence that the attractiveness of male faces and voices may be unrelated (Lander, 2008; Oguchi & Kikuchi, 1997; although see Saxton et al., 2006; Saxton et al., 2009) and may communicate different messages. Speed-accuracy trade-offs are common and can be affected by environmental noise affecting perception (Chittka et al., 2009). Face attractiveness is typically determined in experimental research using stimuli presented immediately on a screen. In approaching a person, visibility may not always be clear either because of distance from the target or environmental conditions.

Vocalisations may better communicate mate quality over distance or through visual noise. For example, detecting emotional expression has been shown to be improved when both the face and voice were congruent and presented together (Collingnon et al., 2008). However, determining emotional expression was predominantly made using a voice when the face was blurred (Collingnon et al., 2008). The relationship between face and voice attractiveness judgements in differing environmental conditions has not yet been explored. It is possible that more weight may be given to face or voice attractiveness respectively in the context of environmental noise. Alternatively, determining attractiveness of a person may take longer or as a result of inefficient processing be made faster but be less accurate.

1.6.2 Summary

Faces and voices could together enhance detection and discrimination of face-voice compound stimuli. Typically, studies have investigated the effect of auditory stimuli on response timing and localisation of a visual target. In response to auditory targets, visual stimuli can impede reaction times (Sinett, Soto-Faraco & Spence, 2008) although this may not be true when stimuli are related. Although localisation can accurately be detected using auditory information, it is less influenced by accompanying visual stimuli when compared to localising visual information accompanied by auditory stimuli (see Recanzone, 2009). While auditory signals may enhance visual perception by decreasing response latency regardless of spatial location, the same may not be true in reverse.

There has been little research on the application of response timing to the attribution of attractiveness. Faces can be detected rapidly although gaze latencies are longer for more attractive faces. Decisions, however can be affected by environmental noise. It is unclear whether, akin to the discrimination of emotion (See Collignon et al., 2008), attractiveness is attributed more rapidly in the presence of a face and voice. However, such decisions may be affected in perceptions of male stimuli because face and voice attractiveness are proposed to be unrelated. Investigating the cognitive benefits of face-voice integration would show how information can be used in a multimodal environment in order to potentially improve the time with which it takes to detect or discriminate the attractiveness of an individual.

1.7 General summary

This review has provided a comprehensive account of both facial and vocal signals. With reference to a framework for signal interaction, this review provides a number of intriguing considerations with which to base experimentation in an effort to resolve the functional nature of multiple signals. There are a number of potential theoretical explanations that could be applied to potential findings. For example, signals may have adaptive value but may be uninformative about the source of the signal or what is being signalled. Moreover, considering signals presented together may be used to estimate the relative influence of face and voice attractiveness with regard to face-voice compound stimuli and thus their respective importance independently. Considering the integration of signals and the potential cognitive benefits of multimodal information also promises to show whether information occurring together is likely to form a unified perception. Such findings are important for methodological considerations of multimodal attractiveness experiments. Moreover, such findings could further elucidate the benefits of multimodal information with regard to detection and discrimination of attractive stimuli.

In an effort to elucidate the function of face and voice attractiveness, it is important that attention is paid to both the methods and exploration of findings. A key element of this research is to investigate modality related effects of visual and auditory information using related face and voice stimuli from each individual participant. The next chapter will therefore begin by detailing the methods used to develop a stimuli database for use in subsequent experiments. Chapter 2 will also describe the manipulation of stimuli specific to each experiment. The aim of experiment 1 in the following chapter will then be to ascertain the relationship between face and voice attractiveness for both male and female stimuli. In addition, experiment 1 will investigate the relative influence of face and voice attractiveness on face-voice compound stimuli attractiveness where vocalisations comprise vowel sounds.

CHAPTER 2: STIMULI DEVELOPMENT

2.1 Introduction

A database of stimuli was created for investigating the relationship between face and voice attractiveness. Previous research investigating female preferences for masculine male faces and voices (Feinberg et al., 2008) used only a small sample of 6 stimuli manipulated on a continuum of sexual dimorphism to create several variations of each. Manipulated face stimuli may produce effects that are not evident when natural faces are used (see Peters, Simmons & Rhodes, 2009) because faces vary on more than one dimension (e.g., feature size/ratio, skin condition). The intention here was to use natural stimuli that had not been manipulated on any dimension; with faces and voices from the same individual. As such, it may be possible to consider the effect of masculinity and the relationship between face and voice attractiveness in an individual male.

This chapter will detail the demographics of participants whose face and voice information comprised the stimuli database (section 2.3) before discussing the methods of stimuli generation, which includes recording equipment and computer software (section 2.4). Section 2.5 then deals with the treatment of stimuli specific to each experimental chapter. However, the following section will begin first by providing information relating to ethical considerations of this research.

2.2 Ethical considerations

Participants were recruited via emails and flyers advertising the opportunity to provide photographs and vocal samples for an experimental stimuli database. Advertisements were placed in locations such as the Nottingham Trent University library and Students Union building. Effort was made to limit the possibility that the sample contained individuals who were known to the target (undergraduate psychology students) experimental population. This made it possible to avoid asking experimental participants to rate the attractiveness of friends or peers. Furthermore, this would avoid any potential confounds of familiarity on attractiveness ratings.

Participants were rewarded with a £10 shopping voucher for taking part. Irrespective of the payment, participants providing stimuli retained their right to withdraw their stimuli from the database at any point. This research was approved by the ethical committee of the division of psychology at Nottingham Trent University.

2.3 Stimuli

Stimuli from 60 participants were collated. Demographics including age and ethnic origin were recorded in addition to whether participants smoke. Smoking has been shown to artificially lower voice pitch (Sorenson & Horii, 2002) and thus it could be a potential confound in vocal attractiveness ratings. Although limited, some research suggests that sexual orientation can also be detected from at least male vocalisations (Linville 1998). Sexual orientation was, therefore, also measured using a version of Kinsey's (1948) scale of sexual orientation. This was a 4 item scale with question relating to identity, romantic attraction, sexual fantasies and behaviour. Participants respond to each question on a 6 point scale ranging from 0 (exclusively heterosexual) to 6 (exclusively homosexual). An estimate of orientation was determined using averaged response to the 4 items. It has been shown that oestrogen cues correlate with female face attractiveness but only when not wearing make-up (Law-Smith et al., 2006). Participants were, therefore, asked not to wear any make-up for the photograph.

2.3.1 Demographics

The stimuli used for experiments in this thesis included only Caucasion participants who did not smoke and reported to be predominantly to exclusively heterosexual. The age of participants used in experiments ranged from 19-31, *M* = 24yrs, *SD* = 3 (male) and 20-34, *M* = 23yrs, *SD* = 5 (female).

2.3.1.1 *Male participants*

The database in total comprised 29 male participants aged between 19 and 42 yrs (*M* = 26, *SD* = 5). All males were predominantly to exclusively heterosexual. The majority of male participants (86%) were white European. 4 males were reported to be at least casual smokers.

2.3.1.3 *Female participants*

The database in total also comprised 31 female participants aged between 19 and 56 yrs (*M* = 24, *SD* = 7). Females were not wearing any make-up for their photograph. The majority (90%) of female participants were white European. 94% of females reported to be predominantly to exclusively heterosexual. 1 female reported to be bisexual and 1 reported to be exclusively homosexual. 3 females reported to be at least casual smokers.

2.4 Stimuli generation

2.4.1 Photographs

Photographs of participants were taken to include the head and shoulders. For the shoot, participants were asked to face the camera and hold a neutral expression. Photographs were taken in a naturally lit room using a Canon US30D camera with an EF-50mm f/1.4 lens under flash lighting, using 2 Canon 430EX flash guns triggered by Wein Ultraslave System on light stands with white diffuser brollies. The images were 3504 x 2336 pixels with 350 pixels per inch (see Figure 2.1).

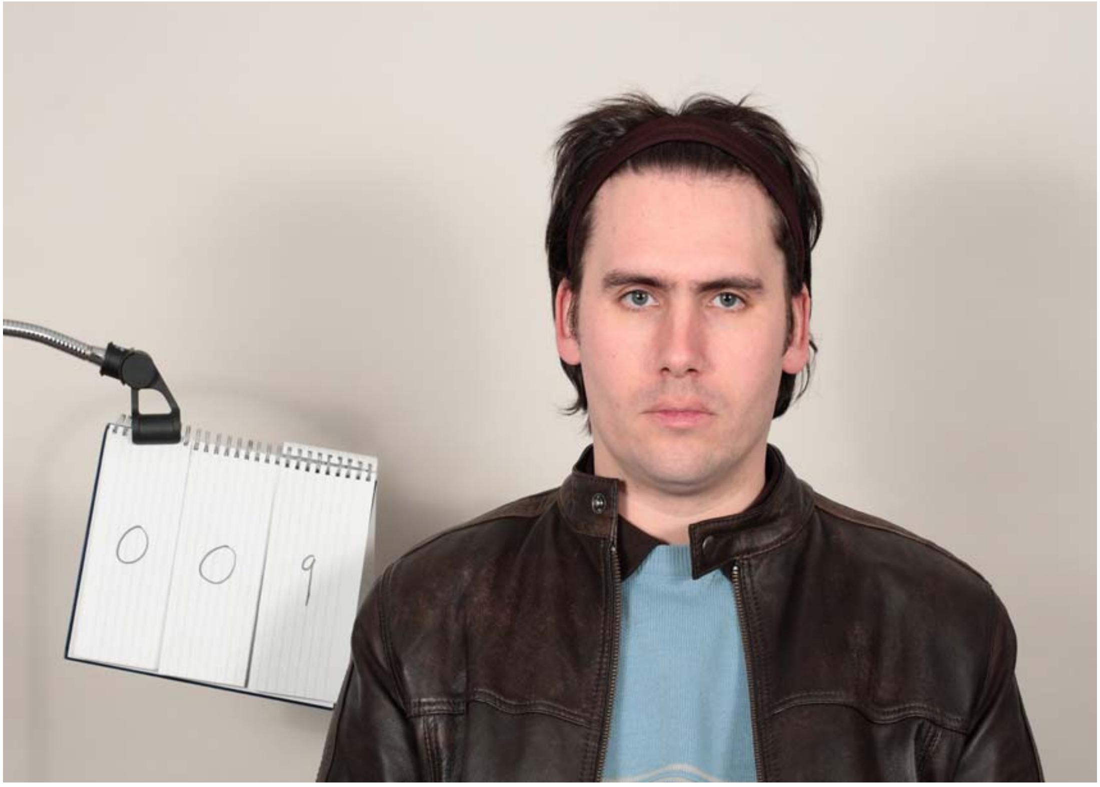

Figure 2.1: *Example of pre-standardised face stimuli (Participant ED009)*

2.4.2 Voice recordings

Vocalisations were recorded in a sound attenuated room. Participants were alone in the room during recording. Voices were recorded at a sampling rate of 48KHz with 16-bit quantization using a PMD 660 digital recorder with an AKG C451B stick microphone (left channel) set to 75Hz roll-off and an AKG C451E rifle microphone (right channel) with CK8 capsule. Participants were sat approximately 75cm from the microphones. Audacity audio editing software (http://audacity.sourceforge.net) was used to separate the vowel sounds and phrases from the recording. Vocal parameters were measured for each vowel and phrase separately using Praat software (www.fon.hum.uva.nl/praat). Using identical settings to Feinberg et al. (2005), voice pitch was measured with the autocorrelations floor set to 60*Hz* and ceiling to 300*Hz*. Average pitch was determined by obtaining pitch for the sound envelope (see Figure 2.2).

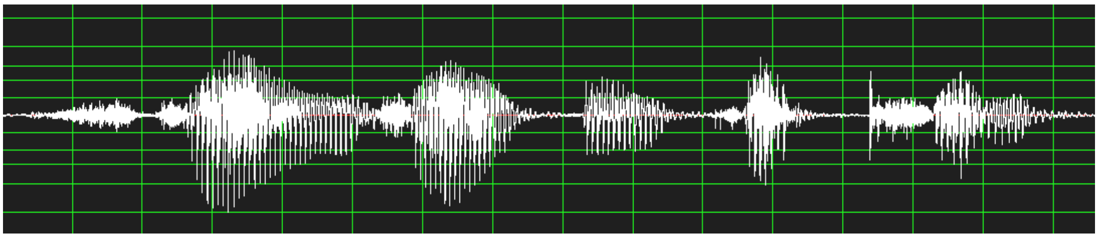

Figure 2.2: *Example of vocalisation envelope for the phrase 'stranger than fiction' (Participant ED009)*

A number of vocal samples were excluded from experiments. For some participants, speech permeated the ceiling and floor levels of the analysis because they spoke too loudly into the microphone. This caused a distorted 'clicking' sound which is likely to confound perceived attractiveness of the sample but also objective measurements. This distortion occurred during vowel sounds and phrases spoken by 4 participants (3 female and 1 male). A number of participants (3 female and 4 male) also reported smoking, which has been shown to lower voice pitch (Sorenson & Horii, 2002). The focus of initial experiments was to ascertain the relationship between attractiveness ratings of natural faces and voices. As such, distorted samples and the voices of smokers were excluded from use in experiments.

Participants were instructed to speak the vowel sounds (a - 'ah'; e - 'eh'; i - 'ee; o - 'oh'; u - 'oo') in a normal speaking voice. These vowel sounds have been used previously in similar studies of vocal attractiveness (e.g. Feinberg et al., 2005). Each vowel was spoken a total of five times with the order counterbalanced. Participants were also instructed to speak the phrase 'stranger than fiction' in a normal speaking voice three times. This phrase was selected because it was deemed to have neutral content. The sample after exclusion comprised 24 male and 26 female vocalisations. For vowel sounds, average pitch was, M = 114.09*Hz*, SD = 13.36 (male) and M = 206.98*Hz*, SD = 20 (female). For the phrase 'stranger than fiction' average pitch was M = 108.69*Hz*, SD = 15.133 (male) and M = 200.06*Hz*, SD = 18.32 (female).

2.5 Experimental stimuli

This section describes the treatment of stimuli specific to each chapter.

2.5.1 Chapter 3

The aim of this chapter was to determine the effect of faces and voices (comprising vowel sounds) in relation to face-voice compound attractiveness using a subset of female (experiment 1a) and male (experiment 1b) stimuli.

2.5.1.1 *Faces*

Photographs of faces were white balanced in Canon Digital Photo Professional in order to remove unnatural colour casting. Treatment of stimuli was then carried out using Photoshop CS2. DeBruine, Jones, Smith and Little (2010) found that non-face cues such as hair can influence perceptions of masculinity/femininity and thus attractiveness preferences. As such, the face stimuli here were isolated and placed on a neutral grey background using the magnetic lasso tool. Faces were then centred and resized (see Figure 2.3), matching across the sample for inter-pupillary distance (width 370 pixels).

Figure 2.3: *Example of standardised face stimuli (Participant ED009)*

2.5.1.2 Sexual dimorphism

Face masculinity was measured using an identical technique to Penton-Voak et al. (2001). Seven measurements were taken from the photographs (see Figure 2.4) including face height, lower face height, face width, lower face width, cheek-bone prominence, eye size and eyebrow height. Each of the seven measures were z-scored based on the population of faces within the experiment. Masculinity was then calculated using the formula: *z(lower face height: face height)-z(face width: lower face height)-z(eye size)-z(mean eyebrow height)-z(cheekbone prominence),* with higher scores indicating greater masculinity. Face femininity was measured using the identical measurements and formula except that scores were reversed so that, higher scores indicated greater femininity (see Feinberg et al., 2005).

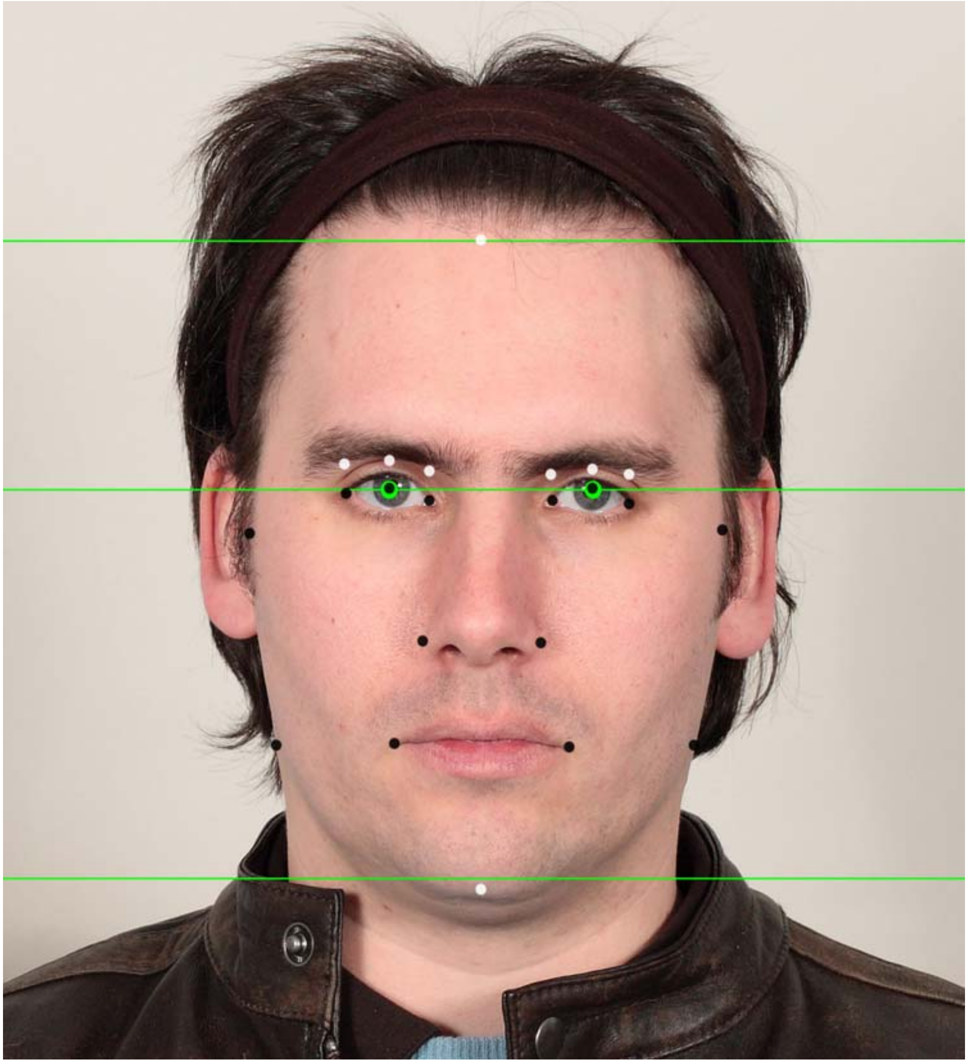

Figure 2.4: *Facial masculinity measurement from points used to calculate face height ratio; face width ratio; eye size; eyebrow height; and cheekbone prominence*

2.5.1.3 Voices

Vocal samples were created for each participant to include each of the 5 vowel sounds. The average pitch for each vowel was selected and pasted into a new sample spaced approximately .1 second apart n the order, a-e-i-o-u. The sample of vowel sounds were mirrored to create stereo samples and converted to a .wav file at 44.1*KHz* sampling rate and 16-bit quantization.

2.5.2 Chapter 4

The aim of this chapter was to determine the effect of faces and voices (comprising the sentence 'stranger than fiction') in relation to face-voice compound attractiveness using a subset of female (experiment 2a) and male (experiment 2b) stimuli.

2.5.2.1 *Faces*

Faces used in experiments 2a and 2b were created identically to those used in experiments 1a and 1b (section 2.5.1.1).

2.5.2.2 *Sexual dimorphism*

Measurements of face masculinity and femininity were identical to those used in experiments 1a and 1b (section 2.5.1.2).

2.5.2.3 *Voices*

Vocal samples comprised the sentence ‘stranger than fiction’ selected for each individual stimulus based on average pitch. Vocal samples were trimmed to have an immediate onset in Audacity, and converted to 44.1*KHz* sampling rate and 16-bit quantization.

2.5.3 Chapter 5

The aim of experiment 3 was to investigate whether females respond faster to male stimuli in compound compared to either face or voice by itself. This experiment also considered whether responding to the compound was affected when the non-target stimulus was related (human) or unrelated (non-human).

2.5.3.1 *Faces*

Faces used in experiment 3 were created identically to those used in experiments 1a and 1b (section 2.5.1.1) except that faces were placed on a white background. White was preferable for this experiment because a number of the distracters were either grey or black and so white allowed for a less biased contrast.

2.5.3.2 *Voices*

Vocal samples comprised the word ‘fiction’ selected for each individual stimulus based on average pitch. The samples were edited using Adobe Audition to have an immediate onset. Each sample was then standardised for length to .5 second and mirrored to produce stereo sounds. Stretching sounds is possible in Audition without distorting measures such as pitch. Samples were converted to .wav files at 44.1*KHz* sampling rate and 16-bit quantization.

2.5.4 Chapter 6

The aim of experiment 4 was to investigate whether the perceptual binding of synchronously presented face and voice information could be disrupted by the presentation of stimuli in in/congruent spatial locations. This experiment also considered whether responding to the compound was affected when the non-target stimulus was related (human) or unrelated (non-human).

2.5.4.1 *Faces*

Faces used in Chapter 4 were identical to those used in experiment 3 (section 2.5.3.1).

2.5.4.2 *Voices*

Voices used in experiment 4 were identical to those used in experiment 3 (section 2.5.3.2). However, samples were not mirrored to produce stereo sounds. Instead, different samples were created to play in only the left or right channels. Editing was carried out using Adobe Audition. Samples were then converted to .wav files at 44.1*KHz* sampling rate and 16-bit quantization.

2.5.5 Chapter 7

The aim of experiment 5 was to investigate whether face and voice attractiveness judgements could be made faster when accompanied by related voice or face information. Stimuli were presented as videos with noise in 3 different video conditions: unimodal stimuli with noise in the related modality (single); bimodal stimuli with noise in the target modality only (asynchronous); and bimodal stimuli with noise in both modalities (synchronous).

2.5.5.1 *Faces*

Faces used in experiment 5 were created using an identical method to those in experiment 1a and 1b (section 2.5.1.1). Faces were placed into a layer extending for 11 seconds and set to fade in at a rate of 1% per second increasing linearly from 0% at 0 seconds to 100% at 10 seconds.

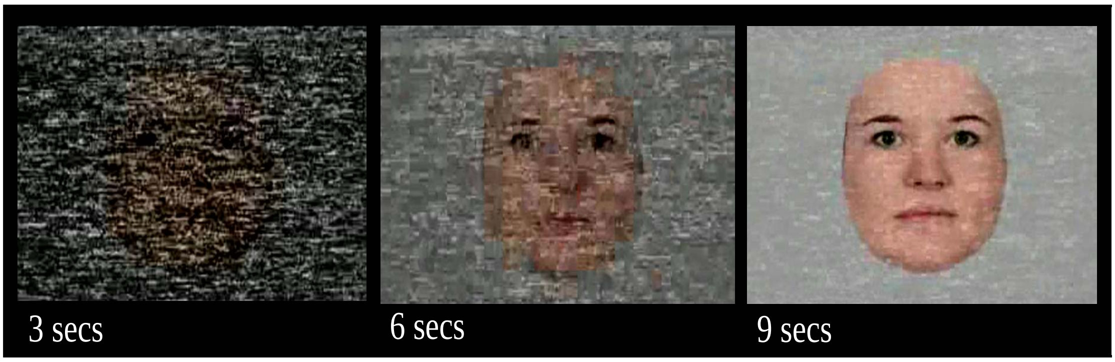

Figure 2.5: *Example of video with background noise and face at 3 time frames (Participant ED0010)*

On a parallel layer, noise was added consisting of random black and white noise recorded from the beginning of video-cassette playback. Noise was faded out linearly (1% per second) from 100% at 0 seconds to 0% at 10 seconds. This meant that stimuli would appear at approximately 4 seconds and be 100% visible at 10-11 seconds (see Figure 2.5). Videos were created in Avid Media Composer 2.5 Videos were converted to .mpeg4 media files.

2.5.5.2 *Voices*

Voices used in experiment 5 were created using an identical method to experiment 2a and 2b (section 2.5.2.3). The sentence 'stranger than fiction' was standardised in Adobe Audition to be 1.57 seconds in length (retaining natural pitch) and looped 7 times in an 11 second video. Voices were set to fade in at a rate of 1% per second increasing linearly from 0% at 0 seconds to 100% at 10 seconds. On a parallel layer, noise was added consisting of a cocktail party (variable frequency inaudible speech).

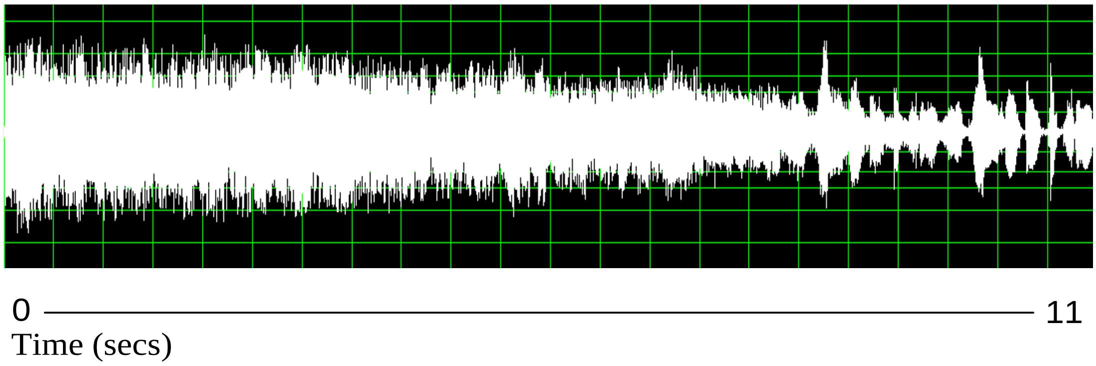

Figure 2.6: *Example of auditory stimuli with cocktail party noise and voice over an 11 second video (Participant ED0010)*

Random frequency noise was considered but was found to be aversive and could possible confound responding. As such, a cocktail party noise was used, which faded out linearly (1% per second) from 100% at 0 seconds to 0% at 10 seconds. This meant that stimuli would be audible at approximately 4 seconds and be 100% audible at 10-11 seconds. Videos were created in Avid Media Composer 2.5 Videos were converted to .mpeg4 media files.

CHAPTER 3: FACES AND VOWEL SOUNDS

3.1 Introduction

In humans, the face and voice comprise signals proposed to have evolved through sexual selection to signal heritable traits that would be beneficial to offspring. Thus far, research has predominantly investigated face and voice signals in isolation (reviewed in Wells et al., 2009). Multiple signals are beneficial, since together they could improve assessments of mate quality and increase the chance of producing healthy offspring through the identification or rejection of suitable/unsuitable partners (Møller & Pomiankowski, 1993). In the natural environment, signals in multiple modalities are likely to occur together. Investigating attractiveness in the presence of multiple signals may therefore prove to be informative about the relative effects of each signal. Moreover, investigating the relationship between multiple signals occurring together may provide evidence with regard to their evolutionary origin and function in sexual selection (Wells et al., 2009).

Multiple signals can take a number of forms (section 1.4) and be informative or non-informative (see Candolin, 2003). Briefly, two forms of informative signals, *back-up signals* and *multiple messages* will be discussed. All signals carry information with some degree of error or dishonesty (Guilford & Dawkins, 1991). Back-up signals are informative because they provide more information with regard to a single trait thus reducing the error interpreting the signal. As such, the attractiveness of back-up signals should at least be related. Two related back-up signals could have various effects on the receiver, producing equivalent or enhanced responses when presented together (Partan & Marler, 1999). Multiple messages are also informative. However, with multiple messages, each signal may communicate information that is independent of its counterpart. Nevertheless, by communicating different aspects of mate quality, together, these signals provide a better assessment of overall mate quality. Multiple messages are, therefore, likely to be unrelated and can have varied effects on the receivers response.

Previous research has shown that face and voice attractiveness have approximately equal influence for both male and female compound stimuli attractiveness (Saxton et al., 2009). Females with attractive faces have higher oestrogen levels (Law-Smith et al. 2006). High voice pitched females also have higher oestrogen than those with low pitched voices (Arbitbol, Abitbol & Abitbol, 1999) suggesting that female voices similarly reflect levels of oestrogen and thus fertility. Evidence has supported the positive relationship between attractive faces and voices in female stimuli (Collins & Missing, 2003; Feinberg et al., 2005; Lander, 2008; Saxton et al., 2009). The relationship between male preferences for female faces and voices suggests that they are back-up signals communicating information with regard to a single trait (i.e. fertility).

While there is concordance between findings investigating female signals, the relationship between face and voice attractiveness in males is equivocal. There is some evidence of a positive relationship between testosterone and attractive male faces (Pento-Voak & Chen, 2004). A relationship also exists between testosterone and male voice pitch (Dabbs & Mallinger, 1999). A number of studies have shown there to be a relationship between preferences for male faces and voices (Feinberg et al., 2008; Saxton, Caryl & Roberts, 2006; Saxton et al. 2009) although two studies found no relationship between male face and voice attractiveness (Oguchi & Kikuchi, 1997; Lander, 2008).

There were methodological differences between inconsistent findings related to male face and voice signals (section 1.5). For example, research that found a relationship between male face and voice stimuli (Feinberg et al., 2008; Saxton, Caryl & Roberts, 2006; Saxton et al. 2009) used a forced-choice design; preferences were calculated from each participant's choice between the most attractive of several pairs of stimuli presented. In contrast, studies that required participants to rate each stimulus independently on a likert-type scale found no relationship between male face and voice attractiveness (Oguchi & Kikuchi, 1997; Lander, 2008). Face and voice attractiveness may not be related in males owing to the function of voices and the evolutionary pressure governing vocal development and propagation in sexual selection (see Wells et al., 2009). Voice pitch is likely to have developed in males as a signal of dominance and aggression through intra-sexual selection pressures

(Clutton-Brock & Albon, 1979; Puts et al., 2006; Puts et al., 2007). Divergent pressures influencing face and voice selection could mean that the attractiveness of faces and voices are unrelated in an individual male.

3.1.1 Aim

Early studies investigating voice attractiveness were conducted using vowel sounds (Collins, 2000; Feinberg et al., 2005). Vowel sounds are produced with an open vocal tract and limited tongue movement, which leads to minimal interference from characteristics such as formant dispersion that can influence vocal judgements (Feinberg et al., 2005). The aim of the present study was therefore to investigate the relationship between face and voice attractiveness in female and male stimuli. In separate experiments, males and females respectively provided attractiveness ratings of voices (using samples of vowel sounds) together with a series of faces. The relationship between face and voice attractiveness ratings and indirect measure of oestrogen/testosterone was also explored. Finally, the present study aimed to provide estimates for the influence of face and voice attractiveness respectively on ratings of face-voice compound stimuli attractiveness.

Consistent with previous research, it was predicted that feminine faces and high pitch voices would be more attractive to males. There would be a relationship between female face and voice attractiveness and together they would contribute to overall face-voice compound stimuli attractiveness. It was also predicted that masculine male faces and voices would be more attractive to females. Together male face and voice attractiveness would contribute to overall face-voice compound stimuli attractiveness. Although previous research has shown inconsistent evidence, the experiment here used similar methodology to Lander (2008); each stimulus was rated independently on a likert-type scale. It was therefore predicted that there would be no relationship between male face and voice attractiveness.

3.2 Method

3.2.1 Design

A repeated measures design was used to investigate attractiveness ratings for faces and voices, presented on their own and together as a compound. Experiments were conducted for female (experiment 1a) and male (experiment 1b) participants separately using opposite sex stimuli.

3.2.2 Participants

The participants were 60 Caucasian students (30 female. *M* = 19yrs, *SD* = 1; 30 male, *M* = 23yrs, *SD* = 5) recruited from Nottingham Trent University. All participants reported to be predominantly or exclusively heterosexual. They received credits as part of a research scheme for taking part.

3.2.3 Stimuli

Forty sets of stimuli (20 male) selected from the database developed for this research (section 2.5.1.1) were used here. The stimuli comprised faces of Caucasian females (*M* = 23yrs, *SD* = 5) and males (*M* = 24yrs, *SD* = 3) with voices matched to each individual. The vocal sample (section 2.5.1.3) comprised vowel sounds ('ah' 'eh' 'ee' 'oh' 'oo') with female (*M* = 206.73Hz, *SD* = 12.64) and male (*M* = 114.9Hz, *SD* = 14.8) average pitch.

3.2.4 Apparatus

The presentation, timing and randomisation of stimuli were controlled by e-prime 2 experimental software. Face stimuli were presented on a 15″ computer monitor. The vocal samples were played at a comfortable volume level through Beyerdynamic DTX 900 headphones. A standard keyboard was used for inputting responses.

3.2.5 Procedure

The participants were seated approximately .5m from the computer facing the screen. After completing a sexual orientation questionnaire, the participants put on the headphones and read the experiment instructions. The experiment was conducted in three counterbalanced conditions (faces, voices, face-voice compounds). The participants rated each opposite sex stimulus for attractiveness on a scale of 1 (not attractive) to 9 (attractive), before moving onto the next condition. The stimuli were presented for 2.5secs each and interspersed with a fixation cross appearing for 2secs. Following each stimulus presentation, participants were prompted to press a number key corresponding to the perceived attractiveness of the stimulus.

3.3 Results

The results of face attractiveness, voice attractiveness and face-voice compound attractiveness were analysed using a two level cross-classified multilevel model. Parameter estimates were obtained in R (R Development Core Team, 2009) using the linear mixed-effects model package (lme4; Bates & Maechler, 2009). Multilevel regression estimates for face-voice compound attractiveness predicted by face attractiveness and voice attractiveness were determined, with participants and stimulus at level 2 and residual variance at level 1. Face and voice attractiveness were centred by level 2 (participant) means to obtain unbiased estimates of their *stimulus* level average effects (Enders & Tofighi, 2007).

3.3.1 Male ratings of female stimuli attractiveness

Average ratings of face attractiveness (M = 4.18, SD = 1.87), voice attractiveness (M = 4.81, SD = 1.85) and face-voice compound attractiveness (M = 4.13, SD = 1.84) for 20 female stimuli can be seen in Figure 3.1.

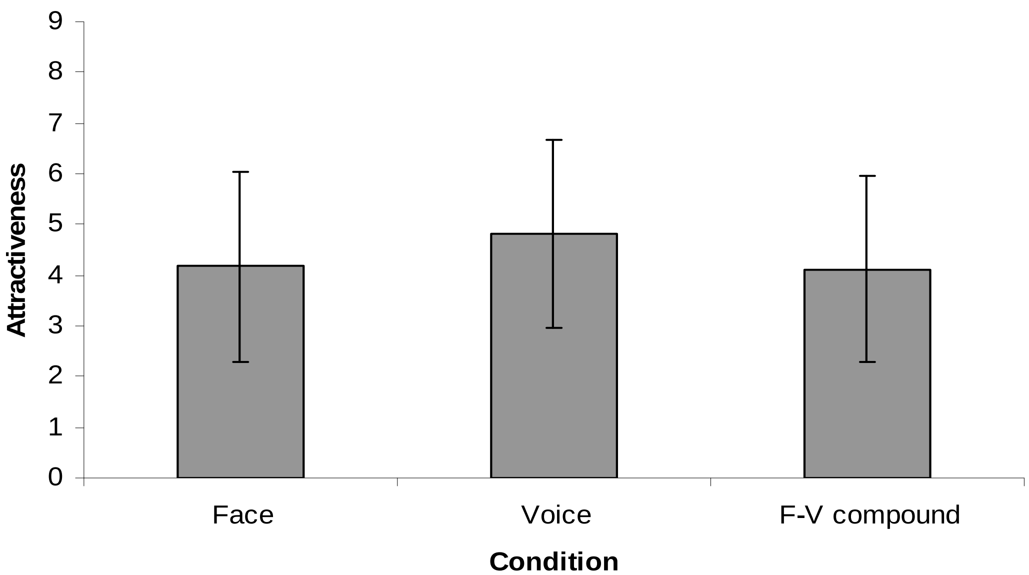

Figure 3.1: *Average ratings of 20 female stimuli for face attractiveness, voice attractiveness and face-voice compound attractiveness*

Fixed effects were obtained for the random intercept model (see Table 3.1). Face attractiveness, $b = .419$, $p < .001$, 95% CI [.348, .49], and voice attractiveness, $b = .085$, $p < .01$, 95% CI [.018, .152], both predicted face-voice compound attractiveness ratings. An interaction between face and voice attractiveness did not improve the model (ΔAIC = 1.4, $\Delta\chi^2$ (1) = .6, $p > .05$) and was thus omitted. Random variance is evident between stimuli (.18), between participants (.9) and is attributed to residual error (1.198). Estimates obtained from an intercept-only model proportioned the variance to be 8%, 40% and 52% respectively. Although there is a large proportion of variance attributed to participants, an attempt to model random slope effects (for face and voice attractiveness varying at the participant level) yielded greater AIC and BIC values and were thus omitted.

	Intercept-only Model		Random Intercept Model	
Fixed Effects	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Intercept	4.125***	.295	3.674***	.208
$Face_c$			.419***	.036
$Voice_c$			.085**	.034
$Face_c$, $Voice_c$				
Random Effects				
Stimulus	1.903		.18	
Participant	.903		.9	
Residual	1.406		1.198	
χ^2, AIC, BIC	2048, 2056, 2073		1927, 1939, 1965	

c = centred at participant level; *** $p < .001$ ** $p < .01$

Table 3.1: *Parameter estimates for a cross-classified 2 level Intercept-only Model and Random Intercept Model predicting female face-voice compound attractiveness with face attractiveness, voice attractiveness and face-voice interaction effects*

The relationships between components of female face and voice signals and attractiveness ratings were also explored. It should be noted that these correlation analyses comprise ratings that are not independent; each participant provided 20 ratings. As such, artificially inflating the degrees of freedom could yield significant results even when the coefficient is small. However, all ratings were centred on the participant averages thus accommodating some of the dependence between ratings from the same individual. Moreover, a small correlation coefficient would still provide some indication of a relationship in absolute terms, even if the degrees of freedom were inflated. The results showed no significant relationship between face attractiveness ratings and stimuli face femininity, $r_{551} = -.05$, $p > .05$, 95% CI: [-.13, .03]. A significant positive relationship was shown between voice attractiveness ratings and stimuli voice pitch, $r_{551} = .15$, $p < .001$, 95% CI [.07, .23]. A significant positive relationship was shown between the attractiveness ratings of female faces and voices, $r_{551} = 0.23$, $p < .05$, 95% CI [.15, .3].

3.3.2 Female ratings of male stimuli attractiveness

A technical error occurred with the experimental program and therefore datum related to one stimulus set was removed. Ratings of face attractiveness ($M = 3.51$, $SD = 1.55$), voice attractiveness ($M = 4.49$, $SD = 1.84$) and face-voice compound attractiveness ($M = 3.54$, $SD = 1.69$) for 19 male stimuli can be seen in Figure 3.2.

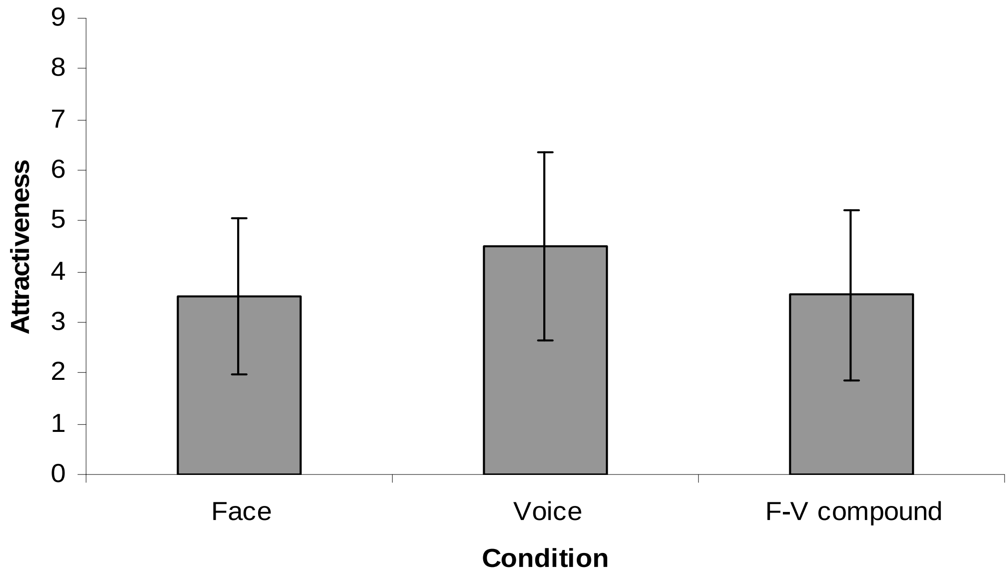

Figure 3.2: *Average ratings of 19 male stimuli for face attractiveness, voice attractiveness and face-voice compound attractiveness*

Fixed effects were obtained for the random intercept model (see Table 3.2). Face attractiveness, $b = .377$, $p < .001$, 95% CI [.293, .461] and voice attractiveness, $b = .189$, $p < .001$, 95% CI [.122, .256], both predicted face-voice compound attractiveness ratings. An interaction between face and voice attractiveness did not improve the model (ΔAIC = -1.4, $\Delta\chi^2$ (1) = 3.4, $p > .05$) and was thus omitted. Random variance is evident between stimuli (.121), between participants (.858) and attributed to residual error (1.467). Estimates obtained from an intercept-only model proportioned the variance to be 5%, 35% and 60% respectively. Although there is a large proportion of variance attributed to participants, an attempt to model random slope effects (for face and voice attractiveness varying at the participant level) yielded greater AIC and BIC values and were thus omitted.

	Intercept-only Model		Random Intercept Model	
Fixed Effects	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Intercept	3.551***	.22	3.546***	.194
$Face_c$			.377***	.043
$Voice_c$			.189***	.034
$Face_c$, $Voice_c$				
Random Effects				
Stimulus	.317		.121	
Participant	.865		.858	
Residual	1.71		1.467	
χ^2, AIC, BIC	2029, 2037, 2054		1975, 1971, 1933	

c = centred at participant level; *** $p < .001$

Table 3.2: *Parameter estimates for a cross-classified 2 level Intercept-only Model and Random Intercept Model predicting male face-voice compound attractiveness with face attractiveness and voice attractiveness effects*

The relationship between components of male face and voice signals and attractiveness ratings were explored. No significant relationship was observed between face attractiveness ratings and stimuli face masculinity, $r_{522} = -.01$ $p > .05$, 95% CI [-.1, .07]. Similarly, no significant relationship was observed between voice attractiveness ratings and stimuli male voice pitch, $r_{522} = -.01^{e-1}$, $p > .05$, 95% CI [-.08, .08]. No significant relationship was observed between face attractiveness ratings and voice attractiveness ratings of the male stimuli, $r_{522} = -.04^{e-1}$, $p > .05$, 95% CI [-.08, .08].

3.4 Discussion

The results of experiments comprising male and female stimuli separately were analysed using multilevel model analyses and provide estimates of face and voice influences on face-voice compound stimuli attractiveness. For both male and female stimuli, face and voice attractiveness positively and independently influenced the attractiveness of face-voice compound stimuli. Of the two modalities, faces had a proportionally greater influence on compound stimuli attractiveness than voices. There was a difference between male and female stimuli such that, male voices had a greater influence on compound stimuli attractiveness compared to female voices. For both male and female models of face-voice compound stimuli attractiveness, there was random variance attributed to differences between stimuli and also considerable variance attributed to differences between participants and to unexplained residual error.

The experiment using female stimuli showed a significant correlation in the predicted direction between female vocal attractiveness and voice pitch. That is, female voices with higher voice pitch were judged as more attractive. However, contrary to prediction, there was no relationship between female face attractiveness and measure of face femininity. Nevertheless, female face and voice attractiveness were shown to be related; this is consistent with previous research (Collins & Missing, 2003; Feinberg et al., 2005; Lander, 2008; Saxton et al., 2009). In contrast, experimental results showed there to be no relationship between face and voice attractiveness ratings for male stimuli. This finding contrasts with some research (Feinberg et al., 2008; Saxton, Caryl & Roberts, 2006; Saxton et al. 2009) but supports others (Oguchi & Kikuchi, 1997; Lander, 2008). Although there was a positive correlation between male face attractiveness and measure of face masculinity it did not reach significance. Contrary to prediction there was also no significant relationship between male vocal attractiveness and voice pitch.

The model results reported here indicate that voices influence face-voice compound attractiveness to a lesser extent than faces. Research conducted by Saxton et al. (2009) found little difference between the effects of voices on compound stimuli compared to faces. Although there were analytical differences between studies (section 1.5), Saxton et al. (2009) also used speech samples from participants introducing themselves. Vowel sounds are useful samples for experiments because there is limited interference from aspects such as formant dispersion that can influence attractiveness judgements (Feinberg et al., 2005). Moreover, they are relatively easier to standardise. However, attractiveness impressions may be more accurate when extracting information from speech.

Although speech contains more information owing to variance in word formation and speed, for example, it is more ecologically valid. The unusual nature of rating vowel sounds could explain why there was no interaction between female face and voice stimuli, despite a relationship between their attractiveness ratings. However, it could also be that effects for face and voice signals on compound stimuli are independent. Nevertheless, variation in pitch may be important for attractiveness judgements, at least in male voices (Hodges-Simeon, Gaulin & Puts, 2010) and could explain the non-significant result found here. The following chapter therefore aims to further explore the putative relationship between attractiveness and femininity/masculinity in female and male faces and voices. By repeating the experiments here using a sample of neutral speech, the next chapter will also consider the influence of more natural vocalisations on the attractiveness of face-voice compound stimuli.

CHAPTER 4: FACES AND SPEECH

4.1 Introduction

The experiments of Chapter 3 showed that female face and voice attractiveness are related (see experiment 1a). In contrast, male face and voice attractiveness were not related (see experiment 1b). For both male and female stimuli, voices comprising vowel sounds influenced compound stimuli attractiveness. However, the voice effect was considerably smaller in magnitude than face effects. The present experiments considered whether estimates of voice effects may be different when auditory stimuli comprise neutral speech.

Vocalisations comprising speech vary in a number of qualities such as formant dispersion related to word formation that may be important for attractiveness attributions (Feinberg et al., 2005). Speech rate can also be influential (Anolli & Ciceri, 2002), possibly because voices conveying positive affect are judged to be more attractive (Raines, Hechtman & Rosenthal, 2006). The semantic content of speech has also been shown to modulate the strength of male preference for female voices (Jones et al., 2008). However, evidence that expressions of interest (i.e. ‘I like you’) have an effect on female preference for male voices (Jones, Feinberg, DeBRuine & Little, 2008; Vukovich et al., 2010) is less clear.

Variation in speech measures such as rate and pitch, for example, may serve to confound the relationship between attractiveness and hormone indicators. However, some variation in voice pitch is related to attractiveness attribution (Anolli & Ciceri, 2002; Bruckert et al., 2006; Oguchi & Kikuchi, 1997). Hodges-Simeon et al. (2010) suggest that in males, a monotone voice may be a more accurate indicator of dominance. Such variation in speech may therefore provide more information with which to discriminate between attractive voices. Limiting confounds such as positive affect induced by semantic content should therefore provide a more ecologically valid estimate of voice contributions to face-voice compound stimuli attractiveness.

It could be argued that dynamic faces paired with speech would provide further ecological validity to findings. Some research has suggested that static and dynamic faces attractiveness judgements are comparable (Roberts et al., 2009). However, others have indicated that dynamic faces may be evaluated differently compared to static images (Lander, 2008; Rubenstein, 2005). However, facial movement can be used to determine a number of factors such as an individual's sex (Morrison, Gralewski, Campbell & Penton-Voak, 2007) and emotional expression (Pollick, Hill, Calder & Paterson, 2003). Moreover, proceptive (e.g. flirting) behaviour is communicated through movement and can also enhance attractiveness (Clark, 2008). Using static facial images may therefore provide more accurate results with regard to invariant attractive properties (i.e. sexual dimorphism) while limiting confounds related to emotion and sexual intention. In addition, investigating relative influence of speech together with static facial images allows for a direct comparison with the findings of the previous experiment.

4.1.1 Aim

The aim of the present study was therefore to repeat experiments 1a and 1b, to further investigate the relationship between face and voice attractiveness in male and female stimuli. Males and females respectively were to provide attractiveness ratings of voices (using samples of speech) together with a series of faces. The relationship between face and voice attractiveness and measures of femininity/masculinity was also explored. Finally, the present study aimed to determine whether the form of auditory stimuli affects estimates of face and voice attractiveness influences on ratings of face-voice compound stimuli attractiveness.

Feminine faces and high pitch voices were predicted to be more attractive to male participants; there would also be a relationship between female face and voice attractiveness and together they would contribute to overall face-voice compound stimuli attractiveness. It was also predicted that masculine male faces and voices would be more attractive to female participants. Together face and voice attractiveness would contribute to overall face-voice compound stimuli attractiveness. However, consistent with previous research (Lander, 2008) and the findings of experiment 1b, it was predicted that there would be no relationship between male face and voice attractiveness.

4.2 Method

4.2.1 Design

A repeated measures design was used to investigate attractiveness ratings of opposite sex faces and voices, presented on their own and together in compound. Experiments were conducted for female (experiment 2a) and male (experiment 2b) participants separately using opposite sex stimuli.

4.2.2 *Participants*

The Participants were 60 Caucasian students (30 females, *M* = 20yrs, *SD* = 4; 30 males, *M* = 21 yrs, *SD* = 3) recruited from Nottingham Trent University. All participants reported to be predominantly or exclusively heterosexual. Students that took part in this experiment had not participated in the previous experiment. They received credits as part of a research scheme for taking part.

4.2.3 Stimuli

The stimuli set in experiments 2a and 2b were identical to the stimuli set used in experiment 1a and 1b (section 2.5.2.1). The vocal sample comprised the phrase ‘stranger than fiction’ (section 2.5.2.3) with female (*M* = 200.53Hz, *SD* = 16.86) and male (*M* = 111.74Hz, *SD* = 15.59) average pitch.

4.2.4 Apparatus

The apparatus used for experiments 2a and 2b was identical to the apparatus used in experiments 1a and 1b (section 3.2.4).

4.2.5 Procedure

The procedure for experiments 2a and 2b was identical to the one used in experiments 1a and 1b (section 3.2.5).

4.3 Results

The model structure used in experiment 2a and 2b was identical to the one used in experiments 1a and 1b (section 3.3).

4.3.1 Male ratings of female stimuli attractiveness

The ratings of face attractiveness (M = 3.9, SD = 1.83), voice attractiveness (M = 4.89, SD = 1.9) and face-voice compound attractiveness (M = 3.86, SD = 1.84) for 20 female stimuli can be seen in Figure 4.1.

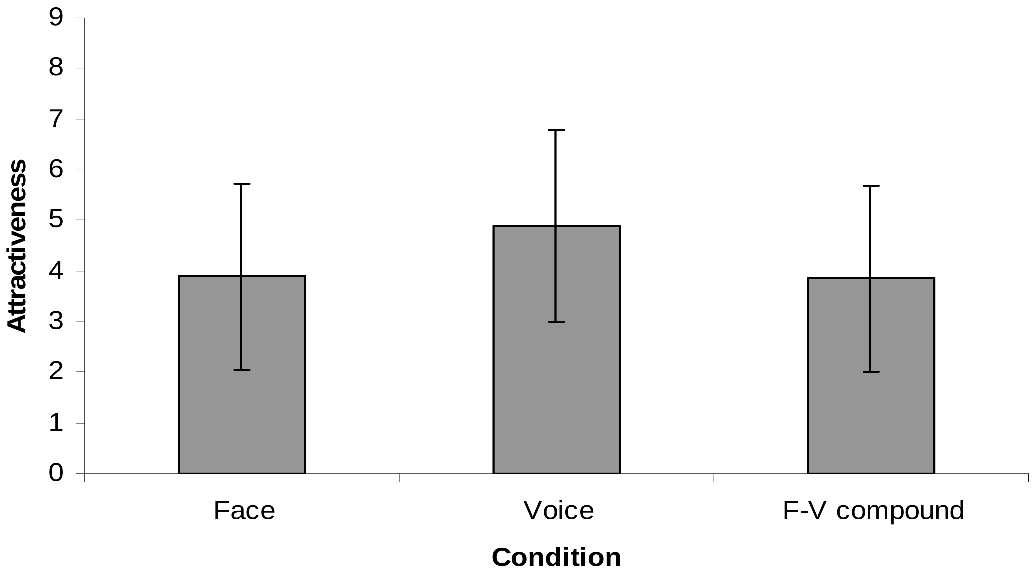

Figure 4.1: *Average ratings of 20 female stimuli for face attractiveness, voice attractiveness and face-voice compound attractiveness*

Fixed effects were obtained for the random intercept model (see Table 4.1). Face attractiveness, b = .433, p < .001, 95% CI [.355, .511], and voice attractiveness, b = .106, p < .01, 95% CI [.046, .166], both predicted face-voice compound attractiveness ratings. An interaction (see Figure 4.2) between face and voice attractiveness improved the model (ΔAIC =6.3, $\Delta\chi^2(1)$ =5.7, p < .001) and significantly predicted face-voice compound attractiveness, b = .041, p < .01, 95% CI .01, .074].

	Intercept-only Model		Random Intercept Model	
Fixed Effects	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Intercept	3.861***	.287	3.841***	.207
$Face_c$			.433***	.04
$Voice_c$			.106**	.031
$Face_c$, $Voice_c$			.041**	.017
Random Effects				
Stimulus	1.03		.251	
Participant	.846		.842	
Residual	1.524		1.295	
χ^2, AIC, BIC	2090, 2098, 2115		1974, 1998, 2019	

c = centred at participant level; *** $p < .001$ ** $p < .01$

Table 4.1: *Parameter estimates for a cross-classified 2 level Intercept-only Model and Random Intercept Model predicting female face-voice compound attractiveness with face attractiveness, voice attractiveness and face-voice interaction effects*

Random variance is evident between stimuli (.251), between participants (.842) and attributed to residual error (1.295). Estimates obtained from an intercept-only model proportioned the variance to be 11%, 35% and 54% respectively. Although there is a large proportion of variance attributed to participants, an attempt to model random slope effects (for face and voice attractiveness varying at the participant level) yielded greater AIC and BIC values and were thus omitted.

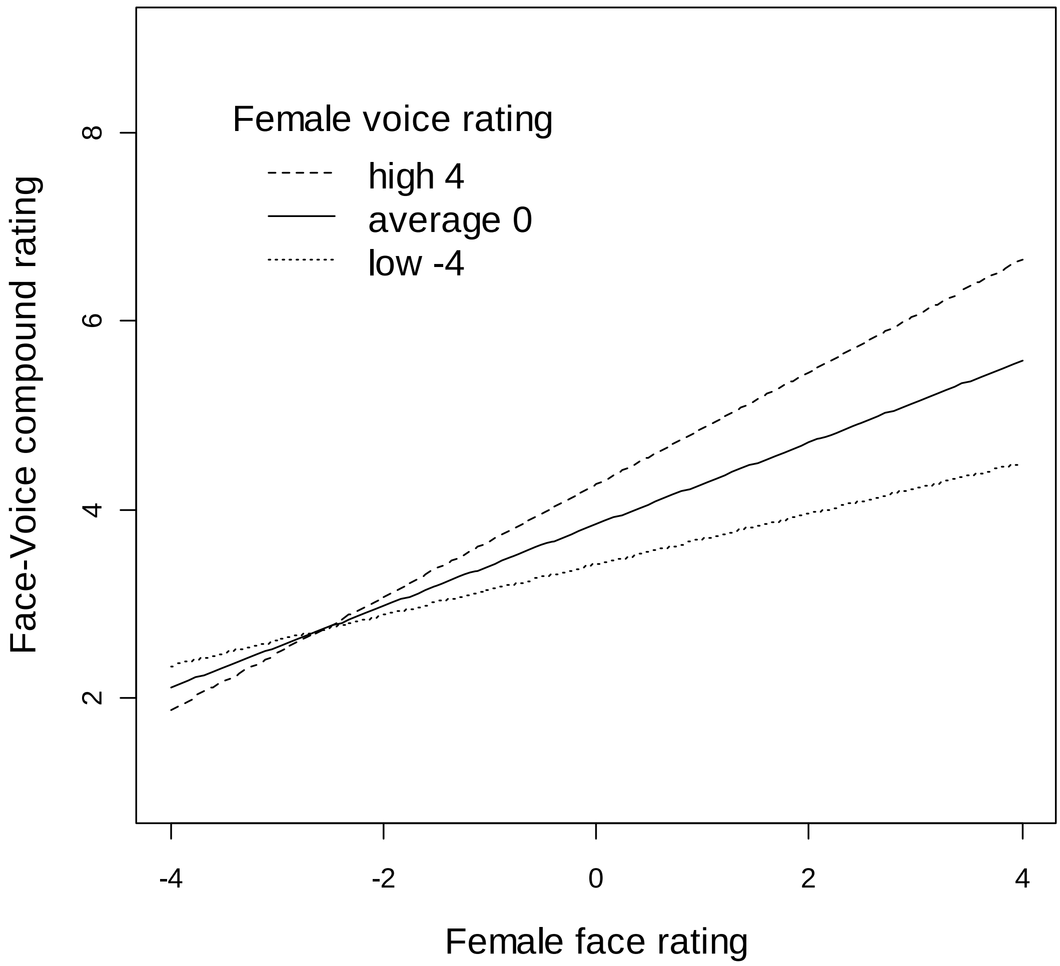

Figure 4.2: *Interaction between male (participant centred) ratings of face and voice attractiveness on face-voice compound attractiveness show that female stimuli with an attractive face and voice are more attractive when presented together*

The relationships between components of female face and voice signals and attractiveness ratings were explored. A non-significant relationship was observed between face attractiveness ratings and stimuli face femininity, $r_{551} = .06$, $p > .05$, 95% CI: [-.02, .14]. A non-significant relationship was also observed between voice attractiveness and stimuli voice pitch, $r_{551} = -.06$, $p > .05$, 95% CI [-.14, .02]. However, a significant positive relationship was observed between face attractiveness ratings and voices attractiveness ratings of the female stimuli, $r_{551} = .19$, $p < .001$, 95% CI [.11, .26].

4.3.2 Female ratings of male stimuli attractiveness

The ratings of face attractiveness (*M* = 3.55, *SD* = 1.8), voice attractiveness (*M* = 4.46, *SD* = 2.1) and face-voice compound attractiveness (*M* = 3.71, *SD* = 1.94) for 20 male stimuli can be seen in figure 4.3.

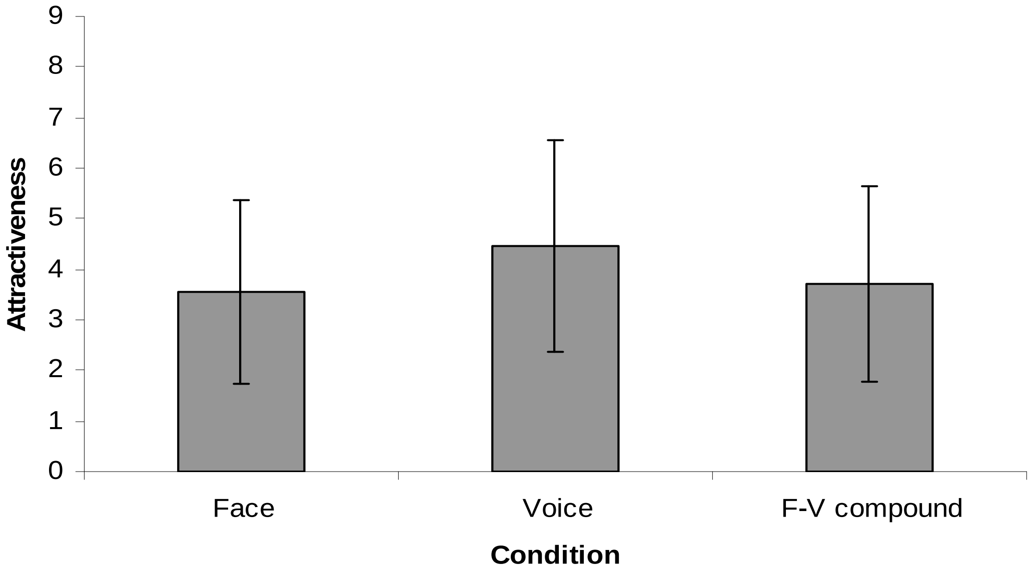

Figure 4.3: *Average ratings of 20 male stimuli for face attractiveness, voice attractiveness and face-voice compound attractiveness*

Fixed effects were obtained for the random intercept model (see Table 4.2). Face attractiveness, *b* = .395, *p* < .001, 95% CI [.321, .469] and voice attractiveness, *b* = .166, *p* < .001, 95% CI [.107, .225], both predicted face-voice compound attractiveness ratings. An interaction between face and voice attractiveness did not improve the model (ΔAIC = .3, $\Delta\chi^2(1) = 1.7$, *p* >.05) and was thus omitted. Random variance is evident between stimuli (.049), between participants (1.76) and attributed to residual error (1.481). Estimates obtained from an intercept-only model proportioned the variance to be 1%, 53% and 46% respectively. Although there is a large proportion of variance attributed to participants, an attempt to model random slope effects (for face and voice attractiveness varying at the participant level) yielded greater AIC and BIC values and were thus omitted.

	Intercept-only Model		Random Intercept Model	
Fixed Effects	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Intercept	3.78***	.274	3.71***	.248
$Face_c$			.395***	.038
$Voice_c$			.166***	.03
$Face_c$, $Voice_c$				
Random Effects				
Stimulus	.308		.049	
Participant	1.76		1.76	
Residual	1.714		1.481	
χ^2, AIC, BIC	2225, 2233, 2250		2116, 2128, 2155	

c = centred at participant level; *** $p < .001$

Table 4.2: *Parameter estimates for a cross-classified 2 level Intercept-only Model and Random Intercept Model predicting male face-voice compound attractiveness with face attractiveness and voice attractiveness effects*

The relationship between components of male face and voice signals and attractiveness ratings were explored using Pearson's correlations. A significant positive relationship was shown between face attractiveness ratings and stimuli face masculinity, $r_{551} = 0.11$, $p < .001$, 95% CI [.03, .19]. A significant negative relationship was also observed between voice attractiveness ratings and stimuli male voice pitch, $r_{551} = -.21$, $p < .001$, 95% CI [-.29, -.14]. However, no significant relationship was observed between face attractiveness ratings and voice attractiveness ratings of the male stimuli, $r_{551} = .03$, $p > .05$, 95% CI [-.05, .11].

4.4 Discussion

The data from each experiment comprising faces and samples of speech were analysed using an identical analyses to Chapter 3. The results of experiments here provide further evidence that face and voice attractiveness positively and independently influenced the attractiveness of face-voice compounds for both male and female stimuli. Similar to the experiments in Chapter 3, there was also random variance attributed to differences between stimuli and also considerable variance attributed to differences between participants and to unexplained residual error. Of the two modalities, faces had a proportionally greater influence on compound stimuli attractiveness than voices. This result is also comparable with the findings of the Chapter 3 and suggests that the influence of voices on compound stimuli attractiveness is similar whether vocalisations comprise vowel sounds or speech.

In contrast to both prediction and results of Chapter 3, there was no significant relationship between female vocal attractiveness and voice pitch. There was also no significant relationship between female face attractiveness and measure of face femininity. Failure to find a relationship between face and voice femininity measures and attractiveness appears to contrast earlier research on both faces and voices (Feinberg et al., 2005). However, male preferences for femininity are influenced by a number of factors including their testosterone levels (Jones et al., 2007; Welling et al., 2008). For example, males with high testosterone are more attracted to feminine female faces (Welling et al., 2008). Some research also found that some males prefer low voice pitch female voices (Leaderbrand, Dekam, Morey & Tuma, 2008; Oguchi & Kikuchi, 1997). The non-significant relationship between attractiveness and female faces and voices found here is therefore unlikely to indicate inaccuracies detecting femininity. Rather, there is likely to be individual differences in male expression of preference for femininity.

Female face and voice attractiveness ratings were shown to be related. Moreover, for female stimuli there was an interaction such that face and voice attractiveness was enhanced by an accompanying attractive voice or face respectively. That is, the attractiveness of a female face was greater when paired with an attractive voice (and visa versa). This interaction was not found in Chapter 3. However, it could be that more natural speech samples facilitate the integration of social face and voice signals. Taken together, the results here and elsewhere (Collins & Missing, 2003; Feinberg et al., 2005; Lander, 2008; Saxton et al., 2009) suggest that female faces and voices are likely to be back-up signals and can be used by a male to more accurately determine fertility.

In contrast, experimental results showed there to be no relationship between face and voice attractiveness ratings for male stimuli. This is consistent with the findings of Chapter 3 and provides support for earlier research (Oguchi & Kikuchi, 1997; Lander, 2008) while contrasting others (Feinberg et al., 2008; Saxton, Caryl & Roberts, 2006;

Saxton et al., 2009). There was a positive correlation between male face attractiveness ratings and measure of face masculinity. There was also a significant negative relationship between male vocal attractiveness ratings and voice pitch. The lack of relationship between male face and voice attractiveness ratings here, therefore, suggests that they are evaluated using different criteria or that indicators of testosterone are simply unrelated within male individuals.

Given the independence of vocal contributions to the attractiveness of compound stimuli and the lack of interaction between faces and voices, however, the function of the male voice could be to facilitate the perception of male faces. The receiver psychology hypothesis, describes signals that evolve alongside more informative signals in order to facilitate detection and discrimination. Rather than elicit any meaningful effect on their own, male voices could simply improve the ability to detect and respond to male attractiveness. The following chapters will therefore investigate whether female responding to a male face or voice would be faster when paired with an accompanying, related human signal. The final chapter will then investigate whether male voices paired with male faces can together facilitate temporal attractiveness judgements.

Considering response latencies in relation to face and voice stimuli is a useful method of determining signal integration. Evidence that response latencies are faster when responding to auditory and visual signals that are presented together compared to responding to either signal on its own (Bernstein, Clark & Edelstein, 1969; Miller, 1982) is a widely accepted method of deducing sensory integration. However, research suggests that auditory information can enhance responding to visual information although the same may not be true when reversed (see Recanzone, 2009). Such evidence, that voices facilitate responding to faces but that faces do not facilitate responding to voices, would suggest that the role of vocalisations could be to simply enhance detection of human face stimuli. The next chapter will therefore begin by investigating whether responding to face-voice compounds provides evidence of sensory integration. Furthermore, the following experiment aims to determine whether responding to a male face is discretely facilitated by the presence of a related male voice.

CHAPTER 5: FACE AND VOICE RESPONSE LATENCIES

5.1 Introduction

The previous chapters (Chapter 3 and Chapter 4) investigated the influence of the face and voice on opposite sex attractiveness ratings of face-voice compound stimuli with both male and female participants. The following chapters, however, will deal exclusively with female participants. In part, the reason for this was pragmatic in that students are encouraged to participate in experiments as part of a research credit scheme and females are more prevalent on the undergraduate psychology degree. Nevertheless, sexual selection research has historically focused on female mate choice owing to the relative amount of parental investment (see Trivers, 1972). That is, females have intrinsically higher investment in their progeny and thus the cost of selecting the wrong partner could be greater. Moreover, females have been shown to both initiate and control the outcome of interactions with opposite sex strangers (Grammer et al., 2000). As such, it would be of interest to consider the cognitive process with which females integrate face and voice information in order to inform a decision to initiate or interact with a potential male mate.

Female face and voice attractiveness appear to be related (see experiments 1a and 2a). Moreover, there is an interaction such that, female faces are more attractive when presented together with an attractive voice (and visa versa). As such, female face and voice are likely to be back-up signals; together providing a more accurate means with which to assess fertility. However, the function of male face and voice attractiveness in experiments 1b and 2b remain equivocal. These findings indicated that male face and voice attractiveness are unrelated. However, they contribute positively and independently to the attractiveness of male face-voice compound stimuli. Together, these results suggest that the male face and voice could be multiple messages; providing a more accurate estimation of overall mate quality. One theory that has yet to be excluded, however, is the receiver psychology hypothesis (section 1.4). That is, male voices may simply enhance the ability to detect and/or discriminate an attractive male face. Understanding the process of face-voice integration could highlight a potential advantage of multimodal processing in relation to person perception. Findings have yet to show how multimodal human-related information affects aspects of perception such as processing speed.

Brain sensory regions have been shown to have enormous plasticity potential (Shimojo & Shams, 2001) which allows for integration of multimodal information. The integration of sensory input can have an important role in perception (section 1.6). Importantly, multimodal information can have simple advantages in terms of enhanced processing speed. For example, responding has been shown to be faster when stimuli comprise bimodal signals (Miller, 1982; Rahne, Bockmann, von Specht, & Sussman, 2007; Vroomen & de Gelder, 2000). Miller (1982) proposed that a greater probability of responding faster to a bimodal target compared to the sum of probabilities for responding to either unimodal target was evidence of intersensory-facilitation.

Inter-sensory facilitation, however, may depend on the target modality. Although responding to a visual target is enhanced by accompanying auditory stimuli (Sinnett, Soto-Faraco & Spence, 2008), responding to an auditory target can be impeded by the presence of a visual stimulus (the visual dominance effect; Colavita, 1974). In a single experiment, Sinnett, Soto-Faraco and Spence (2008) found both inter-sensory facilitation and sensory competition in a single experiment depending on whether the target modality was either visual or auditory respectively (section 1.6). That is to say, responding to a visual target was faster when accompanied by an auditory stimulus while responding to an auditory target was impeded by an accompanying visual stimulus.

The above findings could have important implications for face-voice perception. While there may be an advantage in processing multimodal signals, person perception may only be facilitated when attention is directed toward the face. However, the stimuli used in Sinnett's (Sinnett, Soto-Faraco & Spence, 2008) experiment were unrelated (section 1.6) and target detection arguably occurs more often in a social context when stimuli are related. For example, both face and voice often express congruent human emotional responses in the same person. Face and voice perception also appear to be interrelated. For example, the human auditory cortex is active even when viewing the mouth movements without sound (Calvert et al., 1997). It is therefore, quite possible that bimodal human-related information will facilitate response times rather than impede them, irrespective of target modality. Specifically, visual dominance may be less likely to occur when a target voice is accompanied by a related human face.

5.1.1 Aim

The aim of the present experiment was therefore, to elucidate the effect of unimodal and bimodal presentations on response latencies when targets were either faces or voices. Moreover, this experiment sought to determine the relationship between target modality and response latencies when bimodal stimuli were either related (human) or unrelated (artificial). It was predicted that response latencies would be faster when face targets were presented with artificial auditory stimuli while response latencies would be slower when voice targets were presented with artificial visual stimuli. However, response latencies were predicted to be enhanced when face or voice targets were presented together with voice or face stimuli respectively.

5.2 Method

5.2.1 Design

A repeated measures design was used to investigate response latencies using a go-no go like task (see Sinnett, Soto-Faraco & Spence, 2008; Teder-Sälejärvi et al., 2005) in response to male faces and voices; presented on their own and together with related (human) or unrelated (artificial) auditory/visual stimuli.

5.2.2 Participants

The participants were 20 female students (*M* = 27yrs, *SD* = 6) recruited from Nottingham Trent University. The majority of participants reported to be right handed (75%). All participants reported normal hearing and normal or corrected vision. Students that took part in this experiment had not participated in any of the previous experiments. They received credits as part of a research scheme for taking part.

5.2.3 Stimuli

24 sets (visual and auditory) of *human*, *artificial* and *distracter* stimuli were used. *Visual*: Human visual stimuli comprised 8 male faces chosen randomly from the database (section 2.5.3.1). Artificial visual stimuli were 8 pink circles containing components (two smaller circles and one line) organised in various configurations. Visual distracters comprised 4 animal faces (cat, chimpanzee, dog and gorilla) and 4 musical instruments (clarinet, harmonica, piano and sitar) obtained through a 'google images' search. Images (see Figure 5.1) were standardised for size and isolated on a white background using Photoshop CS2.

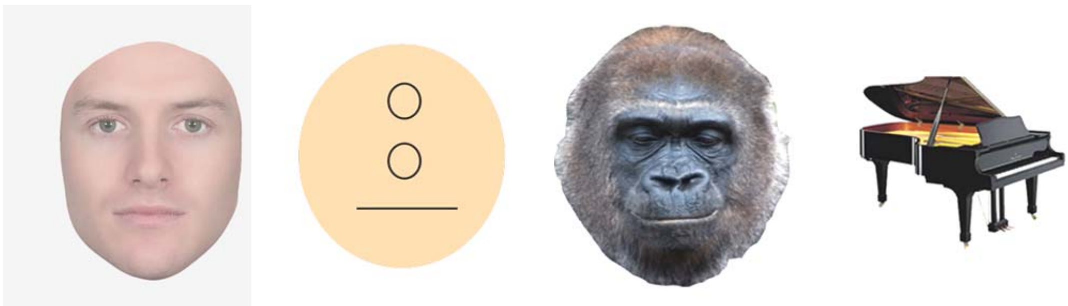

Figure 5.1: *Sample of human (face), artificial (circle configuration) and distracter (animal and musical instrument)visual stimuli*

Auditory: Human auditory stimuli comprised male voices speaking the word 'fiction' (section 2.5.3.2). Voices were selected from the database and were matched to people used for face stimuli. For artificial auditory stimuli, 2 tones (frequency, 110*Hz* and 130*Hz*) within male voice pitch range were generated. Auditory distracters comprised 4 animal and 4 musical instrument sounds matched to the visual stimuli and obtained through a 'google' search for .wav samples. Auditory samples were standardised for length (.5 secs), mirrored to produce stereo sounds and converted to 44.1*KHz* sampling rate and 16-bit quantization using Adobe Audition.

5.2.4 Apparatus

The presentation, timing and randomisation of stimuli were controlled by e-prime 2 experimental software. Face stimuli were presented on a 15″ computer monitor. The vocal samples were played at a comfortable volume level through Beyerdynamic DTX 900 headphones. A standard keyboard was used for inputting responses.

5.2.5 Procedure

The experiment was conducted in two counterbalanced blocks. In block one (face), participants were asked to respond to human face targets and in block two (voice), participants were asked to respond to human voice targets. Participants were instructed to respond to the target modality before the trials began. Stimuli were presented on their own and together with a related visual/auditory sample. Human stimuli were also presented in a unimodal condition and bimodal condition with their related sample. However, human stimuli also occurred in a bimodal condition together with an unrelated (i.e. artificial visual or auditory stimuli) sample (see Table 5.1).

Visual	Auditory	Response
Face		Block1
	Voice	Block 2
Face	Voice	Block1,2
Face	Artificial	Block1
Artificial	Voice	Block2
Artificial		
	Artificial	
Artificial	Artificial	
Distracter		
	Distracter	
Distracter	Distracter	

Table 5.1: *List of experimental stimuli presentations with responding required in block 1 (face) and block 2 (voice) respectively for a unimodal human target, bimodal human target with related stimuli and bimodal human target with unrelated artificial stimuli*

Within each block, slides with visual, auditory and visual with auditory samples were presented on the computer for 2 seconds each in a randomised order. Each stimulus was followed by a random length (between 1 and 4 seconds) inter-trial-interval comprising a white slide with a central fixation cross. Participants were seated approximately .5m from the computer facing the screen. The experiment was a version of a go-no go task and so participants were asked to respond as quickly and accurately as possible by pressing ‘b’ on the keyboard as soon as they saw or heard the instructed target in the relevant modality (whether it occurred by itself or not) while refraining from pressing ‘b’ in the presence of any other stimuli. Response latencies were recorded in addition to errors and omissions. Participants were instructed to use their dominant hand.

5.3 Results

A 2 (target) x3 (condition) repeated measures ANOVA found a significant main effect of target, $F_{1,19} = 17.375$, $p < .01$ (see figure 5.2a); overall responses to faces *M* = 419ms, 95% CI [400, 438] were faster than responses to voices, *M* = 467ms, 95%CI [439, 495]. There was also a significant main effect of condition, $F_{2,38} = 4.967$, $p < .05$. Pairwise comparisons with Bonferroni corrections showed that responses to single targets, *M* = 448ms, 95% CI [427, 468] were significantly ($p < .05$) slower than responses to targets paired with related face or voice stimuli, *M* = 432ms, 95% CI [408, 456]. Responding to targets paired with artificial visual or auditory stimuli, *M* = 450ms, 95% CI [429, 471] were also shown to be significantly slower than responding to targets paired with related face or voice stimuli.

However, there was also a marginally significant interaction between target and condition, $F_{2,38} = 2.969$; $p = .06$. Pairwise comparisons with Bonferroni corrections revealed that responding to face targets paired with artificial auditory stimuli, *M* = 414ms, 95% CI [397, 431] was faster ($p < .01$) than responding to voice targets paired with artificial visual stimuli, *M* = 486ms, 95% CI [456, 515]. Responding to voice targets paired with face stimuli, *M* = 451ms, 95% CI [421, 481] was also shown to be significantly faster ($p < .01$) than responding to voice targets paired with artificial visual stimuli, *M* = 486ms, 95% CI [456, 515].

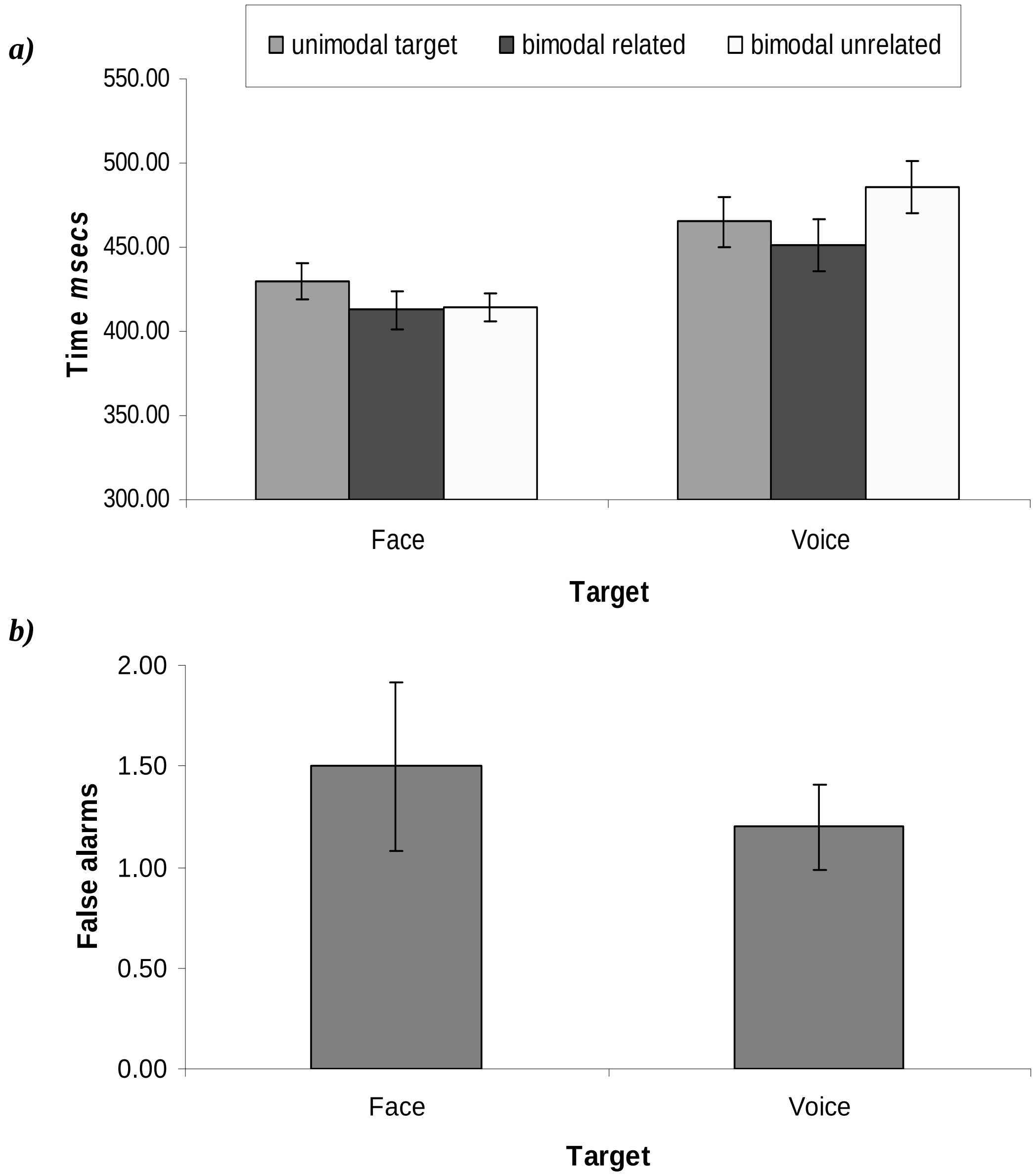

Figure 5.2: *Response latencies with standard error bars (a) when responding to face and voice targets presented on their own, together with related human stimuli or with artificial stimuli; and for (b) the number of errors made when the target was a face or voice*

There was very little difference between the number of errors made (see figure 5.2b) when responding to visual targets, $M = 1.5$, $SD = 1.88$, compared to auditory targets, $M = 1.2$, $SD = .95$, when data were collapsed across conditions, $t_{19} = .224$, $p > .05$. Taken together, responding to face targets appears to be enhanced whereas responding to voice targets appears to be impeded by the presence of artificial auditory or visual stimuli respectively. By contrast, responding to face and voice targets were similarly enhanced when paired with related, human stimuli.

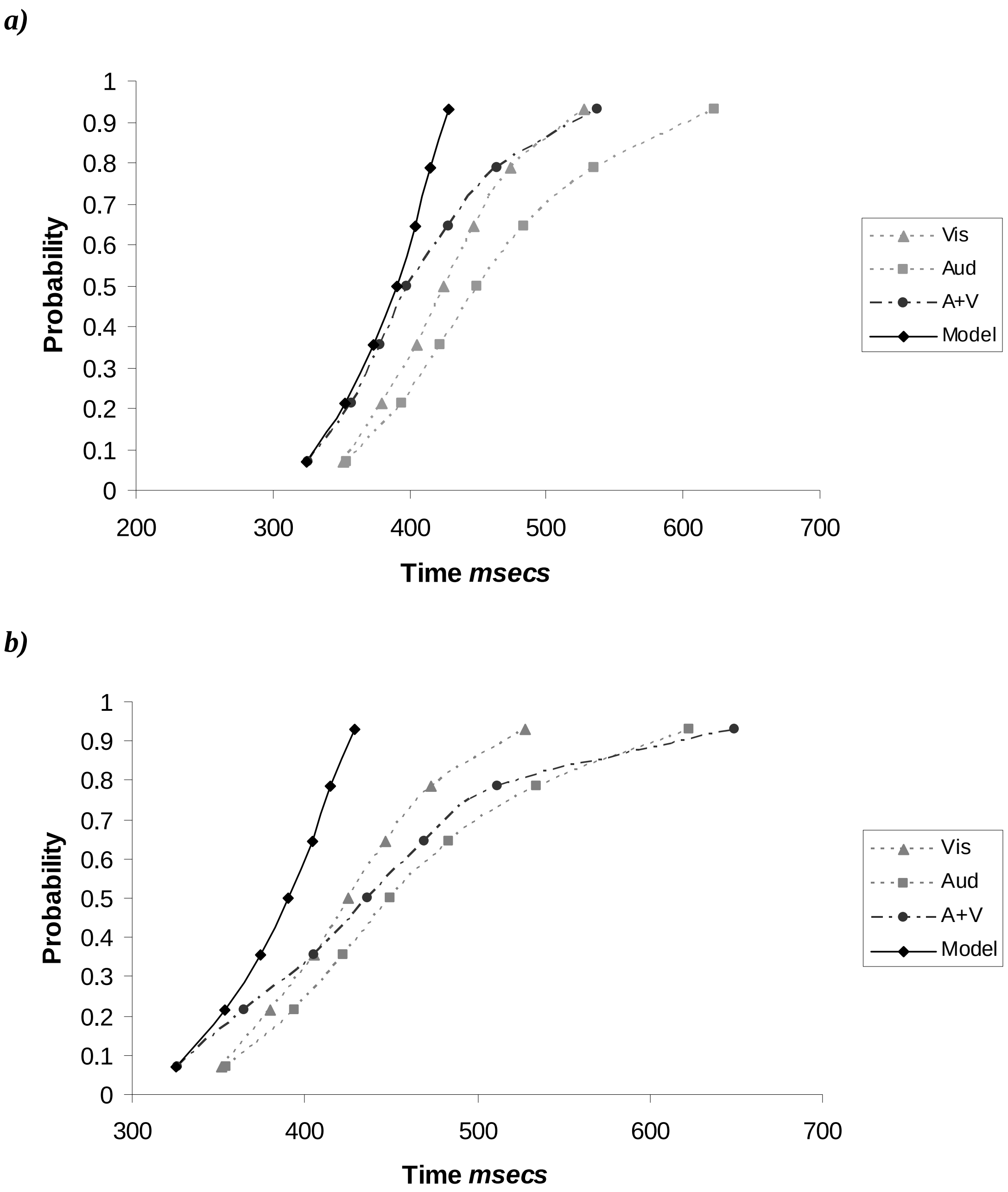

Figure 5.3: *Plots for face (a) and voice (b) targets show the probability distributions of response latencies in relation to visual (face) and auditory (voice) stimuli; presented unimodally, bimodally and compared to the predicted race model*

In order to test for inter-sensory facilitation, the probability distribution of bimodal responding was tested against the race inequality model ($[RT_{face}+RT_{voice}]-[RT_{face}*RT_{voice}]$; see Miller, 1982) at each of the seven quantiles. That is, a test was used to determine whether responding was faster, at any of the quantiles, for bimodal stimuli compared to responding to the predicted race model (summated probability of responding to either of the targets alone). The probability of faster bimodal responses compared to the race model was non-significant ($p > .05$) in each of the seven quantiles for both visual (face) targets (see figure 5.3a) and auditory (voice) targets (see figure 5.3b). Although response latencies were enhanced, these results therefore provide no evidence of inter-sensory facilitation.

5.4 Discussion

Overall, responding to auditory targets was slower than responding to visual targets. In bimodal trials there was an interaction such that, responding to face targets paired with artificial auditory stimuli was faster compared to responding to voice targets paired with artificial visual stimuli. These findings are, therefore, consistent with Sinnett, Soto-Faraco & Spence (2008), providing further evidence of both enhancement and competition such that, an irrelevant auditory stimulus enhances responding to faces while an irrelevant visual stimuli impedes responses to voices.

In bimodal trials where face and voice targets were paired with related human stimuli, however, responding was enhanced. It could be that responses to voices paired with faces were faster because participants were predominantly responding to the presence of a face. However, if this were true, more false alarms responding to voices might have been expected. There was no significant difference between the errors made in the face or voice target conditions thus indicating that faces did enhance responding to voice targets. Although responding to face-voice compounds were enhanced, there was no evidence of inter-sensory facilitation.

Responding to face-voice compounds could be enhanced because they often occur together and are perceptually interrelated (Calvert et al., 1997). Information that occurs together is likely to originate from a single source (Welch & Warren, 1980). However, vocalisations could be used to communicate information over distance. As such, the source of an auditory signal could be perceived as incongruent with visual information. For example, sensory integration can be disrupted by temporal asynchrony (Radeau, 1994). Face and voice integration may also be disrupted by spatial asynchrony. The next chapter will therefore consider responding to face-voice information in the spatial domain, which may reveal a special case for sensory-integration when stimuli comprise information related to person perception.

CHAPTER 6: FACE-VOICE INTEGRATION AND SPATIAL CONGRUENCE

6.1 Introduction

The aim of experiment 3 (Chapter 4) was to determine whether female responding to male face and voice targets would be enhanced by the accompaniment of a related human stimulus, irrespective of target modality. These findings showed faster responding to male face targets presented with unrelated artificial auditory stimuli while responding to male voice targets was impeded by unrelated artificial visual stimuli. These findings were also extended in experiment 3 to show that response latencies were faster, irrespective of target modality, when stimuli were related (i.e. faces paired with voices) and presented synchronously in the same spatial location. Although a face and voice can often easily be attributed to an individual, however, there are instances where such perception could be disrupted. Voices for example, may serve to communicate information over distance or from different spatial locations (e.g. television speakers), which may impact on the integration of multimodal signals.

Two fundamental sources of information that affect perceptual unity are space and time (Radeau, 1994). There is some evidence (section 1.6) to suggest that responding to visual stimuli is inhibited when auditory stimuli occur in an incongruent location (Lee et al., 1991; Simon & Craft, 1970). Imaging studies have also shown distinctive patterns of brain activation in regions related to bimodal stimuli presented in different compared to same spatial locations (Macaluso, et al., 2004; Teder-Sälejärvi et al., 2005). However, Teder-Sälejärvi et al. (2005) found that responding to a visual target could be enhanced when presented together with auditory stimuli irrespective of spatial location. This finding can be explained in terms of the ventriloquism effect (see de Gelder & Bertelson, 2003); that is, visual perception can be affected by auditory stimuli even when occurring in a different location.

While auditory information enhances response to incongruent visual information, the same may not be true in reverse. Integration of visual and auditory spatial information in the superior colliculi (section 1.6) together with higher spatial acuity in the visual field (Shimojo & Shams, 2001) leads to visual dominance. Incongruent audio-visual information biases auditory location toward the visual target (Recanzone, 2009). Typically, studies have therefore investigated the effect of auditory stimuli on response timing and localisation of a visual target (see Recanzone, 2009). However, human voices are an important social signal and can be used to communicate over distance or locate a person for example. Considering response latencies to voice targets when the composite face signal is spatially disparate could provide evidence of their relative importance in the integration of multimodal social information.

6.1.1 Aim

The aim of this experiment was to further understand the conditions with which audio-visual information is integrated. Specifically, by considering processing speed when male faces and voices are spatially disparate, these findings could provide evidence of their relative effects in female perception of social stimuli. The present study will therefore extend the findings of experiment 3 to investigate response latencies when face and voice targets are presented on their own and together with stimuli in spatially congruent and incongruent locations. Moreover, this experiment sought to determine the relationship between target modality and response latencies when accompanying information was either unrelated or related social stimuli. It was predicted that response latencies would be faster when face targets were presented with auditory stimuli, irrespective of relatedness or spatial location. In contrast, visual information less often biases auditory information. It was therefore predicted that responding to voice targets would only be faster when related, face stimuli were presented in the same spatial location.

6.2 Method

6.2.1 Design

A repeated measures design was used to investigate response latencies using a go-no go like task (see Sinnett, Soto-Faraco & Spence, 2008; Teder-Sälejärvi et al., 2005) in response to male faces and voices; presented on their own and together with related human or non-related auditory/visual stimuli.

6.2.2 Participants

The participants were 20 female students (*M* = 20yrs, *SD* = 4) recruited from Nottingham Trent University. The majority of participants reported to be right handed (85%). All participants reported normal hearing and normal or corrected vision. Students that took part in this experiment had not participated in any of the previous experiments. They received credits as part of a research scheme for taking part.

6.2.3 Stimuli

16 stimuli sets (visual and auditory) comprising human and artificial samples were used to create unimodal and spatially congruent and incongruent bimodal stimuli (see Figure 6.1). *Visual*: The human faces (section 2.5.4.1) and artificial visual stimuli were identical to those used in experiment 3. *Auditory*: The human voices (section 2.5.4.2) and artificial auditory stimuli were identical to those used in experiment 3.

6.2.4 Apparatus

The presentation, timing and randomisation of stimuli were controlled by e-prime 2 experimental software. Face stimuli were presented on a 15″ computer monitor on the left or the right of the screen separated by 10° of visual angle. The vocal samples were presented in either the left or the right auditory channel and were played at a comfortable volume level through Beyerdynamic DTX 900 headphones. A standard keyboard was used for inputting responses.

6.2.5 Procedure

The experiment was conducted in two counterbalanced blocks where participants were asked to respond to two different target modalities (face or voice). Stimuli were presented for both targets on the left and right in the conditions unimodal; bimodal with human sample presented in spatially congruent and incongruent locations; and bimodal with artificial sample presented in spatially congruent and incongruent locations (see Table 6.1)

Left	Stimulus	Right
F	1	
V	2	
FV	3	
A^V	4	
A^A	5	
A^V A^A	6	
F	7	V
V	8	F
A^V	9	A^A
A^A	10	A^V
	11	A^V A^A
	12	A^V
	13	A^A
	14	V
	15	F
	16	FV

Table 6.1: *List of experimental stimuli presented on the left and right; unimodal and bimodal congruent and incongruent presentations human face (F) and voice (V) targets, together with artificial visual (A^V) and auditory (A^A) stimuli*

Within each block, slides with visual, auditory and visual with auditory samples were presented on the computer for 2 seconds, each in a randomised order. Each stimulus was followed by a random length (between 1 and 4 seconds) inter-trial interval comprising a white slide with a central fixation cross. The participants were seated approximately .5m from the computer facing the screen. The experiment was a version of a go-no go task and so participants were asked to respond as quickly and accurately as possible by pressing ‘b’ on the keyboard as soon as they saw or heard the instructed target in the relevant modality (whether it occurred by itself or not) while refraining from pressing ‘b’ in the presence of any other stimuli. Response latencies were recorded in addition to errors and omissions. Participants were instructed to use their dominant hand.

6.3 Results

Data for face and voice targets were analysed separately using a repeated measures ANOVA. There was no effect of side for either face ($F_{1,19} = .995$, $p > .05$) or voice ($F_{1,19} = .03$, $p > .05$) targets and so the data was collapsed into one-way ANOVAs with 5 levels; unimodal targets, targets paired with related human stimuli presented in congruent and incongruent spatial locations and targets paired with unrelated artificial auditory/visual stimuli presented in congruent and incongruent spatial locations.

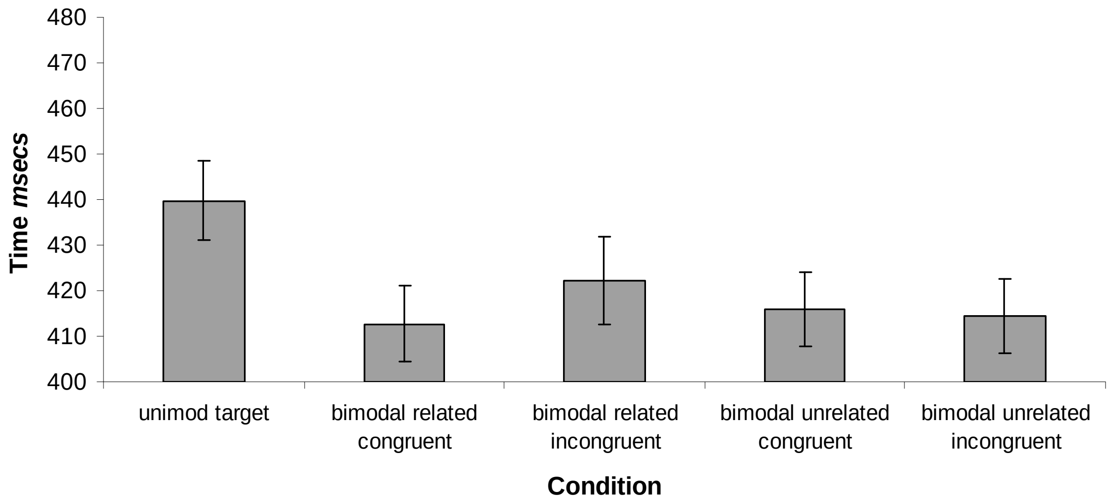

Figure 6.1: *Response latencies with standard error bars in relation to face targets presented on their own, together with related voice stimuli or with unrelated artificial auditory stimuli occurring in a congruent or incongruent spatial location*

Analysis of responding to face targets (see Figure 6.1) revealed a significant effect of condition, $F_{4,76} = 6.159$, $p < .001$. Pairwise comparisons with Bonferonni corrections showed that responding to face targets alone, *M* = 440ms, 95% CI [421, 458] was significantly ($p < .05$) slower than responding to face targets paired with related voice stimuli in congruent, *M* = 413ms, 95% CI [395, 430] but not ($p > .05$) incongruent, *M* = 422ms, 95% CI [440, 443] spatial locations. Responding to face targets alone was also significantly ($p < .05$) slower than responding to face targets paired with artificial auditory stimuli presented in both congruent, *M* = 416ms, 95% CI [399, 433] and incongruent, *M* = 414ms, 95% CI [397, 432] spatial locations. There was no difference ($p > .05$) between responding to face targets paired with related voice stimuli and unrelated artificial auditory stimuli, irrespective of spatial location.

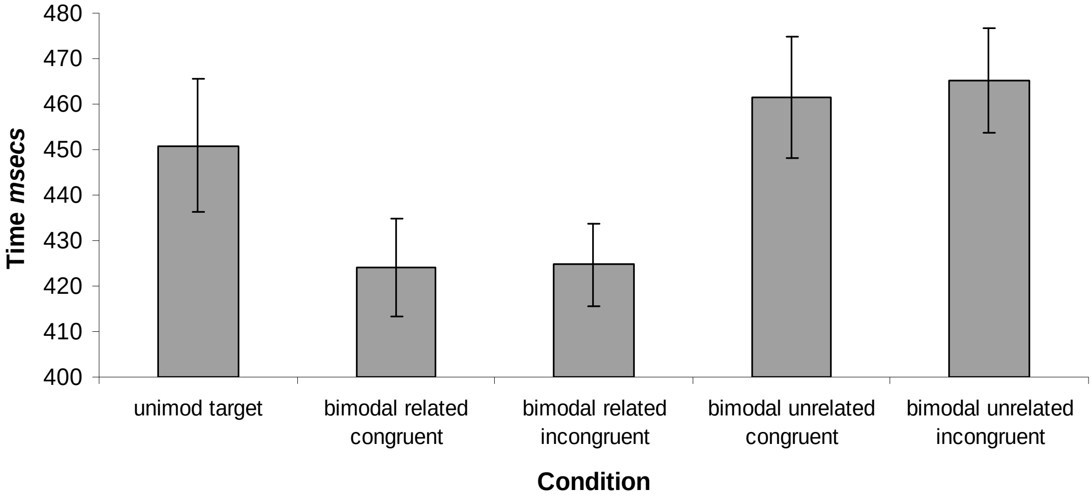

Figure 6.2: *Response latencies with standard error bars in relation to voice targets presented on their own, together with related face stimuli or with unrelated artificial visual stimuli occurring in a congruent or incongruent spatial location*

Analysis of responding to voice targets (see Figure 6.2) revealed a significant effect of condition, $F_{4,76} = 5.882$, $p < .001$. Pairwise comparisons with Bonferonni corrections showed that responding to voice targets paired with related face stimuli in congruent, *M* = 424ms, 95% CI [402, 446] and incongruent, *M* = 425ms, p>.05, 95% CI [406, 443] spatial locations was faster than responding to voice targets alone, *M* = 451ms, 95% CI [420, 481] although these results did not reach significance (p > 05). Responding to voice targets paired with unrelated artificial visual stimuli presented in both congruent, *M* = 462ms, 95% CI [434, 489] and incongruent, *M* = 465ms, 95% CI [441, 489] spatial locations was slower than responding to voice targets alone although similarly, these results did not reach significance (p > .05). There was however, a significant difference (p<.05) between responding to voice targets paired with related face stimuli in both congruent and incongruent spatial locations and responding to voices paired with artificial auditory stimuli presented in incongruent spatial locations.

Faster response latencies to voice trials paired with faces could have been because participants were simply responding to visual information. Analysis revealed more errors in relation to voice target trials, *M* = 5.9, *SD* = 5.13, compared to faces, *M* =4.2, *SD* = 3.09. However, this difference was found to be non-significant, $t_{19} = -1.506$, p>.05. In order to determine whether faster responding to bimodal trials occurred because of inter-sensory facilitation, the probability distribution of bimodal responding was tested against the race model ($[RT_{face}+RT_{voice}]-[RT_{face}*RT_{voice}]$; see Miller, 1982) for face and voice targets separately in both the spatially congruent and incongruent conditions. There was no evidence of a violation of the race model ($p > .05$) for all conditions. That is, the probability of faster responding to face or voice targets when paired with related human stimuli, whether presented in congruent or incongruent spatial locations was not greater than the probability of responding to either target alone. These findings therefore provide no evidence of inter-sensory facilitation.

6.4 Discussion

Overall, the findings showed evidence of both cognitive enhancement and competition with regard to response latencies, dependent on the target modality. Responding to face targets was faster when presented together with unrelated artificial auditory stimuli. Responding to voice targets appeared to be impeded by the synchronous presentation of artificial visual stimuli, although the later finding was not significant. The findings of experiment 3 were replicated to show that responding to voice targets paired with related face stimuli enhances response latencies. Moreover, in contrast to prediction, this was shown to occur irrespective of spatial congruence. There was no difference between the errors made when responding to face or voice targets, which suggests that enhanced responding to voices paired with faces can not simply be explained by a tendency to primarily attend to visual stimuli.

The findings here that face stimuli enhanced response latencies to voice targets irrespective of spatial congruence, although non-significant, would be surprising. However, auditory stimuli tend to exert more influence compared to visual information on temporal order judgements (Scheier, Nijwahan & Shimojo, 1999) owing to higher temporal acuity in the auditory domain (Shimojo & Shams, 2001). In contrast, visual stimuli predominate in spatial tasks owing to higher spatial acuity in the visual field (Shimojo & Shams, 2001). For example, during spatially incongruent audio-visual integration, location is biased toward the visual information (Recanzone, 2009). As such, it was expected that responding to a face target would be enhanced and voice target impeded by related human stimuli presented in an incongruent spatial location.

When face targets were paired with related voice stimuli, responding was only significantly faster when both occurred in the same spatial location. This fails to support the prediction that voices would enhance responding even when voices occurred in an incongruent spatial location. This finding also fails to support earlier research (Teder-Sälejärvi et al., 2005). However, sensory integration research (e.g. Salejarvi et al., 2005) often uses unrelated non-human stimuli such as light flashes and sound bursts. Faces and voices are often perceived together in conversation and are used to detect emotional expression, identify or locate a person. Interpreting voices is likely to require some top-down processing (see Latinus, Van Rullen & Taylor, 2010) and as such, spatial incongruence may be more readily apparent and could disrupt integration. In contrast, unrelated artificial auditory stimuli may only involve bottom-up processing and need not be attended. As such, responding to a target accompanied by a simple signal could be facilitated even when stimuli occur in an incongruent spatial location.

These findings showed that responding to face targets paired with unrelated auditory stimuli was faster even when auditory stimuli occurred in an incongruent spatial location. There was no evidence of inter-sensory facilitation. Nevertheless, enhanced responding to visual information presented together with artificial auditory stimuli, irrespective of spatial congruence, is consistent with the recent findings of Teder-Sälejärvi et al. (2005) and is consistent with the ventriloquism effect (see de Gelder & Bertellson, 2003). That is, auditory information can aid orientation toward and localisation of a visual object (see Recanzone, 2009) when presented in an incongruent location. Audio-visual integration may occur early in the attention process (Colin et al., 2002) and potentially serves to facilitate stimuli detection or location. However, it appears such integration may depend on the nature of the signal. Perceptual binding could be more sensitive to disruption when information has social relevance or requires top-down processes.

The findings here suggest that person specific information is a special case of integration. Auditory stimuli facilitate responding to faces, however, integration may be disrupted when the accompanying stimuli are related voices and occur in a different spatial location. There were small differences in responding to voice targets in the different conditions although few were significant. Nevertheless, visual stimuli impede responding to voice targets while related face stimuli appear to enhance responding, irrespective of spatial location. Together, the results of experiment 3 (Chapter 5) and experiment 4 (Chapter 6) show that face and voice information can be integrated to facilitate response latencies.

The receiver psychology hypothesis, describes signals that evolve alongside more informative signals in order to facilitate detection and discrimination. Rather than elicit any meaningful effect on their own, male voices could simply improve the ability to detect and respond to male attractiveness. In order to test this assumption, the next step would be to consider how such person specific integration translates to discriminative judgements. For example, research has shown that face and voice information facilitates the identification of emotions (Collignon et al., 2008; de Gelder & Vroomen, 1995). Evidence that judgements of male face attractiveness are made faster with the presence of a male voice, but that male faces do not facilitate the attractiveness judgements of male voices would be consistent with a receiver psychology account. The next chapter will therefore investigate the role of face and voice information in the temporal detection and discrimination of attractiveness.

CHAPTER 7: TEMPORAL ATTRACTIVENESS JUDGEMENTS

7.1 Introduction

The findings of experiment 3 (Chapter 4) and 4 (Chapter 5) have shown enhanced responding when face and voice information are presented together. Integration can be disrupted when responding to face targets and accompanying voice information is spatially incongruent. These findings differ from responding to face or voice targets when accompanied by unrelated stimuli. Unrelated auditory stimuli enhance responding to face targets irrespective of spatial location while unrelated visual stimuli appear to impede responding to voice targets. Processing person specific information may be an exception in sensory integration. However, it remains to be investigated whether integrating face and voice information extends to increasing the ability to detect or discriminate attractiveness.

Male face and voice attractiveness do not appear to be related (Lander, 2008; Oguchi & Kukuchi, 1997). That is, face and voice information may communicate different signals with regard to male mate qualities. It is therefore possible that face-voice integration could create a conflict in attributing attractiveness. People have been shown to integrate face and voice information in attractiveness judgements even when asked to ignore one of the modalities (Zuckerman, Miyake & Hodgins, 1991). Since faces have a greater effect on compound attractiveness (see experiments 1b and 2b) it could be that more weight is attributed to face judgements thus voices may have little effect on judgement time. However, determining attractiveness could also take longer as a result of resolving the potential conflict between the differential attractiveness of male faces and voices.

One possible explanation for the function of face-voice integration in attractiveness judgements that has not yet been discounted is the receiver psychology hypothesis (section 1.4.3). Females have been shown to prefer low voice pitch males (Bruckert et al., 2006; Collins 2000; Feinberg et al., 2005; Feinberg et al., 2008; Riding, Lonsdale & Brown, 2006). However, it is possible that male voices simply facilitate the detection or discrimination of male face attractiveness although voices by themselves may elicit no response of their own. For example, Smith, Grabowecky and Suzuki (2007) found that the frequency of a pure auditory tone determined the sex attribution of an androgynous face although the tone by itself was rated as neither male nor female. That is, the tone's pitch was used to discriminate the sex of a human face although by themselves, the tones elicited no response of their own.

Speed accuracy trade-offs are common in the decision making process (section 1.7) and may be particularly relevant in contexts where environmental conditions affect perception. For example, detecting emotional expression is improved when both the face and voice are congruent and presented together (Collingnon et al., 2008). However, determining emotional expression was predominantly made using a voice when the face was blurred (Collingnon et al., 2008). Voices are effective when communicating over distance or where there are impoverished light conditions. It is possible that in such conditions, voice information could be used to determine compound attractiveness. However, given the lack of relationship between male face and voice attractiveness this seems unlikely. Face and voice may not be used to determine the attractiveness of the composite (e.g. voice or face) signal when where one modality is less clear. Despite the interest in attractiveness research, the focus has predominantly been on what constitutes attractiveness rather than how attractiveness is attributed. As such, there is very little on which to base predictions.

7.1.1 Aim

The aim of this experiment was therefore, to tentatively explore temporal attractiveness judgements. Moreover, this experiment sought to determine the effect of background noise on the capacity to detect stimuli and discriminate attractiveness when targets were presented on their own, together with stimuli that was not masked with noise and together with masked stimuli. Targets were presented in video format with visual and/or auditory background noise that degraded linearly over time. Female participants provided responses for face and voice targets separately. The findings of experiments 3 and 4 have shown that responding to male face-voice compounds are faster when presented synchronously in the same location. It was therefore predicted that face and voice targets would be detected earlier when synchronously presented with related voice or face stimuli. The findings of experiments 1b and 2b have also shown that male face and voice attractiveness tend not to be related. It was therefore also anticipated that discrimination of male face or voice attractiveness would not be facilitated when presented in compound.

7.2 Method

7.2.1 Design

A mixed methods design was used to investigate response latencies related to detection and the discrimination of attractive faces and voices. It was decided to use both male and female stimuli in order to determine whether there could be any difference in effects that could be attributed to the detection and/or discrimination of same/different sex stimuli. A series of videos were used to present stimuli that were masked by linearly degraded background noise. Detection and discrimination of attractiveness were made in 3 between measures conditions for face and voice targets separately. The target was presented (single) on its own with background noise; the target was presented with background noise and accompanying stimuli that were not masked (asynchronous); the target was presented with accompanying stimuli which were both masked by background noise (synchronous).

7.2.2 Participants

The participants were 48 female students (*M* = 21.5yrs, *SD* = 5) recruited from Nottingham Trent University. Students that took part in this experiment had not participated in any of the previous experiments. They received credits as part of a research scheme for taking part.

7.2.3 Stimuli

Stimuli sets (faces and voices) of 20 white European males (10) and females (10) were used. Stimuli were selected randomly from the database (Chapter 2). Videos were compiled (section 2.5.5) for face and voice targets respectively in 3 experimental conditions. Videos in the single condition were faces or voices with corresponding visual or auditory noise. Videos in the asynchronous condition comprised a target with corresponding noise together with an accompanying stimulus with no noise. Videos in the synchronous condition comprised both face and voice together with both visual and auditory noise. Each video lasted 11 seconds and comprised a target stimulus together with visual or auditory noise. Random black and white noise was used for the visual stimuli and a cocktail party noise (consisting of mixed-frequency inaudible speech) was used for the auditory stimuli. Simultaneously, noise faded out and stimuli faded in linearly, at 1% per second, with complete audibility/visibility at 10-11 seconds of video clips.

7.2.4 Apparatus

The presentation, timing and randomisation of stimuli were controlled by e-prime 2 experimental software. Face stimuli were presented on a 15″ computer monitor on the left or the right of the screen separated by 10° of visual angle. The vocal samples were presented in either the left or the right auditory channel and were played at a comfortable volume level through Beyerdynamic DTX 900 headphones. A standard keyboard was used for inputting responses.

7.2.5 Procedure

The participants were randomly assigned to one of 3 experimental conditions (see Figure 7.1; single, asynchronous and synchronous). The experiment was conducted in 2 blocks comprising face and voice targets, the order of which was counterbalanced across participants. Stimuli were presented in a random order within each block. Participants were asked to respond twice within each video clip. The first response was to press space bar when able to detect the target (face or voice) stimulus. The second response was to press space bar when able to judge the attractiveness of the stimulus. Following the second response, the video ended and participants were asked for a third response; an attractiveness rating on the scale 1 (not attractive) to 9 (attractive). Each video was separated by a 3 second inter-trial interval. Response latencies for detection and discrimination (attractiveness choice time) were recorded in addition to the attractiveness rating.

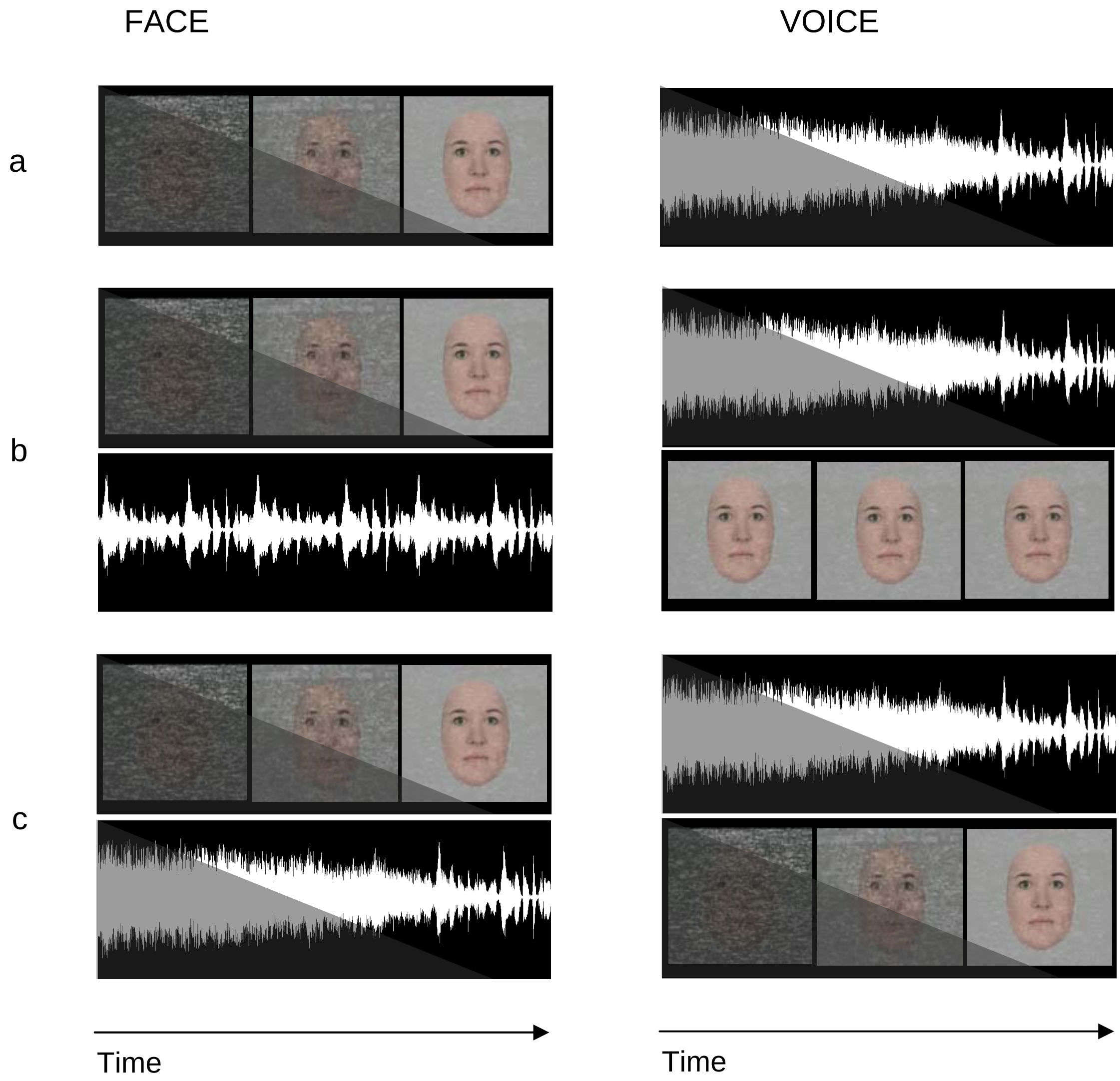

Figure 7.1: *Experimental conditions for face and voice target blocks; a) single, target stimuli emerges as noise reduces; b) asynchronous, target stimuli emerges as noise only presented in the target modality reduces; c) synchronous, target stimuli emerges as noise presented in both modalities reduces concurrently*

7.3 Results

A 2 (target) x 2 (stimuli sex) x 3 (condition) mixed measures ANOVA was used to analyse mean detection responses for stimuli in 3 independent measures conditions; single targets (single), target with accompanying stimuli that was not masked by noise (asynchronous); and target and accompanying stimuli both of which were masked by noise (synchronous). There was a significant main effect of target, $F_{1,45} = 15.594$, $p < .001$, such that, faces, *M* = 4474msecs, 95% CI [4150, 4797], were detected faster than voices, *M* = 5006msecs, 95% CI [4609, 5403]. There was no significant effect of stimulus sex, $F_{1,45} = 1.843$, $p > .05$, and no effect of condition, $F_{2,45} = .014$, $p > .05$ (see Figure 7.2), single, *M* = 4734msecs, 95% CI [4152, 5315]; asynchronous, *M* = 4708msecs, 95% CI [4127, 5290]; synchronous, *M* = 4777msecs, 95% CI [4195, 5358]. There were no significant interactions ($p > .05$).

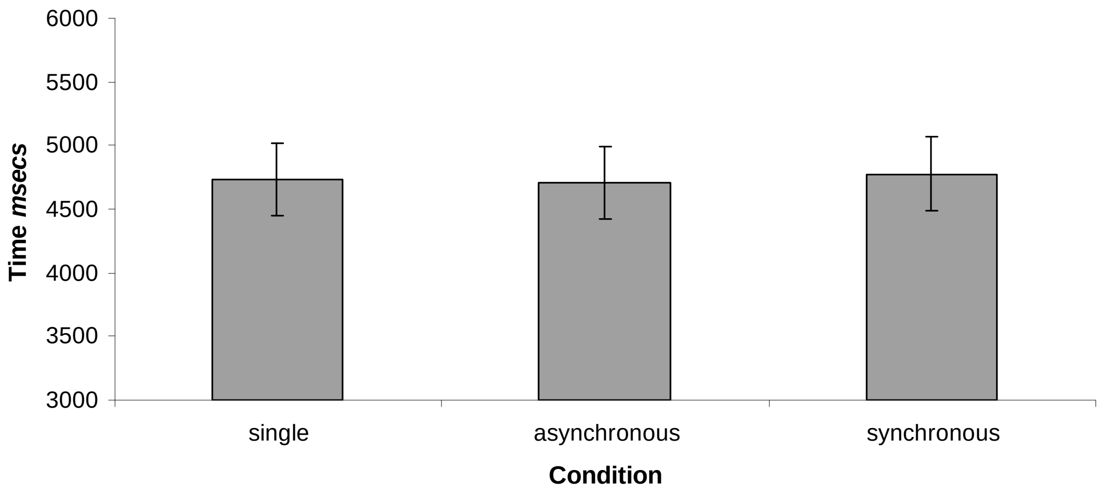

Figure 7.2: *Response latencies with standard error bars for stimuli detection in single asynchronous and synchronous experimental conditions*

A 2 (target) x 2 (stimuli sex) x 3 (condition) mixed measures ANOVA was used to analyse mean attractiveness choice time. Attractiveness choice time was determined by subtracting response latency at response 1 (detection) from response 2 (discrimination). There was no significant, $F_{1,44} = 2.618$, $p > .05$, main effect of target; face, *M* = 3064msecs, 95% CI [2698, 3429]; voice, *M* = 2821msecs, 95% CI [2478, 3163]; and no significant, $F_{1,44} = 1.907$, $p > .05$, main effect of stimuli sex; male, *M* = 2780msecs, 95% CI [2656, 3303]; female, *M* = 2905msecs, 95% CI [2578, 3232]. There was also no significant, $F_{2,44} = .911$, $p > .05$, main effect of condition (see Figure 7.3); single, *M* = 2726msecs, 95% CI [2159, 3293]; asynchronous, *M* = 3235msecs, 95% CI [2686, 3784]; synchronous, *M* = 2866msecs, 95% CI [2316, 3415], and no significant interactions ($p > .05$).

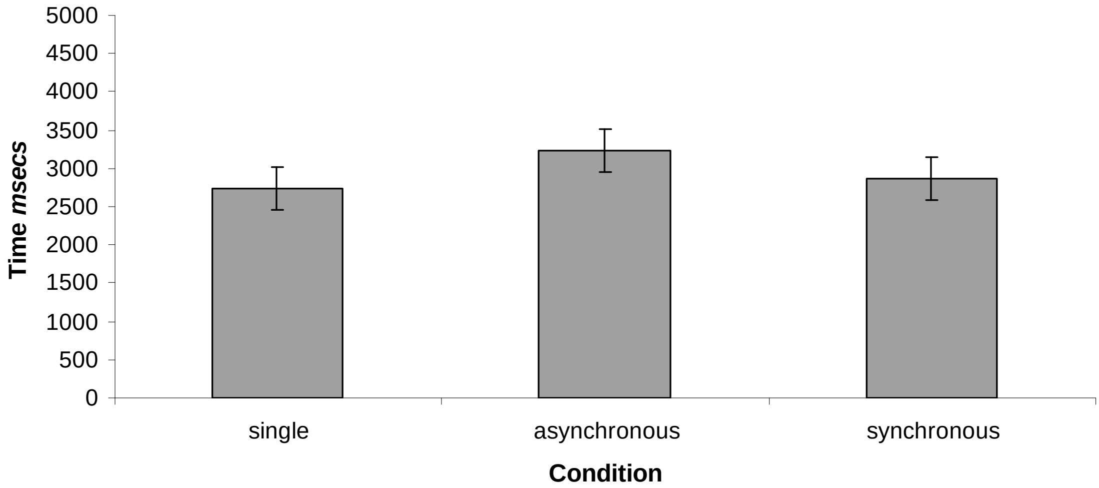

Figure 7.3: *Response latencies with standard error bars for attractiveness choice time in single, asynchronous and synchronous experimental conditions*

Data for attractiveness ratings were pooled across the three conditions and compared to attractiveness choice time for male and female stimuli and for face and voice targets. The analysis revealed no relationship between female voice attractiveness and choice time, $r_{441} = .038$, $p > .05$, 95% CI [-.131, .055]. There was a positive but non-significant relationship between female face attractiveness and choice time, $r_{443} = .086$, $p = .07$, 95% CI [-.001, .177]. However, there was a significant positive relationship between male face attractiveness, $r_{455} = .156$, $p < .001$, 95% CI [.065, .244], male voice attractiveness, $r_{403} = .111$, $p < .05$, 95% CI [.014, .206], and choice time. The female participants took longer to determine the attractiveness of male and female faces although the latter did not reach significance. Female participants also took longer to determine the attractiveness of male but not female voices.

7.4 Discussion

Overall, the results showed that faces were detected faster than voices when presented against background noise. There was no difference between detecting male and female stimuli and no effect of condition. Although faces were detected faster, there was no difference between the time taken to determine the attractiveness of faces and voices. There was also no difference between the time taken to determine male and female attractiveness or between experimental conditions. However, further analysis revealed that there was a relationship between attractiveness ratings and attractiveness choice time. The female participants took longer to judge attractive male and female faces although the latter did not reach significance. The participants also took longer to judge attractive male voices. However, there was no relationship between choice time and attractive female voices.

The absence of faster detection when face and voice were presented together in compound here was contrary to prediction. Faster responding to face and voice targets had been shown previously in experiment 3 (Chapter 5) and 4 (Chapter 6). There was, however, a considerable degree of residual error in responding to the detection of stimuli. One possibility for the degree of residual error is that the participants may have varied in their definition of detection. For example, people may have responded when the outline of a face could be seen and others when more of the features could be detected. However, it is also possible that the variation in responding to detection might have simply been induced by task complexity. The procedure required participants to respond twice during each video. For each response, the definition required two distinct perceptual definitions, detection and attractiveness choice, that could have been confused.

Task complexity could also explain why there was no effect of experimental condition on attractiveness choice time. Participants did not make judgements faster when more information was presented. However, previous research has shown that attractiveness judgements regarding faces can be made as quickly as 100msecs and do not differ significantly from those made at 500msecs (Willis & Todorov, 2006). It could be that attractiveness attributions are automatic and require little effort. The addition of another modality could therefore have had little or no effect. However, female participants here took on average ~3secs to determine stimuli attractiveness. In part, longer choice time is likely to be evident because participants waited until background noise was reduced and more stimuli could be perceived. Nevertheless, choice time was actually ~500msecs slower in the asynchronous condition.

Although there was a considerable difference in choice time when stimuli were asynchronously presented together, the difference was non-significant. Any effect of experimental condition may not have been detectable because there was considerable residual error in judgement time. Such error is likely to have been related to individual differences in responding because of task complexity. However, some of the variance in choice time could have been related to the attractiveness ratings. For example, previous research found that participants took longer to categorise attractive rather than neutral or unattractive faces (Kranz & Ishai, 2006). The findings here similarly showed that choice time was longer for attractive stimuli. While attractiveness decisions can be made early (Willis & Todorov, 2006) participants may not do so when given the choice.

Attractiveness choice time was longer for male faces and voices, and there was some indication of longer choice time for female faces but not voices. Previous research has shown a relationship between gaze duration, attractiveness and arousal (Shimojo, Simion, Shimojo & Scheier, 2003). Moreover, research has shown that longer response time categorising an attractive faces is related to the brain reward circuitry (Kranz & Ishai, 2006). While this has been shown in faces, to speculate, the research here could indicate that information evident in male voices attended to by females are also of intrinsic value. That is, attractive opposite sex voices could similarly activate reward related areas of the brain. Further research would be required in order to satisfy this suggestion. Nevertheless, the findings here show that attractiveness judgements were not made faster when face and voice were presented synchronously. These findings therefore indicate that together, male voices do not simply facilitate the detection or discrimination of male face attractiveness judgements.

CHAPTER 8: GENERAL DISCUSSION

8.1 Summary of aims

The literature in chapter 1 outlines research relating to the nature and function of faces and voices in human sexual selection. With reference to the framework proposed by Candolin (2003), a number of intriguing considerations are highlighted with which to base experimentation in an effort to resolve the functional nature of multiple signals. Investigating multiple signals presented together could be used to estimate the relative influence of face and voice attractiveness with regard to face-voice compound stimuli and thus their respective importance independently. Considering the integration of signals and the potential cognitive benefits of multimodal information also promises to show whether information occurring together is likely to form a unified perception.

A key element of this research was to investigate modality related effects of visual and auditory information using human face and voice stimuli. Chapter 2 detailed the methods used to develop a stimuli database for use in the following experiments. Chapter 2 also described the manipulation of stimuli specific to each experiment. The aim of experiment 1a and 1b (Chapter 3) and experiment 2a and 2b (Chapter 4) was to investigate the nature of both female and male face and voice signals in relation to the framework proposed by Candolin (2003). Accordingly, the aim was to ascertain the relationship between face and voice attractiveness for both female (experiment 1a and 2a) and male (experiment 1b and 2b) stimuli using samples of faces together with vowel sounds (Chapter 3) and speech (Chapter 4). In addition, these experiments considered the relative influence of face and voice attractiveness on face-voice compound stimuli attractiveness for both male and female stimuli.

The findings of experiment 1a and 1b (Chapter 3) and experiment 2a and 2b (Chapter 4) suggest that male and female stimuli could communicate different messages with respect to the framework. The relationship between female face and voice attractiveness is congruent with the back-up signals hypothesis. Together, female faces and voices can be used by a male to more accurately determine fertility. For males, however, judgements of face and voice attractiveness were not related, which is congruent with the multiple messages hypothesis. That is, the face and voice of males communicate different information that can be used by a female to ascertain the overall quality of a potential mate. However, one possibility within the framework that could also explain the function of male face and voice information is the receiver psychology hypothesis. That is, male voices could simply be used to facilitate the detection or discrimination of male faces.

The following experiments therefore dealt with further investigating female perception and the modality related effects of male faces and voices. Experiment 3 (Chapter 5) investigated the effect of unimodal and bimodal presentations on response latencies when targets were either male faces or voices. Experiment 3 also sought to determine the relationship between target modality and response latencies when bimodal stimuli were either related or unrelated. These findings were extended in experiment 4 (Chapter 6) in an effort to understand the conditions with which audio-visual information is integrated. Specifically, by considering processing speed when male faces and voices are spatially disparate, the aim of experiment 4 was to provide evidence of their relative effects on the unified perception of social stimuli. Finally, the aim of experiment 5 (Chapter 7) was to tentatively explore temporal attractiveness judgements. This experiment sought to determine the effect of background noise on the capacity to detect stimuli and discriminate attractiveness when targets comprised both male and female stimuli and were presented on their own and together in compound. Before discussing the findings in relation to current research, the next section will consider the results specific to each experiment.

8.2 Experimental findings

8.2.1 Face and vowel sounds

Experiment 1a and 1b (Chapter 3) was conducted using photographs of faces together with vowel sounds for female and male stimuli. The participants rated the attractiveness of a series of faces, together with voices and face-voice compound stimuli. The results were analysed using multilevel model analyses, providing estimates of face and voice attractiveness influences on perceived face-voice compound stimuli attractiveness. Modeling also produced estimates of random variance attributed to differences between stimuli, between participants and to unexplained residual error. The attractiveness ratings of faces and voices were also analysed in relation to measures of femininity/masculinity.

Face and voice attractiveness positively and independently influenced the attractiveness of face-voice compound stimuli for both males and females. Of the two modalities, faces had a proportionally greater influence on compound stimuli attractiveness than voices. There was a difference between male and female stimuli such that, male voices had a greater influence on compound stimuli attractiveness compared to female voices. For both models, there was random variance attributed to differences between stimuli. There was also considerable variance attributed to differences between participants and to residual error. That is, a large proportion of variance in the attractiveness effects was related to unspecified individual differences and to factors such as measurement error for example.

The results of the experiment 1a (Chapter 3) showed, as predicted, that perceived face and voice attractiveness in the female stimuli were related. A significant positive correlation was also found between female vocal attractiveness and voice pitch. That is, female voices with higher voice pitch were judged as more attractive. However, contrary to prediction, there was no relationship between female face attractiveness and measures of face femininity. The results of experiment 1b (Chapter 3) showed no relationship between face and voice attractiveness ratings in male stimuli. Contrary to prediction there was no relationship between male vocal attractiveness and voice pitch. Although there was a positive correlation between male face attractiveness and measures of face masculinity it did not reach significance.

8.2.2 Face and speech

Experiment 2a and 2b (Chapter 4) was conducted using photographs of faces together with a sample of speech for female and male stimuli. Identical to experiments in chapter 3, the participants rated the attractiveness of a series of faces, together with voices and face-voice compound stimuli. The results were analysed using multilevel model analyses. The attractiveness ratings of faces and voices were also analysed in relation to measures of femininity/masculinity.

Overall the results showed little difference between experiments using either vowel sounds or speech for either male or female stimuli. Face and voice attractiveness positively and independently influenced the attractiveness of face-voice compound stimuli for both males and females. For female stimuli, an interaction was again evident such that, face and voice attractiveness was enhanced by an accompanying attractive voice or face respectively. For both models, there was random variance attributed to differences between stimuli and considerable variance attributed to differences between participants and to unexplained residual error.

The findings of experiment 2a (Chapter 4) provided further support for the prediction that female face and voice attractiveness would be related. However, there was a non-significant correlation between perceived female vocal attractiveness and voice pitch. Contrary to prediction, there was also a non-significant relationship between female face attractiveness and measures of face femininity. Concordant with earlier findings, there was a non-significant relationship between face and voice attractiveness for male stimuli in experiment 2b (Chapter 4). There was, however, a significant negative correlation between male vocal attractiveness and voice pitch. That is, male voices with lower voice pitch were judged as more attractive. There was also a significant positive correlation between male face attractiveness and measure of face masculinity. More masculine faces were judged to be more attractive.

8.2.3 Face and voice response latencies

Experiment 3 (chapter 5) investigated the response latencies of female participants in relation to unimodal and bimodal stimuli when targets were either male faces or voices. Experiment 3 also sought to determine the relationship between target modality and response latencies when bimodal stimuli were either related or unrelated. The findings of experiment 3 showed that overall responding to male voice targets were slower than responding to male face targets. Consistent with prediction, response latencies were reduced in bimodal trials where male face targets were presented synchronously with unrelated artificial auditory stimuli or related voice stimuli. In contrast, response latencies were increased when a male voice target was presented synchronously with unrelated artificial visual stimuli. However, responding to male voices targets was faster when presented synchronously with related human face stimuli.

8.2.4 Face-voice integration and spatial congruence

Experiment 4 (Chapter 6) was devised in an effort to understand the conditions with which audio-visual information is integrated. Specifically, experiment 4 investigated female responding to male face and voice and voice targets that were presented on their own and together with related human stimuli or unrelated artificial auditory/visual stimuli in spatially in/congruent spatial locations. The findings of experiment 4 found that response latencies were reduced in bimodal trials where male face targets were presented synchronously with unrelated auditory stimuli irrespective of spatial location. Responding to face targets presented with related voice stimuli, however, were only enhanced when occurring in the same spatial location. Responding to voice targets paired with unrelated visual stimuli was slower than responses to voice targets on their own, irrespective of spatial location. Responding to voice targets paired with related face stimuli was, however, faster compared to responding to voice targets on their own. This was true irrespective of spatial congruence. However, response latencies for bimodal voice target conditions were not significantly different from responses to voice targets on their own.

8.2.5 Temporal attractiveness judgements

Experiment 5 (Chapter 7) investigated the time taken for female participants to detect and judge the attractiveness of male and female stimuli. Face and voice targets were presented in three experimental conditions. The target was presented on its own with background noise (single); the target was presented with background noise and accompanying stimuli that was not masked (asynchronous); and the target was presented with accompanying stimuli which were both masked by background noise (synchronous).

The findings of experiment 5 (Chapter 7) showed that face targets were detected faster than voice targets although there was no difference between stimuli sex and condition. There was also no difference in attractiveness choice time between face and voice targets, irrespective of stimuli sex or condition. Data for attractiveness ratings were pooled across the three conditions and compared to attractiveness choice time for male and female stimuli and for face and voice targets. There was a positive association between choice time and male stimuli such that, females took longer to judge more attractive male faces and voices. Females also took longer to judge the attractiveness of female faces. However, there was no relationship between choice time and attractiveness for female voices.

8.3 Discussion of findings in relation to current research

8.3.1 Female face and voice attractiveness

The findings of experiment 1a (Chapter 3) and 2a (Chapter 4) using female stimuli showed a correlation between female face and voice attractiveness whether vocal samples comprised vowel sounds or speech. These findings are supported by similar research (Collins & Missing, 2003; Feinberg et al., 2005; Fraccaro et al., 2010; Lander, 2008; Saxton et al., 2009). Feminine faces have been found to be attractive to males (Feinberg et al., 2005; Johnston et al., 2001; Jones et al., 2007; Law-Smith et al., 2006; Perrett et al., 1998; Rhodes et al., 2000) and are related to high oestrogen levels and fertility (Law-Smith et al., 2006). High voice pitch females also have higher oestrogen than those with low pitched voices (Abitbol, Abitbol & Abitbol, 1999) and are preferred by males (Collins & Missing, 2003; Feinberg et al., 2005; Feinberg et al., 2008; Vukovich et al., 2009) suggesting that female faces and voices similarly reflect femininity and fertility.

A positive relationship in experiment 1a (Chapter 3) and 2a (Chapter 4) was found between attractiveness and measures of femininity in female faces. However, the relationship in each case failed to reach significance. Feminine faces have been shown to be attractive whether natural or manipulated (Rhodes, 2006). Moreover, faces with greater femininity were found to be more attractive in a study (Feinberg et al., 2005) where male attractiveness ratings were correlated with the same facial measures of femininity used in experiment 1a and 2a. It is possible there was insufficient variation within the female stimuli used here to detect a relationship between attractiveness and femininity. Nevertheless, the sample of stimuli used in these experiments was taken from a normal population.

Penton-Voak and Chen (2004) reported only a small effect in the ability to discriminate testosterone signals in male faces. Further, it was suggested that discriminating between facial testosterone indicators may be easy, only when the differences are large. That is, people find it difficult to discriminate between faces expressing average testosterone-related facial features. There was variation between female stimuli used in both experiment 1a (Chapter 3) and 2a (Chapter 4). However, such variation may have been too small to discriminate oestrogen indicators. Further investigation would serve to address whether male preference for feminine faces is more evident when differences between expressions of oestrogen is large. Evidence that comparison of extreme facial features is required to differentiate between attractive feminine faces could question the importance of facial femininity. For example, difficulty distinguishing between feminine faces could emphasise the role of direct comparisons in male mating decisions. However, discrepancies identifying femininity in female faces could also emphasise the importance of integrating multiple redundant signals in order to more accurately detect oestrogen and fertility.

The relationship between attractiveness and feminine voices was also problematic. Although experiment 1a (Chapter 3) using vowel sounds showed there to be a relationship between attractiveness and female voice pitch, no relationship was shown in experiment 2a (Chapter 4) when using a sample of neutral speech. This is surprising given the relationship between female voice attractiveness and voice pitch shown elsewhere (Collins & Missing, 2003; Feinberg et al., 2005). However, female vocalisations have been shown to vary in relation to menstrual phase in speech and not vowels (Bryant & Haselton, 2009). The content of speech has also been shown to influence the strength of female voice attractiveness (Jones et al., 2008). Males appear to prefer high voice pitch females that suggest interest (i.e. ‘I like you’) in the receiver (Jones et al., 2008). In addition, there is some evidence to indicate that males prefer female speakers with a familiar regional accent (Coupland & Bishop, 2007). While a controlled experiment may show a clear relationship between female vocal attractiveness and voice pitch, the effect may only be small relative to the dynamic contextual information in speech.

Despite the experimental findings in experiment 1a (Chapter 3) and 2a (Chapter 4) showing inconsistent preferences for feminine faces and voices, results were in the predicted direction. One issue with the present research is that participants were predominantly undergraduate students. Males are proposed to prefer females expressing youth and fertility (Jones et al., 1995). However, this may not apply to males of all ages. Some research found male preference for low voice pitch female voices (Leaderbrand, Dekam, Morey & Tuma, 2008; Oguchi & Kikuchi, 1997). Moreover, females were shown to lower their voice pitch when simulating a sexy voice (Tuomi & Fisher, 1979) and in response to an attractive male face (Hughes, Farley & Rhodes, 2010). This appears to conflict with research (Feinberg et al., 2005) to suggest that males prefer females that indicate (e.g. high voice pitch) fertility/youthfulness. However, since female voice pitch gradually lowers with age (Abitbol, Abitbol & Abitbol, 1999), it could be that females benefit from advertising maturity and sexual experience.

Male face preferences have been shown to be influenced by age related aspects of their parents (Perrett et al., 2002). That is, males with an older mother, for example, prefer faces expressing older characteristics. Moreover, one study found that adolescent males reported intercourse with at least one older female in order to gain sexual experience (Chinake et al., 2002). Factors such as parental age and sexual experience could explain some of the variance in attractiveness effects attributable to individual differences in experiment 1a (Chapter 3) and 2a (Chapter 4). Although female faces and voices are likely to express oestrogen and fertility (Feinberg et al., 2005) they may be used to varying degree by each individual male.

8.3.2 Male face and voice attractiveness

The findings of experiment 1b (Chapter 3) and 2b (Chapter 4) provided contrasting results with regard to the relationship between low voice pitch and attractiveness of male vocal stimuli. Male low voice pitch was only found to be more attractive when voices comprised samples of speech (experiment 2b). This result is likely to have been affected by the composition of vocal stimuli. The vowel sounds used in experiment 1b are useful because there is limited interference from aspects such as formant dispersion that can influence attractiveness judgements (Feinberg et al., 2005). However, there is also little variation in pitch. Voices naturally vary in pitch and such variation may be important for judgements of attractiveness and dominance (Hodges-Simeon et al., 2010). For example, females have been shown to prefer male voices that are low in pitch but show some upward variation (Bruckert et al., 2006). As such, the samples used in experiment 1b may have lacked sufficient variance with which to distinguish between male voices.

In general experiment 1b (Chapter 3) and 2b (Chapter 4) do find support from previous research suggesting that females prefer low voice pitch males (Bruckert et al., 2006; Collins 2000; Feinberg, et al., 2006; Puts, 2005; Puts, 2006; Riding, Lonsdale & Brown, 2006; Saxton, Caryl & Roberts, 2006; Zuckerman & Driver, 1989; Zuckerman, Hodgins & Miyake, 1990; Zuckerman & Miyake, 1993). In accordance with previous research (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999), there was also a positive relationship between face masculinity and attractiveness. Although a positive relationship was found in both experiments, masculine faces were only found to be significantly more attractive in experiment 2b. Nevertheless, both experiment 1b and 2b were consistent in finding there was no correlation between male face and voice attractiveness.

Evidence of no correlation between male face and voice attractiveness is congruent with some research (Oguchi & Kukuchi, 1997; Lander, 2008) but contrasts others (Feinberg et al., 2008; Saxton et al., 2006; Saxton et al., 2009). The discrepancy between findings of a face-voice attractiveness relationship in male stimuli could simply be the result of different methodology used in these studies. Both Feinberg et al. (2008) and Saxton et al. (2006) used a forced choice paradigm where participants continually chose the more attractive of two simultaneously presented stimuli as opposed to rating a single stimulus on a scale. Relative (forced choice) judgements have been shown to be more sensitive in detecting differences between stimuli (Gur et al., 2009). It could be that allowing direct comparisons can provide more accurate information with which to judge stimuli attractiveness. However, the forced choice paradigm has been shown in another study to produce format-induced effects relating to sex differences in jealousy (DeSteno, Bartlett & Salovey, 2002).

Although comparative evaluation may be an important aspect of mate choice, such contexts render decisions to be labile (see Bateson & Healy, 2005). For example, the attractiveness of a target face is influenced by the assimilation of juxtaposed faces (Geiselman, Haight & Kimata, 1984; Wedell, Parducci & Geiselman, 1987). The relationship between findings based on relative and absolute judgments would be an interesting focus of further investigation. Moreover, the validity of the aforementioned methods in relation to mate choice is a matter of debate. Although contrast effects can not truly be eliminated, stimuli judged in relative isolation are nevertheless likely to provide more informative data with regard to individual attractiveness ratings.

One issue with experiment 1b (Chapter 3) and 2b (Chapter 4) is that data regarding ovulation cycle or hormonal contraception use was not obtained for female participants. Studies have shown that female preference for masculine faces (Johnston et al. 2001; Jones et al. 2008; Little et al. 2007) and voices (Feinberg et al., 2006; Puts, 2005) is heightened during peak ovulation phase. Further, masculinity preferences are weaker for females using hormonal contraception (Feinberg et al., 2008). The lack of evidence for a relationship between male face and voice attractiveness could therefore be a result of weaker masculinity preferences owing to the hormonal status of female participants. However, studies of female preferences and the ovulation cycle have typically involved experiments using stimuli manipulated on a single dimension (Peters, Simmons & Rhodes, 2009) such as masculinity (e.g. Little, Jones & Burriss, 2007; Penton-Voak & Perrett, 2000). A recent study found no cyclic preference for masculinity using non-manipulated faces (Peters, Simmons & Rhodes, 2009). As such, the effect of ovulation phase on female preferences may only be small. Nevertheless, weaker preferences owing to hormonal status could explain why the relationships between face masculinity and attractiveness were in the predicted direction but only reached significance in one of the experiments.

The lack of correlation between female attractiveness ratings of male faces and voices in the findings of experiment 1b (Chapter 3) and 2b (Chapter 4) suggest that indicators of testosterone were either unrelated in an individual or that perceived face attractiveness was judged using a different criteria to voice attractiveness. There is some suggestion that male faces are judged differently to male voices. For example, there is evidence of female preference for masculine faces (Keating, 1985; Koehler et al. 2004; Penton-Voak et al., 2001; Scheib et al., 1999), although some research has shown preference for composite feminised male faces (Perrett et al., 1998; Penton-Voak et al., 2004).

The possibility of a preference for a masculine voice and feminine face from the participants used in experiment 1b (Chapter 3) and 2b (Chapter 4) could explain why there is no relationship between male face and voice attractiveness. However, studies showing feminine face preferences have predominantly used faces manipulated on a continuum of sexual dimorphism (Rhodes, 2006). Studies using non-manipulated faces tend to support preference for a masculine face (see Rhodes, 2006). In general, males with high testosterone expressed in low pitch voices (Dabbs & Mallinger, 1999; Hollien, 1960) and masculine faces (Penton-Voak & Chen, 2004) are preferred by females and tend to have greater reproductive success (Apicella, Feinberg & Marlowe, 2007; Hughes, Dispenza & Gallup, 2004; Puts, 2005). Taken together, a correlation between male face and voice attractiveness would have been expected but was not found.

8.3.3 Face and voice attractiveness influences

Evidence of face and voice influences on the perceived attractiveness of both male and female compound stimuli is congruent with recent research (Saxton et al., 2009). However, Saxton et al. (2009) found that face and voice attractiveness had similar contributions to face, voice and body compound stimuli. This may appear surprising since humans are primarily visually oriented animals. For example, witness testimonies research has shown that vocal recognition is poor owing to the overshadow effect of faces (Cook & Wilding, 2001). The findings of Saxton et al. (2009), however, were based on the attractiveness of individual elements (face, voice and body) that were rated by a different group of participants to those that rated compound attractiveness. Moreover, average ratings for each participant were included in the analysis.

Using participant average attractiveness ratings could lead to an ecological fallacy (Robinson, 1950). That is, stimuli averages could be erroneously inferred as representative of individual stimuli attractiveness. Importantly, looking only at group or participant averaged data can produce different size or even direction of a relationship between variables compared to correlations between individual observations. Regressing participant averages could therefore produce misleading estimates of face and voice effects on compound stimuli attractiveness. By comparison, the influence of voices on face-voice compound attractiveness was shown in experiment 1a and 1b (Chapter 3) to be small relative to faces. These findings applied to both male and female stimuli. Moreover, similar results were found in experiment 2a and 2b (Chapter 4) using an identical method. Accommodating multiple sources of variance using statistics such as multilevel models could therefore provide more accurate and robust estimates of effects.

8.3.4 Evidence of face-voice integration

Overall, the results of experiment 3 (Chapter 5) were congruent with earlier research (Miller, 1982; Rahne et al., 2007; Vroomen & de Gelder, 2000) showing that responding to visual stimuli was faster compared to auditory stimuli. In bimodal trials where male face and voice targets were presented synchronously with unrelated stimuli in the opposite modality, responding to face targets was faster compared to responding to voice targets. These results are therefore congruent with Sinnett, Soto-Faraco & Spence (2008) and provide further evidence of both cognitive enhancement and competition dependent on the target modality. Auditory stimuli facilitated responding to faces while visual stimuli impeded responding to voices. However, when bimodal trials were presented synchronously with related human stimuli, responding to both male face and voice targets were enhanced.

The findings of experiment 3 (Chapter 5) were replicated and extended in experiment 4 (Chapter 6) to show that response latencies were reduced when responding to male face targets presented synchronously with unrelated auditory stimuli relative to a face targets alone, irrespective of spatial congruence. Responding to voice targets, however, was slower when presented synchronously with unrelated visual stimuli irrespective of spatial location. This is consistent with evidence that visual dominance can occur when responding to auditory stimuli while facilitation can occur when responding to visual stimuli (Sinnett, Soto-Faraco & Spence, 2008). Visual information can often be biased by auditory stimuli although auditory information is less often biased by visual information (see de Gelder & Bertelson, 2003).

Evidence of enhanced responding in experiment 4 (Chapter 6), to visual information paired with auditory information irrespective of spatial congruence supports earlier research (Teder-Sälejärvi et al., 2005) but contrasts other research in both non-human (Meredith, Huneycutt & McDade, 1989) and humans animals (Lee et al., 1991; Simon & Craft, 1970). For example, the timing of arm movements (Simon & Craft,

1970) and saccadic eye movements (Lee et al., 1991) toward a visual target have been shown to be faster when accompanied with auditory stimuli emanating from a congruent but not incongruent location. This discrepancy is likely to be caused by the different processes involved in planning key-presses compared to reaching (see Adams, Parthoens & Pratt, 2006). Integration may be facilitated by simple bottom-up processes and disrupted by higher level processing involved in a decision to orient and move toward an object. Latinus, Van Rullen and Taylor (2010), for example, found that top-down processing occurred earlier than bottom-up multimodal integration processes in a gender categorisation task using faces and voices. This could explain why in experiment 4, responding to a face target was faster when presented with related voice stimuli in the same but not different location. The integration of related social stimuli could primarily be influenced by top-down processes thus leading to more obvious disruption when information is spatially incongruent.

Although experiment 3 (Chapter 5) and 4 (Chapter 6) showed reduced response latencies where male face and voice targets were presented synchronously (in congruent spatial locations) with voice and face stimuli respectively, there was no evidence of inter-sensory facilitation. According to Miller’s (1982) race inequality model, inter-sensory facilitation is evident where the probability distribution of bimodal response latencies are significantly less than the sum of probability distributions responding to either of the two unimodal targets. Failure to find evidence of inter-sensory facilitation in both experiment 3 and 4 contrasts that of earlier research. For example, inter-sensory facilitation has been shown in similar paradigms (Miller, 1982; Sinnett, Soto-Faraco & Spence, 2008) even when visual and auditory stimuli were presented in incongruent spatial locations (Teder-Sälejärvi et al., 2005).

Inter-sensory facilitation may not have been found in experiment 3 (Chapter 5) and 4 (Chapter 6) owing to the experimental apparatus. Auditory stimuli in experiments 3 and 4 were delivered through headphones. It has been argued that sound presented through headphones is lateralised rather than providing spatial (localised) information (Grantham, 1995). Moreover, presenting information through headphones may have biased responding to auditory stimuli because of a more direct delivery of sound to the brain. Direct delivery of sound through headphones may have subsequently affected the timing of auditory stimuli presentation. Light travels faster than sound and is thus more likely to be perceived first. As such, visual information is more likely to correspond with the time related occurrence of an event (Navarra, Hartcher-O'Brien, Piazza & Spence, 2009). However, differences in sensory processing have been used to estimate that sound will be perceived first for stimuli occurring at distances of up to 12 metres away (see Poppel, 1997). Responding to visual information is unaffected by the asynchrony of accompanying auditory stimuli (Navarra et al., 2009). Responding to auditory stimuli however, is slower when accompanying visual information lags behind onset and faster when visual information precedes onset (Navarra et al., 2009). The direct delivery of auditory stimuli through headphones could therefore explain the lack of inter-sensory facilitation found in experiment 3 and 4; direct delivery of auditory information could have caused visual information to lag behind the onset time.

There was, however, methodological differences between the paradigm used in experiment 3 (Chapter 5) and 4 (Chapter 6) and similar studies investigating inter-sensory facilitation. Miller (1982) combined visual stimuli with a higher frequency (780Hz) constant tone at 70db. Research has shown that intensity of visual and auditory stimuli can affect reaction times (Jaskowski, Rybarczyk & Jaroszyk, 1994; Niemi, 1979). However, high intensity auditory stimuli can have a negative effect on response latency because it can increase arousal (Jaskowski, Rybarczyk & Jaroszyk, 1994). The auditory stimuli used in experiment 3 and 4 were vocalisations in the male speaking range and thus varied in intensity owing to naturally occurring speech variation. Such variation was retained in order to present stimuli likely to occur in a natural environment but may not have expressed sufficient intensity to produce inter-sensory facilitation. It is possible, however, that reaction times were affected independent of intensity owing to arousal. Attractive faces do evoke responses in the brain relating to reward circuitry (Aharon et al., 2001; Kranz & Ishai, 2006; O'Doherty et al., 2003) and humans do look at attractive features for longer (Shimojo, et al., 2003). Although tentative, it is possible that response latencies were weakened as a result of arousal.

Another methodological difference concerns the use of pre-training and an extended testing period. Humans may be capable of adapting responses to the use of multimodal information even when they are presented in incongruent spatial locations. However, spatially and temporally incongruent information is processed differently in the brain (Macaluso, George, Dolan, Spence & Driver, 2004; Salerjavi et al., 2005). For example, face movements related to speech activates areas in the auditory cortex whereas; facial movements unrelated to speech do not (Calvert et al., 1997). Macaluso et al. (2004) found that ventral regions of the brain are involved in processing temporal aspects of multimodal integration, while more dorsal regions are involved in spatial congruence. Although audio-visual information may processed differently when either spatially or temporally incongruent, it appears that this may not be reflected in behavioural experiments. That is, with training and extended testing periods, it remains possible to provide behavioural evidence of inter-sensory facilitation (e.g. Salerjavi et al., 2005) despite contrasting biological evidence. It appears that such experiments may have to be contrived specifically to elucidate inter-sensory facilitation through extended testing/training periods.

The study conducted by Salejarvi et al., (2005) consisted of practice trials before participants completed 16 experimental sessions (each containing 300 stimulus presentations) lasting 1.5 hours; approximately 8 times more trials than the method employed in experiment 3 (Chapter 5) and 4 (Chapter 6). It could be that inter-sensory facilitation may be an effect that is more likely to be found when participants are trained to optimally respond. Individuals do vary in their sensory dominance (see Giard & Peronet, 1999) and in responses to audio-visual tasks (Hairston et al., 2003). That is, visually dominant people may be more able to locate a visual target when an audio stimulus is presented in an incongruent location (Hairston et al., 2003). Moreover, research has shown that repeated exposure to incongruent audio-visual stimuli can bias the localisation of auditory space (Recanzone, 2009). Such plasticity in the human brain means that participants are likely to be capable of optimally responding in multimodal tasks through adaptation to incongruently presented stimuli. As such, the inclusion of extended training periods may be crucial in elucidating inter-sensory facilitation effects where audio-visual stimuli are presented incongruently.

8.3.5 *Detection and discrimination of faces and voices*

The aim of experiment 5 (Chapter 7) was to investigate whether faces and voices together could aid the detection of target stimuli and facilitate the discrimination of attractiveness. There were three experimental conditions where the target was presented on its own with background noise (single); the target was presented with background noise and accompanying stimuli that was not masked (asynchronous); and the target was presented with accompanying stimuli which were both masked by background noise (synchronous). Participants were asked to respond firstly when they could detect the target, and secondly when they were able to judge the attractiveness of the stimulus. Attractiveness choice time in experiment 5 was calculated by subtracting the time participants chose to rate stimuli from the time at which stimuli was detected. This method was intended to provide results of choice time while unbiased by, for example, the late detection of stimuli.

It was anticipated that more than one signal would implicitly aid detection of the target signal. Research findings presented in experiment 3 (Chapter 5) and 4 (Chapter 6) and elsewhere (Miller, 1982; Matsuda, Tsujii & Wantabe, 2005; Rahne, Bockmann, von Specht, & Sussman, 2007; Vroomen & de Gelder, 2000) have shown that responding to visual, compared to auditory stimuli, is faster and that audio-visual stimuli can together facilitate shorter response latencies. In addition, faces and voices have been shown to influence attractiveness judgements even when one signal is ignored (Zuckerman, Miyake & Hodgins, 1991). Response times are also faster when information is congruent. For example, detecting an emotion is faster when the face and voice both portray the same emotion (Collingnon, et al., 2008). However, discrimination is more determined by faces or voices depending on the reliability of the signal (Collingnon, et al., 2008). For emotion discrimination, more reliance on voices was evident when the face was blurred (Collingnon, et al., 2008). It was therefore expected that faces would facilitate voice attractiveness choice time (and visa versa) in the synchronous condition and even when one signal was degraded (asynchronous condition).

The findings of experiment 5 (Chapter 7) showed that faces were detected faster than voices. Detecting faces may have been faster because visual intensity did not vary and thus stimuli presentation may have been more consistent. In contrast, voices varied in intensity owing to the use of natural speech. Further research could utilise more standardised stimuli and record speeded response times in order to investigate bimodal detection in varying auditory/visual noise conditions. However, retaining natural speech in the present research was paramount in order to avoid confounding attractiveness judgements. Although faces were detected faster than voices, responding was not enhanced further by an accompanying signal that was not masked by noise (asynchronous condition) or when both stimuli were masked by linearly degraded background noise (synchronous condition). Moreover, there were no effects of target, stimuli sex, or condition on attractiveness choice time.

There was, however, a considerable degree of residual error in responding to the detection of stimuli in experiment 5 (Chapter 7). There was also a large proportion of residual error in responding to attractiveness choice time. Similarly, the lack of experimental effects in the detection and attractiveness choice time could be explained by the complexity of the experiment. The procedure required participants to respond twice during each video. For each response, there were two distinct perceptual definitions, detection and attractiveness choice, that could have easily been confused. Varied responding could be an indication that the participants found experiment 5 to be an unusual and confusing task. Nevertheless, there could be other possible explanations for the lack of effects in experiment 5.

Research on bimodal responding typically records speeded responses to stimuli that are presented with immediate clarity (e.g. Miller, 1982). Here, participants did not give speeded response times but rather they had to wait until enough stimuli were present to allow detection. The participants were instructed in experiment 5 (Chapter 7) to detect a specific target. In focusing on the target modality, the participants may have been able to ignore an accompanying signal in the period leading to a detection response. However, people are influenced by face and voice information when making attractiveness judgements even when asked to ignore one modality (Zuckerman, Miyake & Hodgins, 1991). Moreover, information occurring together will be integrated since it is likely to be perceived as originating from a single source (see Welch & Warren, 1980). While integration might have been disrupted in the asynchronous condition, enhanced detection would have at least been expected in the synchronous condition.

One possible explanation for the lack of facilitation when attributing attractiveness in bimodal conditions is that, face and voice information are integrated at an early perceptual level (von Kriegstein & Giraud, 2006; Latinus, VanRullen & Taylor, 2010). As such, attributing attractiveness may occur rapidly even where there is only unimodal information. Previous research has shown that humans are capable of making face attractiveness judgements within 100msecs that do not significantly differ from judgements made in 500msecs (Willis & Todorov, 2006). There is no research relating to temporal attractiveness attribution of voices. Nevertheless, if participants were able to make rapid attractiveness judgements then floor effects would have been found. In contrast, choice time was in the order of seconds. Although face and voice may be rapidly integrated and attractiveness can be determined early, participants may take longer when given the choice.

Although there were no effects owing to the experimental conditions, there was an interesting finding in experiment 5 (Chapter 7). That is, choice time was longer for more attractive male faces. There is reason to believe that people may take longer to attribute attractiveness without time restrictions. For example gaze duration is positively related to attractive stimuli and can influence choice (Hall, Hogue & Guo, 2010; Shimojo et al., 2003). Females have been shown to direct attention to both male and female stimuli (Hall, Hogue & Guo, 2010; Maner et al., 2003; Rupp & Wallen, 2007). There was a positive association with choice time and female faces although this did not reach significance. Choice time in experiment 5 was also longer for attractive male voices but not female voices. This is the first finding to show a relationship between the times taken to judge attractive voices.

Females have been shown to outperform males on tasks involving recognition of female faces while performing equally well on tasks involving recognition of male faces (Lewin & Herlitz, 2002; Rehnman & Herlitz, 2006; although see McBain, Norton & Chen, 2009). Attention to opposite-sex characteristics is likely to relate to sexual orientation (e.g. Hall, Hogue & Guo, 2010; Rupp & Wallen, 2007) while attention to same-sex characteristics could be related to competition (Lewin & Herlitz, 2002; Maner et al., 2003). For example, females compete with each other in order to increase attractiveness to males even at the expense of disparaging and disassociating from other females (Fisher, 2004; Tennenbaum, 2002). Moreover, females are more interested in the attractiveness opinions of other females than the opinions of men (Graziano, Jensen-Campbell, Shebilske & Lundgren, 1993). Although female interest may modulate decision time for opposite and same-sex faces, however, the same may not apply to voices.

Despite a positive relationship between choice time and the attractiveness ratings of female faces in experiment 5 (Chapter 7), it should be noted that the result was not significant. However, the time dependent relationship between stimulus and perceiver is modulated by interest (see Isaacowitz, 2006). Females in a long-term relationship are less attentive to other attractive females (Maner et al., 2003). Moreover, females using oral contraception attend to contextual information such as clothing rather than to the attractive features of other females (Rupp & Wallen, 2007). The weak correlation found in experiment 5 between choice time and attractive female faces could have been influenced by the relationship status of female participants or the use of hormonal contraception. Unfortunately, neither of these measures was recorded and thus cannot be used to test this suggestion. Another factor that has not been considered, however, is the self-perceived attractiveness of female participants. For example, in females self-perceived attractiveness predicts socio-sexual attitudes (Clark, 2004) and male face preferences (Little, Burt, Penton-Voak & Perrett, 2001). An interesting focus of investigation would be to consider the relationship between the choice time of females and attractiveness ratings of both male and female faces. Self-perceived attractiveness could be an additional factor modulating the attention and effort expended in attributing attractiveness to both opposite and same-sex faces.

8.4 Implications for attractiveness research

8.4.1 Female face and voice signals

The findings of experiment 1a (Chapter 3) and 2a (Chapter 4) are the first to show an interaction between female faces and voices on compound stimuli attractiveness. Female faces and voices are proposed to express levels of oestrogen that are attractive to males because they indicate fertility (Law-Smith et al., 2006; Thornhill & Gangestad, 1999). The positive relationship between oestrogen levels and attractiveness ratings of female faces and voices has been suggested elsewhere

(Feinberg, 2008) to indicate that these are back-up signals. All signals carry information with some degree of error or dishonesty (Guilford & Dawkins 1991; Møller & Pomiankowski, 1993) and therefore, amalgamating multiple redundant signals can provide a more accurate estimate of a single characteristic (i.e. fertility).

Back-up signals can have varying effects on a response (see Partan & Marler, 1999). The influence of female voices on the attractiveness of face-voice compound stimuli, were shown in experiment 1a (Chapter 3) and 2a (Chapter 4), to be small relative to female face attractiveness. In part, this effect could be small because female voices are variable and change over the ovulation cycle (Bryant & Haselton, 2009). A smaller voice effect could also be due to the redundancy in communicating fertility. Nevertheless, the findings in experiment 1a and 2a show that combining the face and voice of females can have an enhanced effect on perceptions of attractiveness. For example, female face attractiveness was greater when paired with an attractive voice. Females are likely to benefit from the expression of multimodal signals; faces and voices presented together could enhance attractiveness and for males, serve to reduce the cost of mating with a suboptimal partner by increasing the accuracy of detecting fertility.

8.4.2 Male face and voice signals

The lack of relationship between male face and voice attractiveness, shown in experiment 1b (Chapter 3) and 2b (Chapter 4), could arise because they are communicating different unrelated messages with regards to mate quality. Male vocal signals may have developed through intra-sexual pressures (Hodges-Simeon et al., 2010; Puts, 2005). Dominant males, for example, have been shown to lower their voice pitch with regard to a less dominant individual (Puts et al., 2006). A recent study also found that lower voice pitch variation (i.e. monotone) in males predicted the number of sex partners in the last year (Hodges-Simeon et al., 2010). Characteristics of dominance (lower pitch) were shown to be related to mating success over attractiveness (average pitch), suggesting that male vocal displays are more likely to have been influenced by intra-sexual pressure (Hodges-Simeon et al., 2010). However, male vocalisations are also likely to have been shaped by female selection. Signals that evolve through intra-sexual pressures can be co-opted by opposite sex mates for selecting optimal partners (see Burglund, Bisazza, & Pilastro, 1996).

Females may obtain direct benefits such as access to resources and protection from a dominant partner. However, given the negative attributions and aggression related to masculine males (Perrett et al., 1998; Schmitt, Shackleford & Buss, 2001), it is possible that the function of the male vocal signal is context dependent. In social species, some signals have dual function; needing to warn off a rival and attract a mate (West-Eberhard 1979). Males may benefit from dominance displays where there is perceived competition while displaying evidence of pro-sociality, investment potential and low threat in relation to a female. This is congruent with evidence that females prefer a low male voice pitch with some upward variation (Bruckert et al., 2006; Oguchi & Kikuchi, 1997; although see Hodges-Simeon et al., 2010). Further, males who initially modulated their voice pitch upward in a study were shown to be more successful establishing a potential mating relationship (Anolli & Ciceri, 2002).

The pressure of social competition between males could have affected the evolution of the male vocal signal differently to the face thus leading to divergence. That is, a male with a masculine face may not necessarily have a masculine voice. Testosterone is detectable in male faces (Penton-Voak & Chen, 2004) and males with high testosterone have lower pitch voices (Dabbs & Mallinger, 1999). An interesting study would consider the relationship between testosterone levels, voice pitch and face masculinity measures together in a male population. Feinberg et al. (2008) has used stimuli manipulated on a continuum of masculinity to show that females do have correlated preferences for male face and voice masculinity. However, Feinberg et al. (2008) combined stimuli from different people and were thus unable to infer whether preferences for masculine faces and voices occurred in the same individual. Evidence of a relationship between low voice pitch, face masculinity and attractiveness in experiment 2b (Chapter 4) suggests that females do prefer masculine male faces and voices. However, the lack of a relationship between face and voice attractiveness in the experiments here indicates that they are less likely to occur together in an individual.

Rather than selecting indicators of immuno-competence, it could be that females use male vocalisations to assess potential direct benefits such as dominance and protection (low voice pitch). In contrast, evidence of a positive correlation between masculine faces and health (Rhodes et al., 2003) suggests that females use male faces to assess indirect benefits that could lead to healthier offspring through heritable genes. Taken together, different pressures that may have historically shaped the evolution of male face and voice signals respectively and the suggestion that male faces and voice communicate multiple messages mean that face and voice attractiveness are less likely to be related. A dominant male may not necessarily have an attractive masculine face and visa versa.

Together, male faces and voices could be used to gain a more accurate perception of overall mate quality. Since each signal carries an independent element of information, they would both be expected to influence overall attractiveness. Non-redundant signals can interact in several ways when presented together (see Partan & Marler, 1999). The findings of experiment 1b (Chapter 3) and 2b (Chapter 4) show that despite being unrelated, face and voice attractiveness positively and independently contribute to male compound stimuli attractiveness. Moreover, a larger vocal attractiveness effect for male stimuli compared to female voices here could be an indication of its relative importance in female assessments. However, reliance on multiple messages could vary in relation to a number of factors including individual differences. For example, a female concerned with obtaining direct benefits from a partner might be expected to add weight to vocal attractiveness judgements. Further research could investigate individual differences such as the desire for obtaining resources in an effort to elucidate their influence on the face and voice attractiveness effects.

8.4.3 Size and variability of attractiveness effects

Considering the size and variance of effects promises to offer intriguing insights and pose interesting questions with regard to the evolution and function of attractiveness signals. The multilevel model analysis used in experiment 1a and 1b (Chapter 3), 2a and 2b (Chapter 4) is a useful statistical procedure that can aid understanding of the effect sizes and in relation to multiple sources of variance within datum. This is particularly important in repeated measures experiments where there is likely to be variance in effects owing to differences between stimuli and within participants.

The results of experiment 1a and 1b (Chapter 3), 2a and 2b (Chapter 4) revealed a large proportion of random variance attributed to differences between individuals. Variation in attractiveness preferences arise for a number of reasons (see Jennins & Petrie, 1997; Widemo & Saether, 1999) and have been shown to have an important influence on attractiveness ratings compared to shared preferences (Hönekopp, 2006). For example, research has shown that attractiveness preferences are influenced by factors such as parental influence, sexual history and self-perceived attractiveness (DeBruine et al., 2006; Jennions & Petrie, 1997; Pfaus, Kippin & Centeno, 2001; Widemo & Saether, 1999). Typically, attractiveness research assumes that participants are homogeneous (e.g. Saxton et al., 2009) which could yield misleading effects. Further research could include factors related to individual differences in order to elucidate their influence on the direction and size of attractiveness effects.

The direction and size of attractiveness effects in sexual selection research could be important. Attractiveness research has covered a range of elements such as body size (e.g. Smith, Cornelissen & Tovée, 2007; Streeter & McBurney, 2003) purported to influence attractiveness. However, many elements are studied in isolation using manipulated stimuli varying on a single dimension. While there is obvious merit in identifying such elements it is important to consider context. In a rich environment, there are many sources of information that can vary on many dimensions. In addition to their function, investigating signals together in compound promises to elucidate their relative importance.

One factor that could affect the relative importance of attractiveness is the cost associated with different environments. For example, the prevalence of disease (risk of disease/infection is high) makes selection for an optimal immune system more important (see Little, Apicella & Marlowe, 2007). Furthermore, preference for indicators of wealth and resources could be increased where a large proportion of the population are considered to be of low socioeconomic status. For example, Swami and Tovée (2006) found that male preference for female body size increased with hunger and discussed their findings in relation to resource scarcity. As such, some signals may become more important in different cultures or environments. Preferences for facial symmetry (Little, Apicella & Marlowe, 2007) and body shape (Swami & Tovée, 2005; Tovée, Swami, Furnham & Mangalparsad, 2006) have been shown to be influenced by the prevalence of disease and in cultures where resources are limited. In the search for an optimal partner, humans are therefore more likely to use information that allows for the most appropriate signals to be used in a given context.

In certain environments, the effect of some attractiveness signals could diminish. For example, attractiveness signals that express genetic fitness are different from those that signal compatibility (Cotton, Small & Pomiankowski, 2006; Roberts & Gosling, 2003). Compatible genes in humans can be detected through the olfactory sense (Penn & Potts, 1999; Havlicek & Roberts, 2009) and serve to complement the hosts genes in their progeny. Specifically, the compatible genes of two mates would be combined to create stronger pathogen resistance in their child. Selection for attractiveness and compatibility are mediated by the variability in available mates (for a discussion see Mays & Hill, 2004). That is, if all mates are equally attractive, humans would benefit from selecting for signals of compatible gene (and visa versa). Where there is little variation between mates and signals are unrelated (i.e. multiple messages), choice could therefore be influenced more by the most appropriate message. Taking the above into consideration, further investigation of integrated signals may serve to elucidate their relative effects in attractiveness attributions. Furthermore, including multiple sources of variance pertaining to individual differences and cultural or contextual information in multilevel model analyses may provide a more fruitful approach for further attractiveness research.

8.4.4 Integrating face and voice signals

The present section deals with the effects of male face and voice information on female perception and processing speed when the signals are integrated. The evidence from experiment 3 (Chapter 5) showed that responding to male face targets was enhanced whether accompanying stimuli comprised unrelated auditory stimuli or related voice stimuli. Experiment 4 (Chapter 6) showed that response latencies to a male face target presented synchronously with unrelated auditory stimuli were also faster, irrespective of spatial congruency. These findings provide an example of the ventriloquism effect (see de Gelder & Bertellson, 2003). That is, auditory information can influence visual processing irrespective of spatial congruence. The integration of spatially disparate auditory information could be advantageous; facilitating the orientation toward and localisation of a visual object (Recanzone, 2009). However, when face targets were paired with related voice stimuli in an incongruent spatial location, responding was not enhanced. This finding indicates a caveat in sensory integration when stimuli comprise socially relevant stimuli. That is, perceptual binding may be disrupted when face and voice are spatially incongruent.

The integration of social or person related information may be dependent on temporal and spatial varying properties (Lander, Hill, Kamachi & Vatikiotis-Batson, 2007). For example, the identity of an unfamiliar person can be inferred more accurately from the prosody of speech and expressiveness of the facial movement rather than the content of the speech itself (Lander et al., 2007). Moreover, participants in another experiment (Kamachi, Hill, Lander & Vatikiotis-Bateson, 2003) were able to correctly identify a face from a voice (and visa versa) in a delayed matching to sample task but not when facial movements and speech were played backwards. Although voices appear to be a special auditory object in terms of perception (Belin, Fecteau & Bédard, 2004) the content may be less important for the integration of face and voice information. Rather, integrating person related information may be more dependent on identifying causality (see Shutz & Kubovy, 2009).

The integration of causally linked stimuli by temporal or spatial varying properties could lead more readily to perceptual disruption when information is incongruent. For example, temporal order judgements during audio-visual speech patterns are more accurate when sex of the speaker is incongruent (Vatakis & Spence, 2007). Causal integration is likely to be influenced by top-down processes; Litainus, Van Rullen and Taylor (2010) found that both bottom-up and top-down modulation influenced a gender categorisation task involving faces and voices. Specifically, top-down processes were shown to influence early brain activity and modulated visual dominance in accurately recognising gender (Latinus, VanRullen & Taylor, 2010). Visual dominance in face-voice integration could explain why the McGurk effect was shown to be relatively unaffected when the sex of the face and voice are incongruent (Green, Stevens, Kuhl & Meltzoff, 1990; Green, Kuhl, Meltzoff &

Stevens, 1991). There is some indication (Green, Kuhl, Meltzoff & Stevens, 1991) that voices may be extracted before integrating with face information in order to normalise visual perception.

Taking the above into consideration, an interesting variation on experiment 4 (Chapter 6) would be the inclusion of a sex non/matched condition. If vocalisations are extracted before face-voice integration (Green, Kuhl, Meltzoff & Stevens, 1991) then responding to a female face target for example, should be enhanced even when presented in compound with a male face. Another interesting variation on experiment 4 would be to investigate response latencies in relation to dynamic non/matched face and voice stimuli and in spatially in/congruent locations. Should face and voice information be integrated through perceptual causality (Shutz & Kubovy, 2009), then responding to dynamic faces presented with non-matched voice samples should not be enhanced, even when both stimuli occur in the same spatial location. Such experiments are proposed to further enhance understanding of integrating person related stimuli. Nevertheless, it appears that integrating face and voice stimuli may be automatically influenced top-down processes (Latinus, VanRullen & Taylor, 2010) and is likely to differ from integration with simple unrelated auditory/visual stimuli. Since the content of vocalisations may be less important (Green, Kuhl, Meltzoff & Stevens, 1991), one possibility that has not yet explored is whether integration with male voices could simply be used to facilitate the detection or discrimination of male faces.

8.4.5 Attractiveness judgements and choice time

The aim of experiment 5 (Chapter 7) was to either eliminate or provide support for the receiver psychology hypothesis. That is, to determine whether the function of male voices is to simply facilitate the detection or discrimination of male face attractiveness. The previous section discussed the integration of male face and voice information and their effect on the processing speed of female participants when signals are integrated. However, experiment 5 showed that for female participants, face and voice together do not enhance the detection or discrimination of attractiveness. There was considerable residual responding that could indicate that the experiment was too complicated. Nevertheless, the findings of experiment 5 indicate that male faces do not facilitate the temporal attribution of attractiveness.

Rather, they are likely to constitute multiple messages, together providing a more accurate estimation of overall mate quality.

The additional findings of experiment 5 (Chapter 7) tentatively add further weight to this proposal. For example, a positive relationship was found between attractiveness ratings and choice time for male faces and voices. Previous research has shown a relationship between gaze duration, attractiveness and arousal (Hall, Hogue & Guo, 2010; Shimojo et al., 2003). Attractive faces have intrinsic value related to sexual orientation (Kranz & Ishai, 2006) that elicits brain responses relating to reward circuitry (Aahron et al., 2001; O'Doherty et al., 2003). Longer choice time is therefore likely to indicate the inherent importance of processing opposite-sex faces. Although attractive male voices have been correlated with more sexual partners and more children (Apicella, Feinberg & Marlowe, 2007; Hughes, Dispenza & Gallup, 2004; Puts, 2005), there has been little research suggesting that voices have similar intrinsic value. This is the first finding to show that longer choice time is also associated with more attractive male voices.

Male and female voices have been shown to activate distinct areas of the brain (Sokhi, Hunter, Wilkinson & Woodruff, 2005). One study also found that self-reported arousal in a sample of heterosexual females was greater in relation to erotic prosody spoken by the opposite and not same-sex individuals (Ethofer et al., 2007). Moreover, this effect corresponded with greater responses in brain regions related to auditory perception and arousal (Ethofer et al., 2007). The semantic content of such speech appears to be important (Ethofer et al., 2007; Bliss-Moreau, Owren & Barrett, 2010). However, the stimuli used in experiment 5 (Chapter 7) comprised neutral speech and thus, there may be sufficient information inherent in pitch to be of importance to female listeners. Further research would be required to determine whether pitch alone can activate the brains reward circuits and elicit arousal.

8.5 Conclusions

In conclusion, the research here has provided evidence with regard to the modality related effects of face and voice information and the perception of human attractiveness. Female face and voice attractiveness appear to be related and are likely to be back-up signals. Together, female faces and voices interact thus modulating the attractiveness of face-voice compound stimuli and provide a more accurate estimate of oestrogen and fertility. In contrast, male face and voice attractiveness appear to be unrelated. When presented together, male voices are integrated with male faces and serve to enhance the response latencies of females. However, such integration can be disrupted when face and voice are spatially incongruent. Although male voices do enhance responding to male faces they do not enhance the detection or discrimination of attractive male faces. Rather, longer choice time determining more attractive stimuli suggests that both male faces and voices signal information relevant to female decisions. Male faces and voices positively and independently influence the perception of compound stimuli attractiveness. As such, they are likely to constitute multiple messages. While faces are proposed to signal health, male voices are proposed to communicate information relating to dominance. Together, male faces and voices provide a more accurate estimate of overall mate quality. Multimodal attractiveness is still in its relative infancy. Considering aspects of sensory integration promises to add further insight into the cognitive processes involved in person perception. Furthermore, studies investigating the integration of different modalities and in different contexts may provide a more informative approach to understanding their evolution, function and importance in human attractiveness perception.

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APPENDIX A: STIMULI ATTRACTIVENESS AND MEASUERMENTS

Attractiveness	
Face	*2.97(1.59)*
Voice	*4.15(2.04)*
F-V compound	2.95(1.72)
Measurement	
Masculinity	*-1.31*
Pitch: Vowels	*76.87Hz*
Pitch: Phrase	*76Hz*

Attractiveness	
Face	*2.75(1.42)*
Voice	*5.61(1.7)*
F-V compound	*3.09(1.59)*
Measurement	
Masculinity	*-.6*
Pitch: Vowels	*106.44Hz*
Pitch: Phrase	*106.09Hz*

Attractiveness	
Face	*3.19(1.5)*
Voice	*3.89(1.96)*
F-V compound	*3.08(1.55)*
Measurement	
Masculinity	*.67*
Pitch: Vowels	*123.07Hz*
Pitch: Phrase	*123.27Hz*

Attractiveness	
Face	*3.52(1.59)*
Voice	*3.76(1.9)*
F-V compound	*3.44(1.69)*
Measurement	
Masculinity	*-.06*
Pitch: Vowels	*124.1Hz*
Pitch: Phrase	*128.37Hz*

Attractiveness	
Face	*2.6(1.26)*
Voice	*4.41(2.02)*
F-V compound	*3.16(1.54)*
Measurement	
Masculinity	*1.19*
Pitch: Vowels	*109.31Hz*
Pitch: Phrase	*108.35Hz*

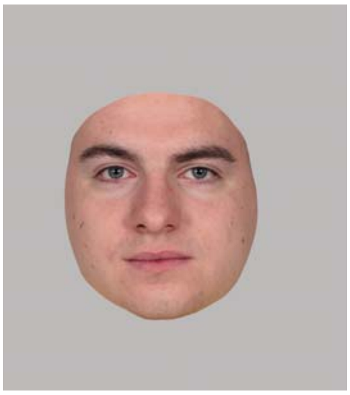
Attractiveness	
Face	*3.33(1.48)*
Voice	*3.8(1.75)*
F-V compound	*3.34(1.59)*
Measurement	
Masculinity	*.03*
Pitch: Vowels	*137.84Hz*
Pitch: Phrase	*132.39Hz*

Attractiveness	
Face	*3.05(1.42)*
Voice	*4.38(1.89)*
F-V compound	*3.31(1.47)*
Measurement	
Masculinity	*1.05*
Pitch: Vowels	*121.06Hz*
Pitch: Phrase	*119.35Hz*

Attractiveness	
Face	*3.79(1.8)*
Voice	*5.48(1.67)*
F-V compound	*4.06(1.76)*
Measurement	
Masculinity	*2.86*
Pitch: Vowels	*95.03Hz*
Pitch: Phrase	*88.79(Hz)*

Attractiveness	
Face	*3.16(1.46)*
Voice	*4.34(1.76)*
F-V compound	*3.34(1.58)*
Measurement	
Masculinity	*-3.68*
Pitch: Vowels	*115.62Hz*
Pitch: Phrase	*108.83Hz*

Attractiveness	
Face	*3.6(1.55)*
Voice	*4.9(1.94)*
F-V compound	*4(1.71)*
Measurement	
Masculinity	*1.37*
Pitch: Vowels	*118.62Hz*
Pitch: Phrase	*113.92Hz*



Attractiveness	
Face	*2.98(1.49)*
Voice	*4.9(2.04)*
F-V compound	*3.39(1.59)*
Measurement	
Masculinity	*-2.57*
Pitch: Vowels	*105.31Hz*
Pitch: Phrase	*99.1Hz*

Attractiveness	
Face	*4.44(1.71)*
Voice	*3.96(2.03)*
F-V compound	*3.94(1.83)*
Measurement	
Masculinity	*.86*
Pitch: Vowels	*120.71Hz*
Pitch: Phrase	*124.73Hz*

Attractiveness	
Face	*3.54(1.41)*
Voice	*4.89(2.02)*
F-V compound	*3.62(1.74)*
Measurement	
Masculinity	*.15*
Pitch: Vowels	*109.61Hz*
Pitch: Phrase	*104.69Hz*

Attractiveness	
Face	*5.09(1.69)*
Voice	*4.35(1.88)*
F-V compound	*4.73(1.81)*
Measurement	
Masculinity	*-.13*
Pitch: Vowels	*115.22Hz*
Pitch: Phrase	*104.46Hz*

Attractiveness	
Face	*3.9(1.55)*
Voice	*4.85(1.92)*
F-V compound	*4.72(1.81)*
Measurement	
Masculinity	*1.52*
Pitch: Vowels	*109.36Hz*
Pitch: Phrase	*98.57Hz*

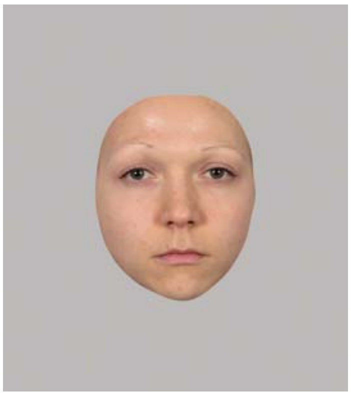
Attractiveness	
Face	*3.03(1.33)*
Voice	*4.81(1.97)*
F-V compound	*4.58(2.22)*
Measurement	
Masculinity	*-5.16*
Pitch: Vowels	*107.24Hz*
Pitch: Phrase	*100.92Hz*

Attractiveness	
Face	*3.9(1.75)*
Voice	*4.7(1.94)*
F-V compound	*3.49(1.78)*
Measurement	
Masculinity	*2.04*
Pitch: Vowels	*144.05Hz*
Pitch: Phrase	*140.6Hz*

Attractiveness	
Face	*3.77(1.5)*
Voice	*3.71(1.61)*
F-V compound	*4.25(1.91)*
Measurement	
Masculinity	*-.71*
Pitch: Vowels	*128.52Hz*
Pitch: Phrase	*116.2Hz*

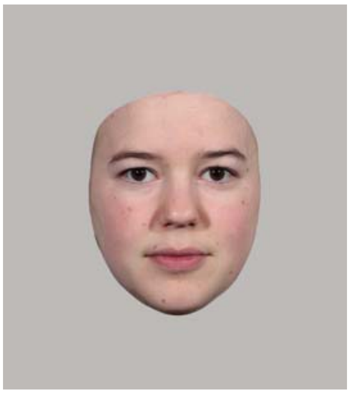
Attractiveness	
Face	*1.92(.92)*
Voice	*3.93(2.02)*
F-V compound	*3.74(2.08)*
Measurement	
Masculinity	*2.12*
Pitch: Vowels	*114.41Hz*
Pitch: Phrase	*128.88Hz*

Attractiveness	
Face	*3.54(1.56)*
Voice	*4.21(1.8)*
F-V compound	*2.28(1.42)*
Measurement	
Masculinity	*.36*
Pitch: Vowels	*110.17Hz*
Pitch: Phrase	*111.23Hz*



Attractiveness		
	Face	*3.73(1.56)*
	Voice	*5.57(1.89)*
	F-V compound	*4.02(1.57)*
Measurement		
	Femininity	*2.13*
	Pitch: Vowels	*187.75Hz*
	Pitch: Phrase	*169.58Hz*

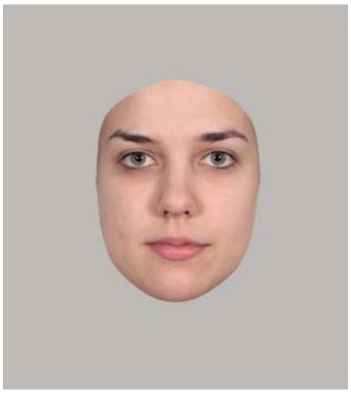
Attractiveness		
	Face	*3.33(1.33)*
	Voice	*4.67(1.56)*
	F-V compound	*3.28(1.5)*
Measurement		
	Femininity	*.27*
	Pitch: Vowels	*223.27Hz*
	Pitch: Phrase	*223Hz*



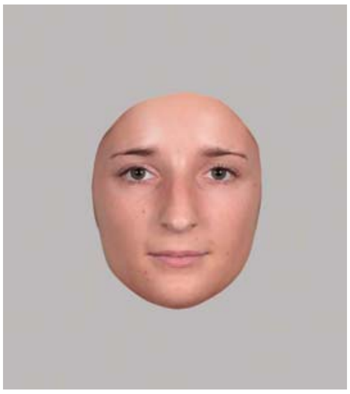
Attractiveness		
	Face	*3.55(1.56)*
	Voice	*6.03(1.35)*
	F-V compound	*3.92(1.64)*
Measurement		
	Femininity	*1.01*
	Pitch: Vowels	*224.09Hz*
	Pitch: Phrase	*198.41Hz*

Attractiveness		
	Face	*3.8(1.56)*
	Voice	*4.3(2.22)*
	F-V compound	*3.5(1.56)*
Measurement		
	Femininity	*1.94*
	Pitch: Vowels	*215.62Hz*
	Pitch: Phrase	*202.94Hz*

Attractiveness
Face 5.63(1.49)
Voice 5.9(1.51)
F-V compound 5.67(1.7)
Measurement
Femininity .63
Pitch: Vowels 198.58Hz
Pitch: Phrase 189.29Hz



Attractiveness
Face 5.2(1.75)
Voice 4.87(1.69)
F-V compound 4.95(1.67)
Measurement
Femininity -1.54
Pitch: Vowels 192.67Hz
Pitch: Phrase 215.81Hz



Attractiveness
Face 5.4(1.47)
Voice 5.38(1.58)
F-V compound 5.02(1.62)
Measurement
Femininity -1.3
Pitch: Vowels 220Hz
Pitch: Phrase 215.93Hz

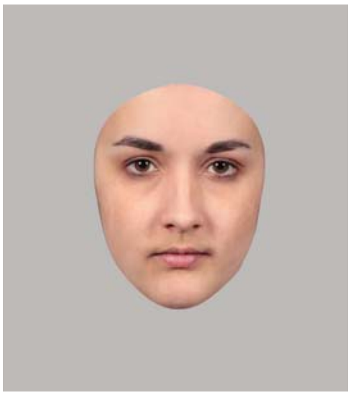
Attractiveness
Face 2(.98)
Voice 4.43(1.78)
F-V compound 2.47(1.2)
Measurement
Femininity -1.41
Pitch: Vowels 193.91Hz
Pitch: Phrase 198.88Hz

Attractiveness		
	Face	*4.35(1.32)*
	Voice	*5.18(1.64)*
	F-V compound	*4.08(1.76)*
Measurement		
	Femininity	*-.13*
	Pitch: Vowels	*179.61Hz*
	Pitch: Phrase	*195Hz*

Attractiveness		
	Face	*2.18(1.3)*
	Voice	*3.62(1.55)*
	F-V compound	*2.32(1.31)*
Measurement		
	Femininity	*-2.32*
	Pitch: Vowels	*197.45Hz*
	Pitch: Phrase	*189.34Hz*

Attractiveness		
	Face	*2.72(1.23)*
	Voice	*4.95(1.52)*
	F-V compound	*2.98(1.34)*
Measurement		
	Femininity	*.43*
	Pitch: Vowels	*191.96Hz*
	Pitch: Phrase	*194.65Hz*

Attractiveness		
	Face	*6.4(1.32)*
	Voice	*5.73(1.62)*
	F-V compound	*6.13(1.67)*
Measurement		
	Femininity	*1.41*
	Pitch: Vowels	*218.3Hz*
	Pitch: Phrase	*211.6Hz*



Attractiveness	
Face	*5.07(1.66)*
Voice	*5.08(1.66)*
F-V compound	*4.9(1.71)*
Measurement	
Femininity	*-1.59*
Pitch: Vowels	*218.99Hz*
Pitch: Phrase	*208.68Hz*

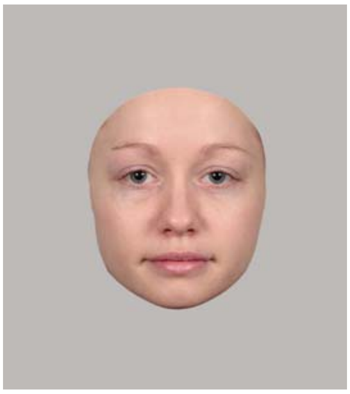
Attractiveness	
Face	*3.43(1.56)*
Voice	*2.67(1.41)*
F-V compound	*2.75(1.33)*
Measurement	
Femininity	*3.15*
Pitch: Vowels	*213.23Hz*
Pitch: Phrase	*206.06Hz*

Attractiveness	
Face	*3.52(1.39)*
Voice	*5.47(1.49)*
F-V compound	*4.03(1.41)*
Measurement	
Femininity	*-2.23*
Pitch: Vowels	*219.92Hz*
Pitch: Phrase	*189.96Hz*

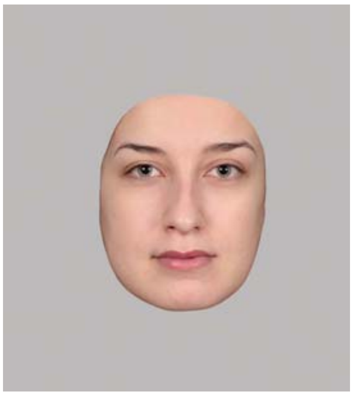
Attractiveness	
Face	*3.48(1.41)*
Voice	*4.7(1.79)*
F-V compound	*3.45(1.35)*
Measurement	
Femininity	*-.37*
Pitch: Vowels	*224.59Hz*
Pitch: Phrase	*190.28Hz*

Attractiveness
Face *3.08(1.17)*
Voice *4.35(1.72)*
F-V compound *3.45(1.35)*
Measurement
Femininity *.27*
Pitch: Vowels *169.98Hz*
Pitch: Phrase *166.45Hz*

Attractiveness
Face *4.22(1.55)*
Voice *4.52(1.41)*
F-V compound 2.98(1.41)
Measurement
Femininity *-3.69*
Pitch: Vowels *205.42Hz*
Pitch: Phrase *211.43Hz*



Attractiveness
Face *4.33(1.68)*
Voice *5.37(1.92)*
F-V compound *4.3(1.27)*
Measurement
Femininity *3.69*
Pitch: Vowels *244.01Hz*
Pitch: Phrase *237.91Hz*



Attractiveness
Face *5.37(1.78)*
Voice *4.18(1.97)*
F-V compound *4.33(1.75)*
Measurement
Femininity *-.35*
Pitch: Vowels *195.21Hz*
Pitch: Phrase *195.45Hz*

APPENDIX B: GUIDE TO MULTILEVEL MODELLING

B.1 Multiple Regression

Multiple regression is a useful statistical technique for investigating the relationship between a number of predictors and an outcome variable. Multiple regression can be formally defined as [a] where an outcome y can be approximated from the mean (intercept; β_0) plus a slope, determined by a number of predictors ($\beta_1 \ldots \beta_k$) multiplied by a response (x). The term e refers to residual error. For example, the present research concerns predicting overall attractiveness using the predictors face and voice attractiveness. In addition to providing estimates of face and voice effects, multiple regression also yields an estimate of the variance in overall attractiveness explained by the face and voice attractiveness.

[a] $y = \beta_0 + \beta_1 x + \ldots \beta_k x + e$

Multiple regression in this context, however, has a number of weaknesses. First, while the outcome variable is assumed to be a random factor from a larger random population, the predictors are not. This is problematic when considering that the face and voice stimuli used are themselves a random sample from a random population. Not only does this limit generalisation beyond the stimuli used in this experiment but may also lead to inaccurate estimates of the variance. Second, perceptions of attractiveness can vary greatly between people. Variance owing to individual differences is not accommodated in multiple regression but could be crucial to understanding variances in the relationship between the predictors and the outcome variable.

In the present example, two sources or levels of variation have been identified, stimuli and individual differences that could affect the variance in predictors and therefore the outcome variable. An illustration might consider the relationship between overall attractiveness and the predictor face attractiveness to be linear (see Figure B.1). However, as discussed this relationship does not account for variance in face attractiveness that may differ between stimuli.

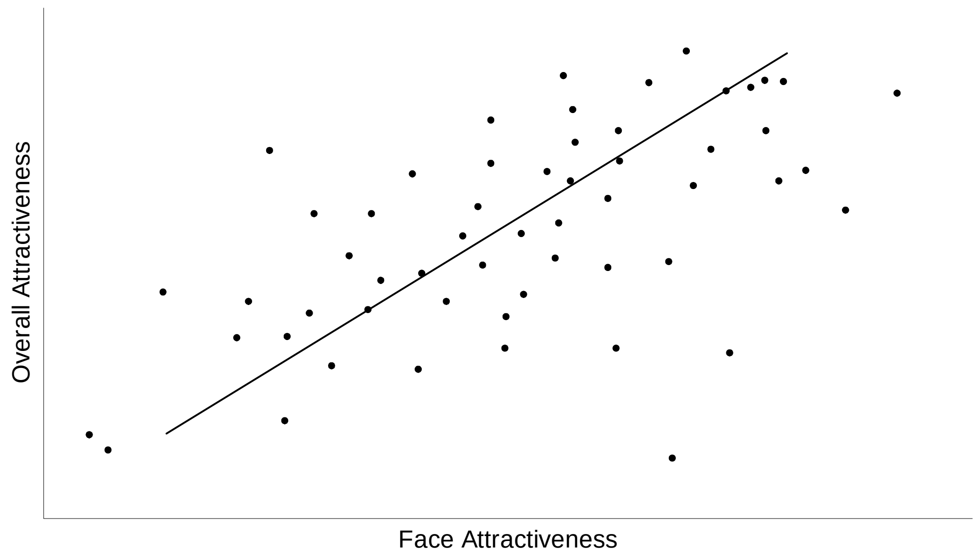


Figure B.1: *Relationship between overall attractiveness and face attractiveness predictor*

It is possible that at this level (stimuli), there exists a relationship between face attractiveness and overall attractiveness (see Figure B.2). Here, the face attractiveness effect on overall attractiveness is smaller for stimuli when ratings of face attractiveness are low.

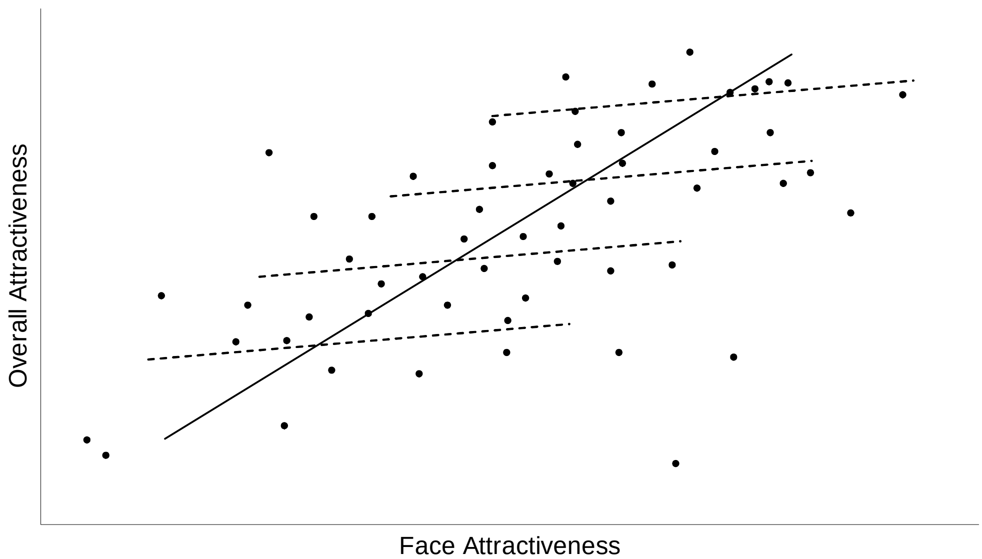


Figure B.2: *Relationship between overall attractiveness and face attractiveness predictor varying within stimuli (n = 4)*

In addition, another source of variation in attractiveness ratings might be evident because of differences between people. This is particularly important in a repeated measures design where multiple responses are gathered from a single individual. Since it is particularly important to use the results to generalise beyond the participants that take part in the study it is imperative that consideration be given to variance at the individual level. For example, consider the data again in Figure B.3. Here, the effect of face attractiveness on overall attractiveness appears smaller for participants that give low face attractiveness ratings.

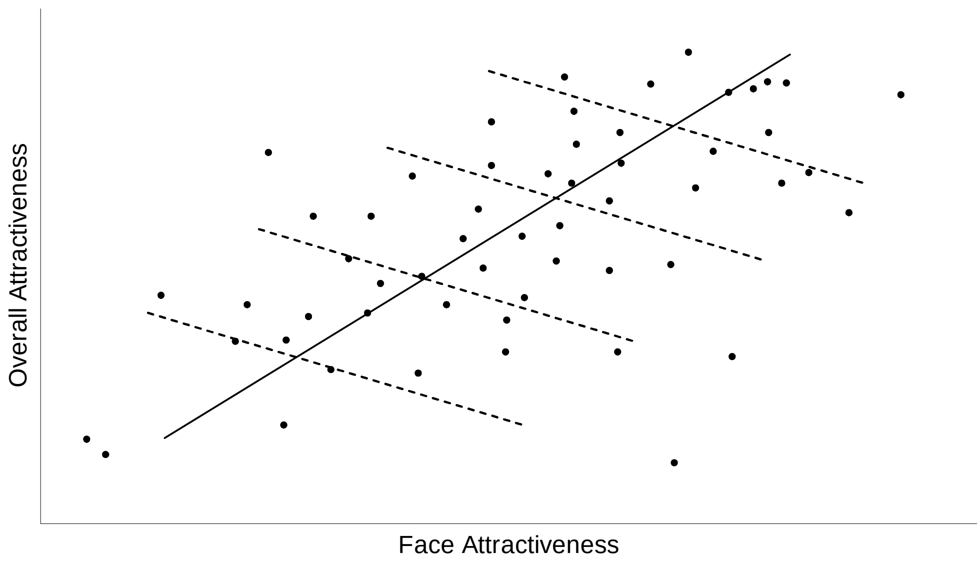


Figure B.3: *Relationship between overall attractiveness and face attractiveness predictor varying between participants (n = 4)*

Considering these two sources of variation simultaneously in a multilevel model therefore enables the researcher to ascertain more realistic estimates of face and voice attractiveness effects on overall attractiveness, that can be generalised beyond the stimuli and participants contained within the study.

B.2 Multilevel Models

Multilevel models can be defined, similar to multiple regression with the formula [b]. This is referred to as the fixed part of the formula and is similar to multiple regression in that the outcome variable, overall attractiveness, is predicted by the mean (intercept; b_0) plus the predictors face attractiveness (b_1) + face attractiveness (b_2) multiplied by the observation (x). There are differences however. The term i here refers to the stimuli level (level 1) where y_i is the rating of overall attractiveness of the ith stimulus. Level 1 contains the highest number of units. In an example where data were used to investigate variance in exam scores of pupils nested in schools, pupils would be level 1.

[b] $y_i = b_0 + b_1x + b_2x + e_i$

It is possible to extend this model to account for individual differences by adding another level, j (individuals; level 2). This yields equation [c], which is the intercept at the stimulus level plus departures owing to variance at the individual level. The formulae can be summed to create equation [d] with B0 $\beta_0 + \beta_1x_{ij} + \beta_2x_{ij}$ being the fixed effects part and $u_{0j} + e_{ij}$ being the random effects part. Here, u_{0j} represents the residual variance at level 2 while e_{ij} represents the residual variance at level 1.

[c] $b_{0j} = b_0 + u_{0j}$

[d] $y_{ij} = b_0 + b_1x_{ij} + b_2x_{ij} + u_{0j} + e_{ij}$

The variance parameters are assumed to have a normal distribution with a variance σ^2, written as N~(0, σ^2). The variance parameters σ^2_u and σ^2_e can be summed to show the total residual variance. Furthermore, it is possible to work out how much variance is attributable to a specified level. The relationship between variance is termed intra-class correlation coefficient (ICC). In the present example, the ICC for variance at the individual level would be σ^2_u / $\sigma^2_u + \sigma^2_e$.

In addition to considering departure from the intercept owing to individual differences, it is possible to further look at departures in the slope of the predictors at the individual level. This is implemented by adding [e]; summing the formulae becomes [f]. This produces further variance parameters (σ^2_{u1} and σ^2_{u2}) in addition to parameters $\sigma_{u1,1}$ $\sigma_{u1,2}$ and $\sigma_{u2,2}$ which represent the covariance between variance parameters (see [g]). This is important because not only can the variation in fixed effects owing to random effects of stimuli and individuals be considered, it also allows for interpretation of the relationship between random effects.

[e] $b_{1j} = b_1 + u_{1j}$ and $b_{2j} = b_2 + u_{2j}$

[f] $y_{ij} = b_0 + b_1x_{ij} + b_2x_{ij} + u_{0j} + u_1x_{ij} + u_2x_{ij} + e_{ij}$

[g] $$u \begin{vmatrix} \sigma^2_{u0} & & \\ \sigma^2_{u1} & \sigma_{u1,1} & \\ \sigma^2_{u2} & \sigma_{u1,2} & \sigma_{u2,2} \end{vmatrix}$$

$$e \begin{vmatrix} \sigma^2_{e0} \end{vmatrix}$$

B.2.1 Refining interpretation of fixed effects

When predictors vary at multiple levels it may be necessary to refine them in order to consider their effect at a particular level. For example, the effect of face attractiveness on overall attractiveness contains variance at both the stimuli and individual level. We might want to constrain the face attractiveness effect to look at the variance between individuals only. This is accomplished by centering face attractiveness at level 2. That is, entering face attractiveness into the model as the response (*x*) subtracted by an individual's mean face attractiveness score (*m*). A model including level 2 centered responses for face and voice attractiveness predictors therefore becomes [h].

[h] $y_{ij} = b_0 + b_1(x_{ij}\text{-}m_{x1j}) + b_2(x_{ij}\text{-}m_{x2j}) + u_{0j} + e_{ij}$

If it is of interest to look further at the level 2 effects, that is, whether individual's face $b_1(x_{ij}\text{-}m_{x1j})$ and voice $b_2(x_{ij}\text{-}m_{x2j})$ attractiveness responses predict overall attractiveness, it is possible to add the individual's mean response as a predictor. This model would therefore become [i].

[i] $y_{ij} = b_0 + b_1(x_{ij}\text{-}m_{x1j}) + b_2(x_{ij}\text{-}m_{x2j}) + b_1m_{x1j} + b_2\, m_{x2j} + u_{0j} + e_{ij}$

B.2.2 Nested and cross-classified multilevel models

The present model [i] allows for a simultaneous analysis of the variance in face and voice attractiveness in relation to overall attractiveness at both stimuli and individual levels. The structure incorporates repeated measures; ratings of *n* stimuli nested within the *i*th individual. This is appropriate where individuals are exposed to different stimuli of which ratings are nested within an individual (see Figure B.4). As another example, analysis might include exam scores of pupils that are nested within different schools.

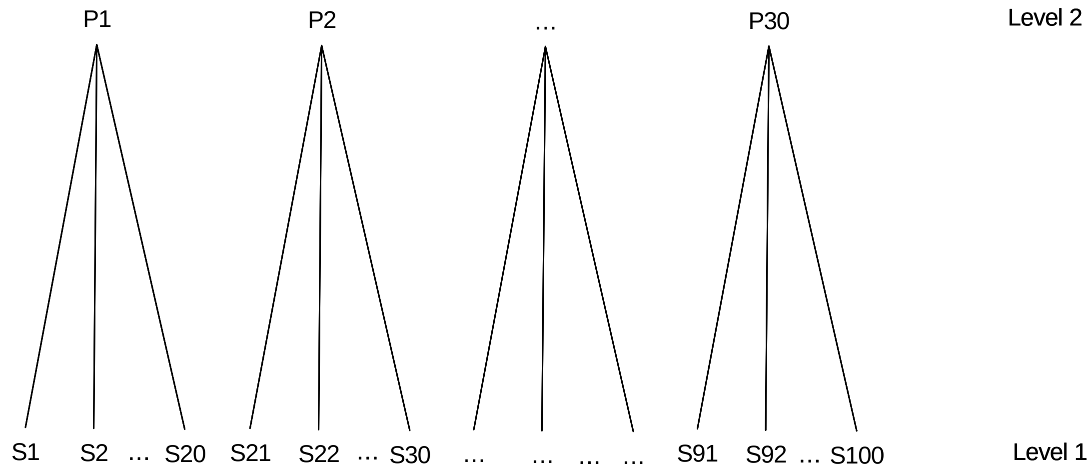


Figure B.4: *Nested structure with the attractiveness ratings of stimuli (n=100) nested within participants (n = 30)*

Continuing with the school example, it is possible that students might come from the same neighbourhood and as such, the structure is complicated because there are sources of variance in exam scores that may be attributable to both schools and neighbourhood that have been erroneously separated out in the current model structure. In the present example, a repeated measures design where participants rate the attractiveness of the same stimuli means that there may be an association between ratings of face and voice attractiveness because each individual is rating the same set of face and voice stimuli (see Figure B.5). It is therefore necessary to acknowledge the cross classification of levels in the model.

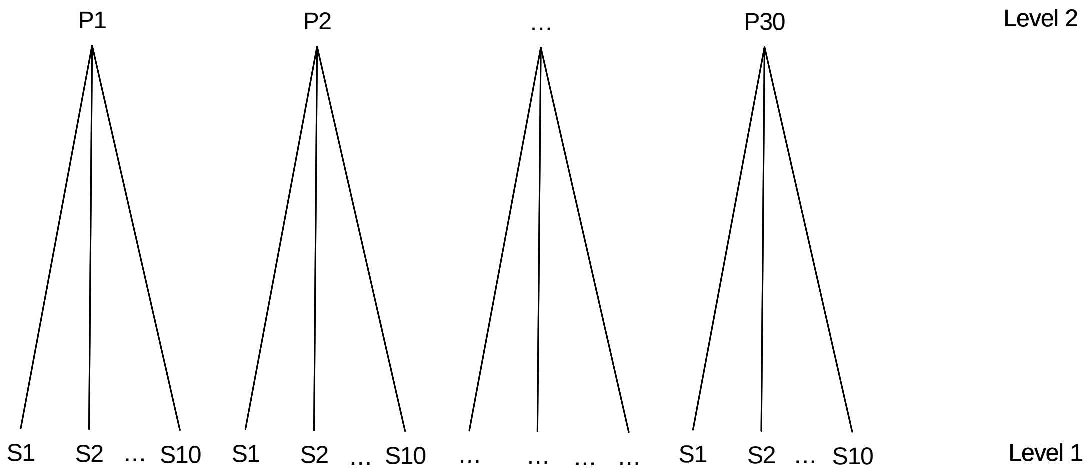


Figure B.5: *Cross-classified structure with the attractiveness ratings of stimuli (n=10) rated by participants (n = 30) in a repeated measures design*

A cross-classified model can be achieved by creating another level, level 3 to identify where units are crossed. An example formula for a simple cross-classified model with no predictors would be [j] yielding the random variance parameters σ^2_u and σ^2_v. Level 1 (i) units are nested within level 2 (u_{0j}). Level 3 (v_{0j}) is a dummy variable set up to identify where units are cross-classified; where level 1 units belong to level 2. In the present example, this would mean that the level 3 units would be 1, where the predictors face and voice attractiveness (*i*th stimulus) are rated by the *j*th individual.

[j] $$y_{ij} = b_0 + v_{0j} + u_{0j} + e_{ij}$$

No fixed effects are estimated for level 3. Rather, random slopes are fitted to the level 3 dummy predictors. The slopes variance are constrained to be equal with zero covariance ($\sigma^2_{v,u} = 0$). This defines the parameters as independent. In this manner it is possible to calculate a single variance for cross-classified stimuli and individual effects at level 2 by summing the parameters σ^2_u and σ^2_v therefore accommodating associations arising from the same stimuli being rated by each individual. In this model, the term e_{ij} represents the residual variance.

B.3 Model estimation

Model estimation is an iterative process implementing an algorithm. The function is to determine the values of parameters that most likely fit the data. As such, it is termed Maximum Likelihood (ML). ML estimates parameters by finding the joint density function of each observation. The resulting value is one that maximises the probability that observations fall within this distribution. An assumption of ML however, is that the variances are known. While ML is relatively accurate at predicting fixed effect parameters, the assumption that the true value of a parameter is known can lead to bias and underestimating the variance and covariance parameters. An alternate method of estimation is Restricted Maximum Likelihood (REML). REML assumes that the true value of a parameter is not known and as such, computation is improved by adjusting for uncertainty. In practice ML computation is preferred for estimates fixed effects while REML is typically used to estimate random effects.

B.3.1 Assessing model fit

There are several ways with which to assess model fit that when used together can be complimentary. In addition to estimating variance parameters, ML and REML also compute a likelihood statistic for the model. Likelihood is the first point of reference assessing model fit with higher likelihood representing a higher probability for the model. This provides a simple way with which to compare models. Each fixed effect added to the model increases the degrees of freedom (*df*) by 1. Random effects are more complicated because extra *df* are added for covariances. For example, in the simple model $y_i = b_0 + u_{0j} + e_{ij}$ adding a fixed effect predictor to a model with two levels will increase the *df* by 1 for the parameter b_1x_{ij}. Adding a random effect for the predictor at level 1, however, will increase the *df* by 2 because of the random variance for the fixed effect predictor (σ^2_{u1}) plus the covariance with the level 1 variance ($\sigma_{u0,1}$).

Comparing models can therefore be accomplished by looking at the deviance in the likelihood statistic between the two models. Deviance is defined as -2 multiplied by the log likelihood ($-2ln(L)$). The deviance between models has an approximate χ^2 distribution with *df* equal to difference in the number of parameters in the model.

Comparing models where χ^2 = $-2ln(L)1$ / $-2ln(L)2$ and df are (df_1-df_2) yields a probability of <.05 suggests that the model with smaller deviance is a better fit.

Another way to assess mode fit is to reference Akaike's information criterion (AIC) and Bayesian information criterion (BIC). AIC is related to $-2ln(L)$ but penalises for multiple parameters by subtracting 2 multiplied by the number of parameters from the full $-2ln(L)$; AIC = $2k-2ln(L)$. A model with lower AIC value indicates a better fit. Because a model with additional parameters is likely to have greater explanatory power simply because there is more information, referencing AIC in order to assess model fit is useful for comparison with the deviance.

BIC similarly accommodates differences in the amount of information in model comparisons by penalising for parameters but more strongly than AIC. BIC is derived from the formula BIC = $kln(n)$ $-2ln(L)$ where k is the number of parameters and n is the number of observations. The implementation of BIC is of some debate because it is unclear at which level the n is derived. It is suggested that for comparison of fixed effects, n should represent level 1 observations and higher level observations for random effects. A model with lower BIC value indicates a better fit. Deviance, AIC and BIC can therefore be complimentary in assessing goodness of fit between models. Agreement between all three methods is an obvious indication of better fit. However, it might be necessary to use discretion and caution interpreting models where the methods disagree.

B.4 Interpreting models

The first stage of interpreting models is to calculate an intercept only model. That is, a model containing only the outcome variable (y) with the random effects and no predictors. This allows for an estimation of variance in the model at each of the levels by calculating the intra-class correlation coefficient (ICC). In the present example, the data is from a repeated measures experiment where female participants rated a series of male faces, voices and a face plus voice compound (overall attractiveness). Overall attractiveness is the outcome (y) varying at 2 levels; level 1 is the residual while both stimuli and participants are at level 2. Because participants rate the same set of faces and voices in the experiment, the design is specified as a cross-classified model with the formula [k]. The results of the intercept only model can be seen in Figure B.6.

[k] $y_{ij} = b_0 + v_{0j} + u_{0j} + e_{ij}$

overall ~ (1 | stim) + (1 | part)

v_{0j}	(stim)	0.273
u_{0j}	(part)	0.805
e_{ij}	(residual)	1.623

Figure B.6: *Intercept only model for overall attractiveness*

From the intercept only model it is possible to calculate the ICC by subtracting the variance of a specified level from the summation of variance at all of the levels. For example, the variance at the stimuli level as a proportion of the total variance would be $P_1 = \sigma^2_u / \sigma^2_u + \sigma^2_v + \sigma^2_e$. In the present example, variance is proportioned such that, stimuli accounts for 10%, and individuals account for 30% of the total variance, with unobserved error or residual error (60%) accounting for the majority of variance in the model. It is further possible to calculate the proportion of variance of a specified level in relation to another e.g. $P_2 = \sigma^2_u / \sigma^2_u + \sigma^2_v$. For example, taking out residual error, it appears that individuals (75%) account for a greater proportion of the explained variance than stimuli (25%).

The next step is to add predictors in a step-by-step fashion, assessing the model fit with the addition of each parameter. The object is to determine the simplest model that best fits the data. In addition to fixed effects, predictors can be allowed to vary at random levels. However, predictors need not be allowed to vary at all levels. It may be necessary to allow predictors to vary only at levels of interest to the research. In the present example, the subject of interest is considering the fixed effects of face and voice attractiveness in predicting overall attractiveness. Here, the interest is allowing the effects to vary at the individual level in order to consider the random effects and the relationship between face and voice attractiveness effects at the individual level. This allows for interpretation of the effect of face and voice attractiveness on overall attractiveness while considering the random effects owing to the sample of individuals representing that of a larger population. The correlation between random face and voice attractiveness effect therefore yields an interpretation of the relationship between face and voice attractiveness effects of a random population of individuals.

Following the intercept only model, the simplest model derived from the data fitted with ML estimates includes the fixed effects face and voice attractiveness. Both face and voice attractiveness predictors are centred using participant averages in order to look at the variance in effect between stimuli. Fixed effects are assumed to have a normal distribution. As such, it is possible to obtain an approximate significance test by calculating the ratio of the parameter to the standard error (*SE*) of the parameter in relation to a normal z distribution ($b \,/\, SE_b$ *approx* $= \square z \sim \mathrm{N}\square 0,1\square\square$). A parameter greater than 1.96 the *SE* is significant at p<.05. Further, the parameter +/- 1.96 multiplied by the *SE* can be used to calculate 95% confidence intervals (CI).

In the random intercept model (see Table B.7), the predictors face and voice attractiveness are significant at p<.001. Overall attractiveness can therefore be predicted from the mean 3.312 (95% CI: 2.951, 3.673) plus a face attractiveness response multiplied by .386 (95% CI: .298, .478) and voice attractiveness response multiplied by .149 (95% CI: .084, .214). An interaction between face and voice attractiveness did not improve the model and was thus omitted. While face and voice predict overall attractiveness, this model shows that face has a greater effect than voice on overall attractiveness. The absence of an interaction between the two signals suggests that these signals contribute independently to overall attractiveness.

	Intercept-only Model		Random Intercept Model	
Fixed Effects	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Intercept	3.312***	.21	3.312***	.184
$Face_c$			.388***	.046
$Voice_c$			.149***	.033
$Face_c$, $Voice_c$				
Random Effects				
Stimulus	.273		.085	
Participant	.805		.808	
Residual	1.628		1.462	
χ^2, AIC, BIC	1998, 2006, 2024		1926, 1938, 1964	

c = centred at participant level; *** $p < .001$

Table B.1: *Parameter estimates for a cross-classified 2 level Intercept-only Model and Random Intercept Model predicting male face-voice compound attractiveness with face attractiveness and voice attractiveness effects*

The random effects show that there is minimal random variance in effects between stimuli (.084). There is greater proportional random variance between participants (.808) suggesting a positive departure from the mean (intercept) owing to individual differences. The residual random variance (1.462) is proportionally higher, indicating a large portion of unexplained variance in the data. This might be expected since perceptions of attractiveness are influenced by many elements, of which only two (cf. face and voice attractiveness) are included in this model. Future studies may investigate the nature of this unexplained variance by including further items in the analysis.

There was no improvement of the model when random slopes were added (evident by lower AIC and BIC values) and thus they were omitted. Nevertheless, while approximate significance can be ascertained for the fixed effects using *SE*, this can not be performed for random effects. *SE* are not computed for random effects because they are often highly skewed. Asymmetric distribution therefore renders significance tests based on the *SE* inaccurate. Subsequently, CI for random effects are also avoided.

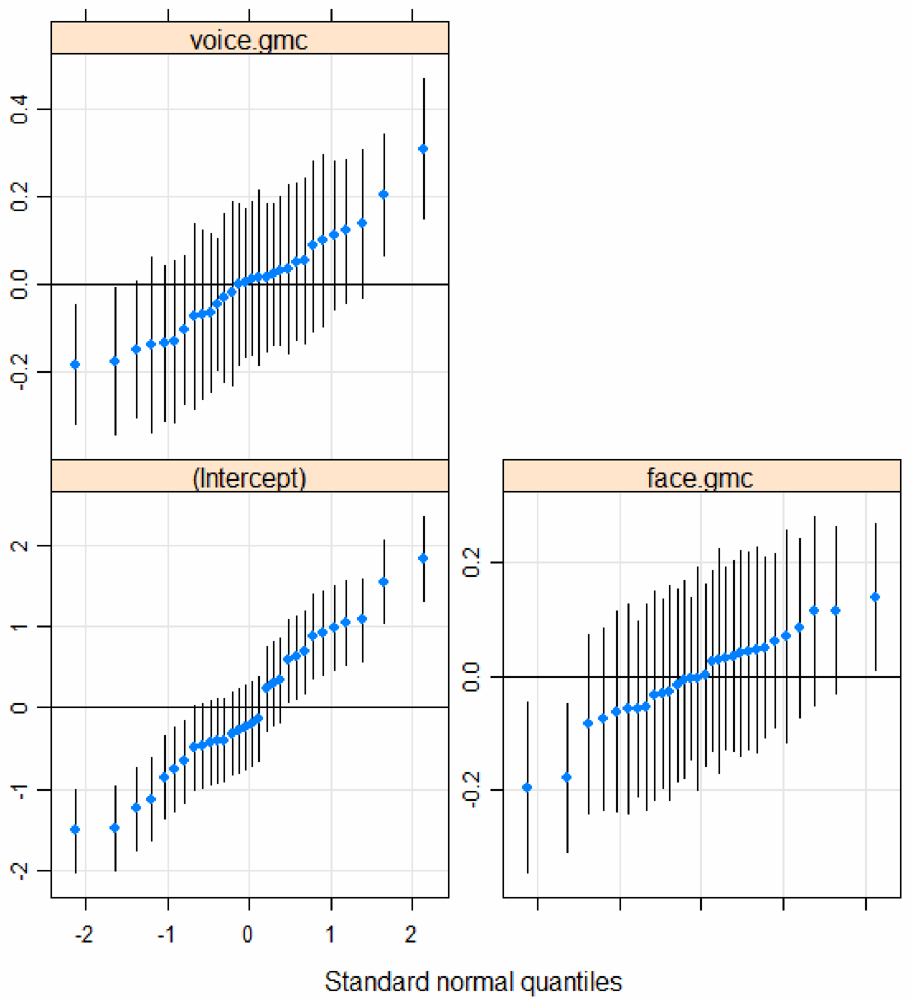


Figure B.7: *Caterpillar plots showing random variance in the intercept, face and voice effects at the participant level*

The caterpillar plots (see Figure B.7) shows a hypothetical example of the potential ranked participant effects for the intercept, face and voice attractiveness random effects at the participant level with 95% CI. It is possible to see from these plots that the effects are not normally distributed (indicated by a departure from linearity). Further, the plots display the variance in random effects by each individual. CI that do not overlap with the mean 0, indicate a significant difference. Several participants appear to differ from the mean showing that there is variance in departures from the intercept owing to individual differences. For the random face and voice effects however, few participants differ from the mean. This provides some indication that there is little random variance for face and voice effects and qualifies rejection of a more complex (random slope) model in favour of the simpler (random intercept) model.

In addition to looking at the random effects, correlation between random slopes and intercepts can indicate patterns in the data. The correlation between random intercept and slope is calculated by σ^2_{u1} / sqrt(σ^2_{u0} x $\sigma_{u0,u1}$). For example, a negative correlation between a random intercept and slope indicates that individuals with a high intercept have lower slopes (see Figure B.8a). In the present example, this would indicate that for participants with higher overall attractiveness ratings, the face attractiveness effect will be smaller for stimuli rated as high attractiveness. In contrast, the correlation between the participant level variance and voice attractiveness effect is positive. This indicates that for participants with higher overall attractiveness ratings, the voice attractiveness effect will be greater for stimuli rated as high attractiveness (see Figure B.8b).

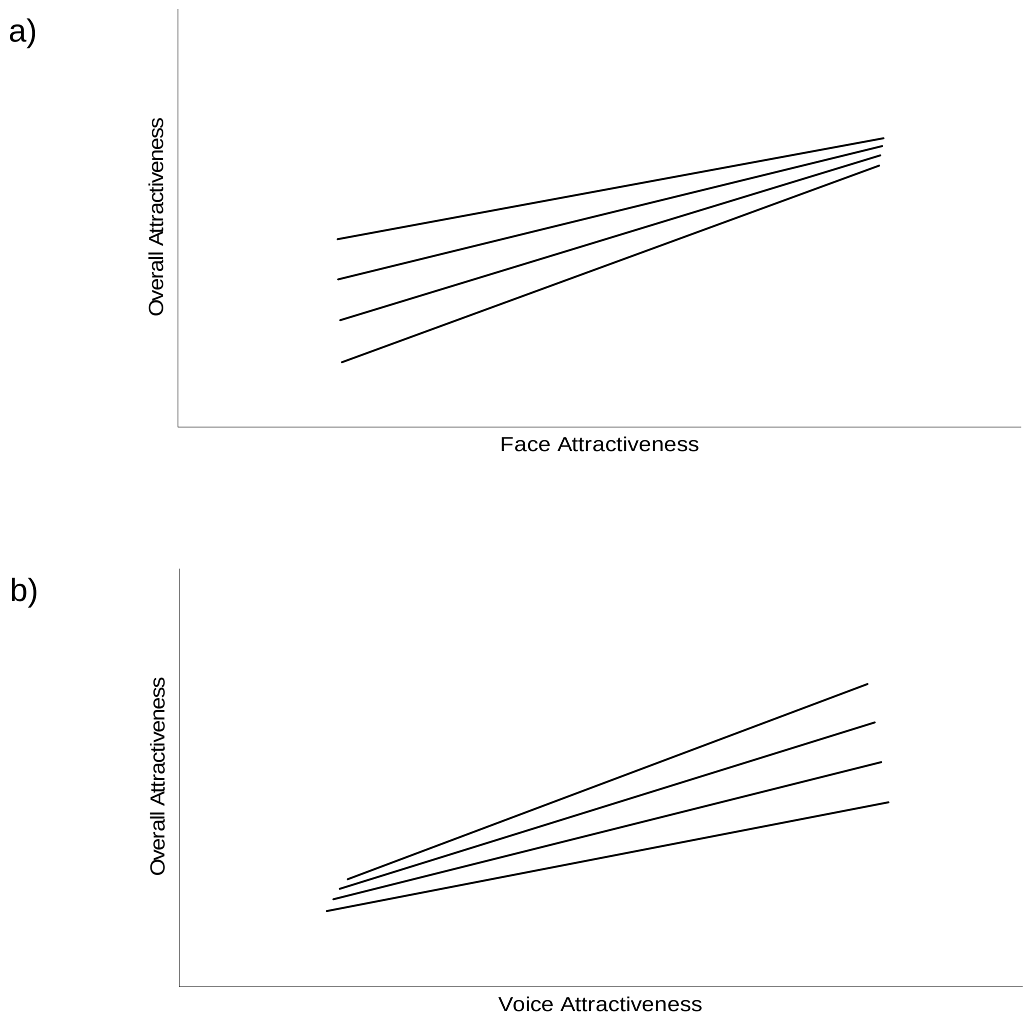


Figure B.8: *Relationship between random intercept and slope when the correlation is a) negative and b) positive*

From data, it is therefore possible to consider the relationship between random slopes. In the present face-voice attractiveness experiment, the correlation between face and voice effect slopes could be negative. This could indicate a shift in the size of effects, such that, the effect of voice attractiveness is higher compared to a diminished face effect for attractive stimuli. However, this could also be the result of differing levels of variance. For example, ceiling or floor effects in attractiveness ratings may yield little variance. The intercept only model ICC shows that there is little variance between stimuli in the data for the model (see Table B.7). A negative correlation between random participant level variance and random face attractiveness effect could be the result of low face attractiveness ratings evident from the raw data. In contrast, greater variance in voice attractiveness ratings could yield the variance in random voice effect in relation to overall attractive stimuli. This could produce the appearance that the face effect is low and voice effect is high for overall attractive stimuli. Caution should therefore be exercised in interpreting the relationship between random effects. In order to aid interpretation, consideration should be given to the ICC and variance in raw data.

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APPENDIX C: PUBLISHED ARTICLE

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MULTIPLE SIGNALS IN HUMAN MATE SELECTION: A REVIEW AND FRAMEWORK FOR INTEGRATING FACIAL AND VOCAL SIGNALS

T. J. WELLS*, A. K. DUNN*, M. J. T. SERGEANT AND M. N. O. DAVIES

Nottingham Trent University

Abstract. Evolutionary adaptation in variable environments is likely to give rise to several signals that can be used to identify a suitable mate in multisensory organisms. The presence of multiple signals for sexual selection could be advantageous, limiting the chance of mating with a suboptimal partner and avoiding the costs of inferior progeny. Despite extensive research into isolated signals of attractiveness, the amalgamation of multiple signals in sexual selection is poorly understood, particularly in humans. Inferences regarding both the function and importance of such signals are therefore tentative unless the effects are considered together. Here, the literature regarding two evolved signals of attraction (cf. faces and voices) is reviewed in relation to a framework (CANDOLIN 2003) for signal integration. It is argued that the functional nature of signals of attractiveness would be better studied through manipulation and experimentation with both single and multiple signals. Considering the prevalence of traits in relation to their combined effects may well provide a more fruitful and informative approach to human mate selection.

Keywords: face, voice, attractiveness, multiple signals, sexual selection

INTRODUCTION

There are two sources that can impact on traits evolving by means of sexual selection (DARWIN 1871: 2004): males and females compete within sex (intrasex) and between sexes (intersex) in order to successfully mate. Each source of competition exerts an influence on the prevalence of behavioural displays and/or physical characteristics that signal reproductive fitness and the means to overcome a rival. Sexual selection is likely to give rise to multiple sources of information that can be used to

* Corresponding authors: T. J. WELLS, timothy.wells@ntu.ac.uk; A. K. DUNN, andrew.dunn@ntu.ac.uk

identify a suitable mate in multisensory organisms, in order to facilitate both sending and receiving of such messages in variable environments. The presence of multiple signals for sexual selection could be advantageous since together they could limit the chance of mating with a suboptimal partner (MØLLER and POMIANKOWSKI 1993), thus avoiding the costs of inferior progeny. However, to date, research has mainly focused on single signals of attractiveness. Since it is unlikely that signals of attractiveness are assessed in isolation, particularly in the presence of other potentially useful information, inferences regarding their function and relative importance are consequently tentative. The aim of this paper is to apply a theoretical framework, outlined by CANDOLIN (2003), to examples from the attractiveness literature most commonly researched in isolation (cf. faces and voices) so as to consider their influence on human mate choice when combined. However, this is not simply a review of two well researched signals of attractiveness. Rather, this is an attempt to consider the relevance and adaptive function of multiple signals in human mate selection in a way that might inform future research.

ATTRACTIVENESS: FACES

The most commonly studied source of information used for human mate choice is the face. Evidence of cross-cultural agreement on what constitutes an attractive male or female face (CUNNINGHAM et al. 1995; RHODES et al. 2001), suggests that facial characteristics may have evolved through sexual selection pressures to signal indirect genetic benefits. Humans show distinct preferences for three varying properties of the face; averageness, symmetry and sexual dimorphism (RHODES 2006; THORNHILL and GANGESTAD 1999).

AVERAGENESS

Averageness as a feature of attractiveness was discovered by GALTON (1879), who overlaid photographs of faces to create a more attractive composite face. A composite face is termed average, because the addition of faces forms a single image and produces a face that is closer to a theoretical average of a population (RUBENSTEIN, LANGLOIS and ROGGMAN 2002). More recently, a number of studies have used a mathematical technique to create average faces that are perceived to be more attractive (LANGLOIS and ROGGMAN 1990; RUBENSTEIN, KALAKANIS and LANGLOIS 1999). It is proposed that averageness reflects an innate capacity to process conspecific faces and as such, there is likely to be a perceptual bias for processing faces closer to a prototype (LANGLOIS and ROGGMAN 1990). That is, humans are likely to prefer average looking faces because they are easier to process than novel faces.

Indeed, the brain processes information that is closer to a prototype much more efficiently (WINKIELMAN et al. 2006). Furthermore, averaged birds, fish and even non-living objects are perceived to be more attractive (HALBERSTADT and RHODES

2000; HALBERSTADT and RHODES 2003) and elicit positive affect (WINKIELMAN and CACIOPPO 2001). Babies show a preference for looking at average faces, which suggests that processing conspecifics are innate, although the development of an average in itself is based on visual experience (RUBENSTEIN et al. 1999). Consequently exposure to faces that deviate from a population average can lead to adaptation to a different facial average (COOPER et al. 2006; WEBSTER et al. 2004). Such adaptations have been shown to increase both normality and attractiveness attributions (RHODES et al. 2003).

The importance of average faces, however, appears at odds with the intuitive notion that novel faces stand out. Indeed, newborns show a preference for looking at novel faces that masks the effect of averageness (RHODES et al. 2002). Whilst likely to be innate, the ability to form prototypical representations of a face emerges around 3 months old (DE HANN et al. 2001) and exposure to novel facial stimuli at this time allows for improved discrimination between faces (PASCALIS et al. 2005). As they develop, babies form a facial prototype based on the faces they are exposed to. This leads to the own-race effect, that is, superior memory for the facial features of those in their environment (TANAKA, KIEFER and BUKACH 2003). This is an effect that can be reversed with exposure to other faces (SANGRIGOLI et al. 2005). Attractive faces based on a fixed average would be maladaptive in the event of seclusion within a population of non-average people. Flexible prototypes are, therefore, advantageous since it allows for more accurate discrimination within and adaptation to a population.

SYMMETRY

Symmetry is an attractive feature of faces because it reflects inherent developmental stability. That is, symmetry indicates immunocompetence: the capability to resist disruption of normal symmetrical development (KOWNER 2001). There are 3 types of symmetry evident in development (KOWNER 2001): *Directional* symmetry leads to traits favouring a particular side, such as the development of Broca's area on the left brain hemisphere. *Antisymmetry* is also directional although the side is random. Handedness, for example is a form of antisymmetrical development. Although a useful example, it should be noted that true antisymmetrical traits have a 50% chance of developing on either side. Thus, given the predominance of right handed individuals handedness is not a true form of antisymmetrical development.

Fluctuating asymmetry (FA) is randomly produced deviation from a symmetrical norm and is purported to be an important indicator of genetic fitness because traits that have bilateral symmetry are controlled by the genome (e.g. GANGESTAD and THORNHILL 1999; KOWNER 2001). As such, each side is equally susceptible to aberration. For example, the human body frame should develop symmetrically, however, because FA is determined by a mix of genetic and environmental factors (KOWNER 2001) the body tends to develop asymmetrically. FA is likely to affect traits that attract a mate because sexual selection is directional (KOWNER 2001).

That is, selection is driven by opting for partners that express a favourable trait. Low FA as a viable indicator of inherent fitness is, therefore, likely to lead to distinct preferences for symmetrical features. Indeed, evidence suggests that symmetrical faces are more attractive (GRAMMER and THORNHILL 1994; JONES et al. 2001; MEALEY, BRIDGSTOCK and TOWNSEND 1999; PERRETT et al. 1999; RHODES et al. 1998; RHODES, SUMICH and BYATT 1999; RHODES et al. 2001; THORNHILL and GANGESTAD 1993; THORNHILL and GANGESTAD 1999).

However, low FA is putatively related to genetic fitness and should therefore be heritable. One problem is that often only single features are measured for FA, which is relatively weak when considering individual differences in heritable developmental stability (KOWNER 2001). It is unlikely that sexual selection would depend on symmetry as a signal unless multiple symmetries were involved (KOWNER 2001). Data on the weak relationship between FA in two separate traits (POMIANKOWSKI and MØLLER 1995; although see GANGESTAD and THORNHILL 1999) suggests the prevailing research on a single trait may have limited implications for the assessment of an individual's developmental stability by a potential partner. On their own, single traits might not be reliable indicators of developmental stability *per se*. Rather, preferences for single symmetrical traits might simply reflect directional pressures for traits pertinent to sexual selection. Partners chosen for having an attractive symmetrical face, for example, are likely to influence the expression of symmetry in faces that may become independent of indicators of overall developmental stability.

The problem with FA as an indicator of fitness is that heritability is both population and environmentally dependent (MARKOW and CLARKE 1997). Differences in FA owing to population stratification and environmental fluctuations mean that estimates of heritability may not be accurately comparable within a species. Moreover, the measurement of FA is subject to error (MERILA and BIORKLUND 1995; PALMER and STROBECK 1986). FA is typically calculated from the variation in measurement of one side subtracted from the other, with asymmetry indicated by a deviation from zero (Right side – Left side = 0). However, not all asymmetry develops as a result of instability. Developmental noise, such as the rate of cell growth, can lead to subtle aberrations from symmetry and subsequently measurement error in FA owing to poor immunocompetence (PALMER and STROBECK 2003). There is also greater variation in the size of larger features and, therefore, increased potential measurement error (see PALMER and STROBECK 2003). Such instances of variation and measurement error are problematic for estimating the heritability of FA.

Another problem arises from evidence that some measurements include directional and not fluctuating asymmetry (MARKOW and CLARKE 1997). For example, SIMMONS et al. (2003) have shown that some facial features are larger on the right side. Not accounting for such directional asymmetry has lead some researchers to conclude that perfect symmetry is not attractive (LANGLOIS, ROGGMAN and MUSSELMAN 1994; SWADDLE and CUTTHILL 1995). However, the faces used in these experiments were created by forming a chimera: mirroring one side of the face. Chimeric faces appear unusual because they mirror elements of the face that should develop asymmetrically. A recent experiment, using computer techniques to create a symmetrical face that maintains inherent directional symmetry, have shown that faces with low FA are perceived to be more attractive than faces with high FA (RHODES et al. 1998). Failure to control for directional symmetry can, therefore, lead to further measurement error in estimating the heritability of developmental stability. Although subject to error, the attractiveness of symmetry and the concept of developmental stability need not be rejected. Rather, it is essential that stringent criteria are considered when measuring FA (see PALMER and STROBECK 2003).

SEXUAL DIMORPHISM

Sexual dimorphism occurs in human faces because of relative levels of circulating hormones. The development of masculine features appears to be related to higher concentrations of testosterone (PENTON-VOAK and CHEN 2004), which exert an influence on the exaggeration of features such as strong jaw line, thick eyebrows, and smaller eyes. By contrast, the development of feminine facial features appear to be related to higher concentrations of oestrogen (LAW-SMITH et al. 2006). As a result, female faces typically have small chins, high cheek bones and large round eyes; features that signal neoteny (BERRY and MCARTHUR 1985; JONES et al. 1995), youthfulness and fecundity (JONES et al. 1995).

Female preference for indicators of testosterone are likely to be beneficial because testosterone is an immunosuppressant (GROSSMAN 1985). That is, high levels of testosterone serve to lower the immune system rendering an organism more susceptible to bacterial and/or parasitic infection. ZAHAVI (1975) proposed that the expression of such ornaments are an indication of genetic fitness owing to an organism's survival despite bearing this handicap. Since high levels of testosterone can have a detrimental effect on an organism's immune system, it is possible that the evolution of masculine facial features are ornaments driven by the selective pressures of females to choose healthy mates (GANGESTAD and THORNHILL 1999). By contrast, male preferences for indicators of oestrogen are likely to be beneficial, because oestrogen is related to fertility (JONES et al. 1995). As such, female faces may have evolved to reflect healthy, fecund females (THORNHILL and GANGESTAD 1999). Hence, males and females should show preferences for traits that indicate high levels of oestrogen and testosterone respectively.

Males do show a preference for feminine features (PERRETT, MAY and YOSHIKAWA, 1994; PERRETT et al. 1998; RHODES, HICKFORD and JEFFEREY 2000) and females show a preference for masculine features (JOHNSTON et al. 2001; PENTON-VOAK and PERRETT 2000; PENTON-VOAK et al. 1999) that appear to be universal (CUNNINGHAM et al. 1995; PERRETT, MAY and YOSHIKAWA, 1994; PERRETT et al. 1998). However, these findings are equivocal. Putative benefits of hormone mediated fitness indicators are likely to lead to preferences for exaggerated traits. Conversely, average male faces were deemed to be more attractive than the same images displaying extreme masculine features (RHODES, HICKFORD and JEFFERY 2000). Although exaggerated masculine faces are perceived to be more dominant, they are no more attractive to females (SWADDLE and REIERSON 2002). Moreover, some studies have shown that females perceive feminised male faces to be more attractive (PERRETT et al. 1998; RHODES, HICKFORD and JEFFREY 2000; LITTLE and HANCOCK 2002).

Sexually dimorphic male and female faces are deemed to be attractive (as discussed). Moreover sexual dimorphism and attractiveness are believed to indicate health (GANGESTAD and THORNHILL 1999). However, different results have been obtained with regard to how well people are able to determine the actual health of individuals based on faces; using similar methodologies KALICK et al. (1998) found no relationship between attractiveness and actual health of participants whereas SHACKLETON and LARSEN (1999) found just such a relationship. Nevertheless, people tend to rate attractive faces as more healthy (GRAMMER and THORNHILL 1994; KALICK et al. 1998). In females, attractiveness ratings relate to perceived health and to perceived fertility (FINK, GRAMMER and MATTS 2006; FINK, GRAMMER and THORNHILL 2001; LAW-SMITH et al. 2006) despite no relationship with actual health (RHODES et al. 2003). Conversely, in men, no correlation was found between attractiveness ratings and ratings of perceived health (BOOTHROYD, 2005) despite a relationship between attractiveness and actual health (RHODES et al. 2003).

Whilst such discrepancies may be the result of differences in the samples tested (or other methodological differences), it may be that health is not as important as previously suggested; for example, males may attribute importance to fertility rather than to health (JOHNSTON and FRANKLIN 1993). Moreover, indicators of health other than sexual dimorphic features, such as skin condition (FINK, GRAMMER and MATTS 2006; FINK, GRAMMER and THORNHILL 2001; JONES et al. 2004), can be subject to changes owing to short-term hormonal fluctuations and nutrition (BOELSMA et al. 2003; GARG et al. 2001), it is possible that differences in perceived health are based more on immediate assessments of diet and hormonal status, for example, rather than long-term phenotypic quality. Alternatively, it may be that people are not accurate at detecting actual health in faces, especially in female faces. If this is the case, the finding that attractive faces are perceived as more healthy may be a halo effect – attractive people are attributed with positive features such as, in this case, good health. Future work will need to elucidate further what participants are rating when they rate for 'health', and to determine which components of 'health' are important in influencing ratings of attractiveness and in turn, mate selection.

AVERAGENESS, SYMMETRY, SEXUAL DIMORPHISM OR ALL THREE?

Average faces may be preferred on the grounds that there is a perceptual bias for processing prototypical faces. Symmetrical faces are also attractive as they are believed to reflect inherent developmental stability. Problematically, average faces also tend to be symmetrical (ALLEY and CUNNINGHAM 1991). GRAMMER and THORNHILL (1994) found symmetrical but not average faces to be attractive. However, the composite faces used in the GRAMMER and THORNHILL (1994) study were constructed from up to 16 faces. Given that LANGLOIS and ROGGMAN (1990) found a composite face constructed from 32 faces to be more attractive, the faces used in the GRAMMER and THORNHILL (1994) study may be less average (RUBENSTEIN et al. 2002). Further investigation has found that averageness and symmetry are exclusive facets (JONES, DEBRUINE and LITTLE, 2007; RHODES, SUMICH and BYATT, 1999). RHODES, SUMICH and BYATT (1999) found that averageness and symmetry correlated in the stimuli used. However, both symmetry and averageness accounted for a significant proportion of the variance in attractiveness when the other was partialled out (RHODES, SUMICH and BYATT 1999). Changes in averageness also altered the perception of attractiveness when symmetry was held constant (RHODES, SUMICH and BYATT 1999). Together, these findings show that both averageness and symmetry appear to independently contribute to the perception of attractiveness.

Whilst average faces are attractive, however, not all attractive faces are average (THORNHILL and GANGESTAD 1999). Attractiveness can also be defined in terms of exaggerated sexually dimorphic traits – those which have exaggerated features (e.g. small nose, high cheek bones and full lips on a woman; thick brow, square chin, prominent jaw line on a man) on an average face (ALLEY and CUNNINGHAM 1991; BAUDOUIN and TIBERGHIEN 2004; DEBRUINE et al. 2007; PERRETT et al. 1994; RHODES et al. 1999). Compared to female faces, for example, normal male faces are more attractive than averaged composite faces owing to averageness being perceived as more feminine (GRAMMER and THORNHILL 1994).

Female preference for feminine male faces could reflect strategic sexual selection. Although high testosterone males purportedly provide genetic benefits, dominant males are associated with negative characteristics such as dishonesty and aggression (PERRETT et al. 1998), and are less likely to invest in their offspring (GANGESTAD and SIMPSON 2000; GRAY et al. 2002). Female preferences for male faces change in accordance with menstrual phase (reviewed in JONES et al. 2008): attraction to masculine features and symmetry are more pronounced for short-term partners and when the probability of conception is high (DANEL and PAWLOWSKI 2006; JOHNSTON et al. 2001; LITTLE et al. 2007; LITTLE, JONES and DEBRUINE 2008; PENTON-VOAK and PERRETT 2000; PENTON-VOAK et al. 1999), suggesting pronounced sensitivity to indicators of genetic fitness when they are most salient for producing healthy progeny.

In contrast, there is evidence of female sensitivity to facial signals indicating potential paternal investment (RONEY et al. 2006). Moreover, preferences for healthy faces was found to be strongest during low fertility and pronounced for pregnant women (JONES et al. 2005). Cyclic preferences are, therefore, likely to be adaptive. Females are able to maximise genetic fitness of their offspring in the short-term and/or select for paternal investment, or increase the likelihood of a successful pregnancy in the long-term (JONES et al. 2008; JONES et al. 2005; PENTON-VOAK et al. 1999).

In summary, attractive faces appear to vary independently across three dimensions; averageness, symmetry and sexual dimorphism. Each are important features of the human face that have been related to increased mating success in both males and females (RHODES, SIMMONS and PETERS 2005). Moreover, the attractiveness of a perceived partner can vary in relation to female menstrual phase. Such shifts may reflect an adaptive strategy for selecting optimal genetic fitness when the probability of conception is high, whilst selecting for investing males and/or a successful pregnancy when the probability of conception is low. Research must, therefore, consider such elements of variance in an effort to elucidate the form and function of facial attractiveness.

ATTRACTIVENESS: VOICES

Vocal communication serves a variety of functions in many animals, including advertising for a mate, intimidating a rival and signalling an alarm call in the presence of a predator (OHALA 1984). Many animals use acoustics to assess the characteristics of the sound-producer (FITCH 1997). Recently, Evolutionary Psychology has witnessed growing interest with the assessment of vocal parameters as a potential signal to genetic fitness in the domain of human mate selection.

Vocalisations in humans occur through the modulation of auditory frequencies as they travel through the vocal apparatus. The principle components involved are the vocal folds or vocal cords, situated in the larynx, which vibrate to modulate the flow of air to produce acoustic energy. The resulting sound then travels through the vocal tract where certain frequencies can be amplified or shaped in the cavities.

The sound created by vibrations of the vocal cords is termed pitch. Although this auditory sensation is referred to in terms of a musical scale, pitch is perceptual. That is, pitch is a subjective attribute that cannot be measured directly. Pitch is the perception of fundamental frequency (F0); the lowest frequency in a period, of which each harmonic component in a spectrum of complex sound is a multiple. For example, the 3rd harmonic in a spectrum of sound will be 3 times the frequency and 1/3 the amplitude of the F0. A F0 of 100Hz, therefore, would have a 3rd harmonic of 300Hz at 1/3 the amplitude, and a 5th harmonic of 500Hz at 1/5 the amplitude. Several aspects determine F0, including vocal fold length and applied tension to the folds (TITZE 1994). In humans, the F0 is sexually dimorphic, such that adult males (on average) speak at a lower vocal pitch than adult females (TITZE 1994). This sexual dimorphism occurs owing to developmental differences in pubertal androgens (HOLLIEN 1960). In males, the size of the vocal folds increases rapidly in relation to body size under the influence of high levels of testosterone (HOLLIEN 1960). It is the longer vocal folds in males relative to females that result in a lower pitch, which emerges as a secondary sexual characteristic.

The filtering of acoustic energy from the vocal folds passes through the vocal tract resulting in formant frequencies. Vocal characteristics change during puberty. However, vocal folds increase independently and at a greater rate than the vocal tract (HOLLIEN 1960). Voice pitch correlates with body size but disappears after puberty (HOLLIEN 1960). In contrast, the vocal tract develops relative to skeletal size (BRUCKERT et al. 2006; FITCH 1997; FITCH and GIEDD 1999; FITCH 2000). Formant dispersion (Df; the difference between formant frequencies in a sound) correlates with body size, and larger animals have smaller Df (FITCH 1997; FITCH 2000). Although vocal characteristics such as Df could be used to accurately assess the size of a mate (BRUCKERT et al. 2006), females do not appear to use it. Rather, females tend to agree on body size attributions but do so inaccurately using F0 rather than Df (BRUCKERT et al. 2006): females associate low voice pitch with large body size.

VOCAL SIGNALS AND SEXUAL SELECTION

Voice pitch is an element of vocal information that is important for the attribution of attractiveness (ZUCKERMAN and MIYAKE 1993). Measures of voice quality, including pitch (deepness, squeakiness and throatiness) and impact (monotonous, loudness and resonance) have been shown to be influential in the attribution of attractive voices (ZUCKERMAN and MIYAKE 1993). A number of studies have also shown that pitch preferences are directional, that is, males prefer higher pitched voices in women (COLLINS and MISSING 2003; FEINBERG et al. 2005) and females prefer low pitched voice in men (BRUCKERT et al. 2006; COLLINS 2000; RIDING, LONSDALE and BROWN 2006; ZUCKERMAN and DRIVER 1989; ZUCKERMAN, HODGINS and MIYAKE 1990; ZUCKERMAN and MIYAKE 1993). There is also some evidence to suggest that women show a preference for male voices that have a degree of variability in pitch (e.g. ZUCKERMAN and MIYAKE 1993; BRUCKERT et al. 2006). For example, BRUCKERT et al. (2006) found that females preferred male voices that varied upwards and had a mean low fundamental frequency. However, RIDING et al. (2006) found no preference for pitch variability. Thus, the issue of attractiveness in relation to variation in vocal signals remains unresolved and outside the scope of this review. Nevertheless, the signal variation could prove to be an important aspect of what determines an attractive voice.

The function of sexual dimorphism in voices is of evolutionary significance. Sexual dimorphism in male voices is testosterone dependent, which is itself an immunosuppressant (GROSSMAN 1985). In relation to ZAHAVI's (1975) Handicap

Theory, like sexual dimorphism in faces, the evolution of voice pitch might be a signal driven by selective pressures of females to choose healthy mates. A central prediction here is that females should prefer males with a low pitch, and that this signal of fitness is at least honest. That is, voice pitch is a reliable indicator of genetic quality that is selected by females.

The putative significance of voice pitch is illustrated by a female sensitivity bias for processing low pitched sounds. Females appear to be more able than males to identify a natural voice from two samples where one is filtered to remove higher frequencies (HUNTER et al. 2005). That is, females are more likely to identify a natural voice than men using predominantly low frequency tones. Moreover, there is evidence of a more pronounced sensitivity to lower pitch during the ovulation stage of their menstrual phase (HAGGARD and GASTON 1978). This bias occurs alongside a preference for masculine voices that develops in conjunction with reproductive capability in young females (SAXTON, CARYL and ROBERTS 2006) and is also more pronounced when the probability of conception is high (PUTS 2005; FEINBERG et al. 2006; PUTS 2006). Preference for low voice pitched males that develops in conjunction with a females' ability to conceive and at a time when conception is most likely, provides firm evidence that voice pitch is of reproductive significance in terms of female mate choice. As an indicator of fitness, testosterone traits such as voice pitch should also co-occur with other testosterone dependent characteristics. Indeed, voice pitch does appear to correlate with measures of body symmetry (HUGHES, HARRISON and GALLUP 2002; HUGHES, PASTIZZO and GALLUP 2008) and desirable characteristics such as shoulder-to-hip ratio in men and waist-to-hip ratio in women (EVANS, NEAVE and WAKELIN 2006; HUGHES, DISPENZA and GALLUP 2004). A recent study has also found that low voice pitch is related to reproductive success in an indigenous tribe of hunter-gatherers (APICELLA, FEINBERG and MARLOWE 2007).

There is an abundance of evidence to support the notion that voice pitch has reproductive significance. However, there may be grounds to be cautious about the importance of voice pitch for female selection of male partners and the function of the signal itself. SNOWDON (2004) argues that criteria including variance within the population, the ability to discriminate and cyclic preferences during high conception risk suggests evolutionary significance and sexual selection of a signal. Although strong evidence suggests that voice pitch is a viable indicator of male fitness, to date, there is no direct evidence that females are actively selecting based on this signal.

Unless the presence of a signal (e.g. voice pitch) leads to copulation, then according to SNOWDEN (2004), such signals might only be a social preference rather than a sexually selected trait. Recently, JONES et al. (2008) found that the phrase 'I like you' modulated the attractiveness of female voices perceived by males but not females. This finding demonstrates that communicating social interest could provide additional information that modulates preferences for attractive female (high pitched) voices (JONES et al. 2008). However, one question presides over the influence of preferences on actual mating behaviour. In a study using mice (a comparable social species), GUBERNICK and ADDINGTON (1994) found that given a choice of two potential mates, female mice develop a preference for one male mouse over the other (irrespective of oestrus). However, such preferences translated to actual mating in only 50% of cases. Moreover of those that mated, only 60% mated with their preferred partner. In short, preferences do not necessarily lead to mating, and mating may not occur with the preferred mate. Further, recent studies investigating preference ratings and behavioural measures in humans have shown that people expend more effort for opposite sex faces that elicit responses in brain regions associated with reward, despite rating same sex faces as equally attractive (AHARON et al. 2001; LEVY et al. 2008). That is, 'liking' can be dissociated from 'wanting' (ROBINSON and BERRIDGE 2000). The aesthetic qualities of a face judged on a simple preference scale may not represent features actually selected for sexual relationships.

It is possible that female preferences for male voice pitch may not, therefore, actually reflect a signal that ultimately leads to copulation. At present, there is no evidence that voice pitch is a signal that elicits sexual arousal. Although there is evidence that men with low voice pitch have more sexual partners (HUGHES, DISPENZA and GALLUP 2004) and more children (APICELLA, FEINBERG and MARLOWE 2007), voice pitch is one signal amongst many that could have been used. Evidence that social interest can modulate the perceived attractiveness of female voices (JONES et al. 2008) could be of no consequence if the mate is perceived to be physically unattractive. Thus it is necessary to be cautious about what may be concluded with regard to putative signals of attractiveness from studies using simple rating scales and in the presence of only one signal.

The function of voice pitch as a reliable indicator for mate assessment could also be clarified, since it is subject to aberrations as a result of relaxed muscle control over the course of a day (TITZE 1994) and emotional/arousal state (BANSE and SCHERER 1996; MILLOT and BRAND 2001; RUSSELL, BACHOROWSKI and FERN´ANDEZ-DOLS 2003). A number of studies have further shown that males modulate their voice pitch as a function of perceived dominance (PUTS, GAULIN and VERDOLINI 2006) and attractive female faces (DUNN, WELLS and BAGULEY in prep.). Rather than indicating genetic fitness, it is suggested that variation in voice pitch originally developed through intra-sexual pressures as a symbol of dominance and aggression (CLUTTON-BROCK and ALBON 1979; OHALA 1982; PUTS et al. 2006; PUTS et al. 2007).

Rather than attractiveness per se, the emergence of voice pitch as a signal of dominance through intra-sexual pressures may render it more useful as an indicator of personality. Voices have been shown to influence personality attribution (ZUCKERMAN and DRIVER 1989; ZUCKERMAN et al. 1990). Females tend to rate medium F0 voices from manipulations of 1.3 (high), 0 (medium) and 0.7 (low) their normal level, as more benevolent (RIDING et al. 2006). Furthermore, vocal attractiveness (low pitch) was shown to significantly affect judgments of dominance (ZUCKER-

MAN and DRIVER 1989; ZUCKERMAN et al. 1990). Evidence of reproductive success in low pitched hunter gatherers (APICELLA, FEINBERG and MARLOWE 2007) could, therefore, reflect selection for dominance and social rank. This may be particularly important in populations where access to resources is paramount. Rather than selecting for genetic quality, it could be that females in the tribe are selecting for partners capable of providing food for their offspring.

Evidence that voice pitch correlates with symmetry and other putative sexually selected traits, suggest that F0 could be a potential indicator of genetic quality (EVANS, NEAVE and WAKELIN 2006; HUGHES, HARRISON and GALLUP 2002; HUGHES, DISPENZA and GALLUP 2004; HUGHES, PASTIZZO and GALLUP 2008). Given that voice pitch can vary in a number of different contexts, however, F0 as a reliable indicator of quality is potentially inaccurate. Female preferences for low voice pitch may be a more important factor in attributing dominance. This would be particularly useful since female preferences for masculinity are cyclic (FEINBERG et al. 2006; PUTS 2005; PUTS 2006). Masculine, dominant men are less likely to invest in and support their offspring (GANGESTAD and SIMPSON 2000; GRAY et al. 2002). It is, therefore, possible that a less pronounced desire for low F0 in male voices during low conception risk (FEINBERG et al. 2006; PUTS 2005; PUTS 2006) could reflect a cyclic preference for females to select for indicators of investment potential. Indeed, RONEY et al. (2006) found that male interest in children predicted female attractiveness ratings of male faces in a long-term mating context. However, attractiveness and pro-social attributes were found to negatively correlate with male participants' ability to engage in child directed speech (determined by a higher average F0) when asked to give directions to an imaginary child (PENTON-VOAK et al. 2007). These results are discussed in terms of a possible halo effect. That is, attractive faces are attributed with attractive traits. Such findings suggest that voices may not be an important aspect of attractiveness if they can be influenced by physical appearance.

Evidence strongly suggests that voice pitch may be a signal indicating genetic quality that is selected for by females. However, few studies have considered direct evidence that females actively select based on such preferences. Although females show directional preferences for testosterone dependent traits such as faces and voices, few studies have also considered their combined effect on attractiveness. If research is to elucidate their function in human mate selection, it is therefore necessary to consider integration of these signals.

MULTIPLE SIGNALS: A FRAMEWORK FOR SIGNAL INTERACTION

Human attractiveness in single modalities has been researched thoroughly. The importance and function of these putative signals of genetic quality are used in human mate selection, however, is limited in that little is known about the combined effect of multiple signals in humans. In their work on multiple signals, PARTAN and MARLER (1999) propose a framework (see *Figure 1*) within which the effect of signals can be integrated. It is proposed that multiple signals can be divided into *redundant* and *non-redundant* signals. Redundant signals are proposed to transmit the same information and as such, lead to a more accurate assessment of a mate or facilitate the most appropriate signal in different environmental conditions. Such signals can, therefore, be equivalent or multiplicative in their effect. In contrast, non-redundant signals transmit more information per message and can have different effects on the receiver. Non-redundant signals tend not to be related to each other. As such, they are likely to express different aspects of a mate that leads to a variety of responses from the receiver. For example, two signals may have effects that are independent of each other, one signal may be more dominant, one signal may modulate the perception of another, or the combination of two signals may lead to the emergence of a new response. However, ROWE (1999a) criticised the framework for presenting the argument that each signal, whether redundant or non-redundant, elicits a response on its own. It is possible that signals may produce no response on their own but serve to enhance another signal. As such, the signal may be an unreliable and uninformative signal to fitness.

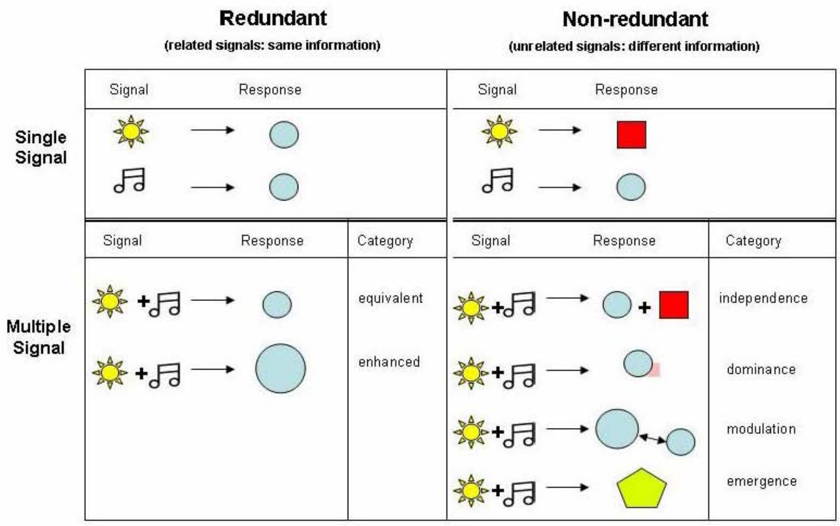

Figure 1. A framework for multiple signals adapted from PARTAN and MARLER (1999)

CANDOLIN (2003) extends the work of PARTAN and MARLER (1999) with more inclusive categories with which multiple signals can be defined (see *Figure 2*). Multiple signals may be *adaptive*, such that, the presence of more than one signal reduces mate choice costs and errors. Alternately, they may be *non-adaptive*: having no influence on fitness and are simply remnants of past selection. Signals could also be *maladaptive*, by appeal to a pre-existing bias that aids sexual selection but is costly to the receiver. According to CANDOLIN (2003), signals can be further grouped into two categories, depending on their content. Signals may be *informative* (providing information about mate quality) or *uninformative* (providing unreliable indicators about mate quality) although they can still be adaptive, have no influence or be maladaptive. The following section will discuss theories relating to adaptive informative signals and adaptive uninformative signals (see *Figure 2*).

Nature of signal	Information Content	Signal Type Hypotheses	Proximate benefit
Adaptive	Informative	*Multiple messages (1)*	Assessment of overall quality
	Informative	*Back-up signals (2)*	More accurate assessment
	Informative	*Fisherian signals (3)*	Heritable attractiveness
	Uninformative	*Receiver psychology (4)*	Facilitates mate assessment
Non-adaptive	Uninformative		No effect
Maladaptive	Uninformative		Costly

Figure 2. Categories of multiple signals hypotheses adapted from CANDOLIN (2003)

Note: Hypotheses relating to *species recognition* and *unreliable signals* have been omitted since (a) this review is not concerned with avoiding mating with other species and (b) unreliable signals have no direct benefits, but are proposed to call attention to other signals CANDOLIN (2003). As such, unreliable signals could be subsumed by receiver psychology.

ADAPTIVE INFORMATIVE SIGNALS

The Multiple Messages hypothesis proposes that signals reflect different information about mate quality (MØLLER and POMIANKOWSKI 1993). For example, a deep voice indicates high testosterone whilst good skin quality signals health. Together, multiple messages can provide an estimation of overall quality. However, multiple messages could also signal different elements within different time frames (HILL et al. 1999; MØLLER et al. 1998). Some signals may change more rapidly or at different stages in life and as a result may become more prominent in mate selection

(CANDOLIN 2003). It is possible that changes developing over a long period (for example age related changes in FA) may be more important indicators of indirect genetic (those that increase offspring viability) benefits (CANDOLIN 2003). In contrast, signals (for example skin condition as an indicator of current health) subject to dynamic changes might reflect direct (those that reflect immediate benefits such as protection or resources) benefits (CANDOLIN 2003).

Multiple messages that reflect independent qualities could also be used differentially, such that, females could weight them differently in terms of importance (CANDOLIN 2003). Factors that might affect such choice are whether females choose direct or indirect benefits. For example, a female with access to resources need not select for direct benefits if she is already capable of providing for her children. Furthermore, weighting mate choice signals may also be determined by the environmental context: audition, for example, is likely to be used in conditions of impoverished light. Females are also less likely to use signals of fitness where there is little variation between mates or the signals themselves are difficult to detect given perceptual or environmental constraints (COTTON, SMALL and POMIANKOWSKI 2006; ROBERTS and GOSLING 2003). For example, indicators of genetic fitness can differ from compatible genes (those which complement the host genes in progeny), in that, two high quality phenotypes may not sufficiently differ on dimensions such as specific immune resistance that, when combined, would create stronger immune defence. In certain conditions, where the costs of poor immunity are high, it may benefit partners to mate with someone that is of lower quality but higher compatibility (for a discussion see MAYS and HILL 2004). Moreover, there are different costs associated with varying environments: the relative prevalence of disease (risk of disease/infection is high) makes selection for an optimal immune system more important. Females are therefore more likely to use information that allows for the most appropriate signals to be used in a given context. Where offspring fitness is paramount, females are more likely to select using attractiveness signals: where resistance to disease and infection is important, females are more likely to use signals of herterozygosity. However, both selection criteria are mediated by the variability in available mates. That is, if all mates are equally attractive, females would benefit from selecting for signals of compatible gene. Such condition dependent mating has been shown in mice (ROBERTS and GOSLING 2003), whereby mice will mate based on the variability of genetic fitness and compatible signals. That is, mice will mate using fitness signals where the variability in compatibility is low and visa versa.

The Back-up signals hypothesis proposes that multiple signals allow for a more accurate assessment of a mate (MØLLER and POMIANKOWSKI 1993). Although variable dishonesty is expected in signals (GUILFORD and DAWKINS 1991), the presence of more than one reliable signal makes cheating less likely to be effective. The belief here is that all signals reflect the same underlying trait, such as levels of testosterone, albeit with a certain degree of error. As such, back-up signals should correlate with each other. There is a similarity between multiple messages and back-up signals in that, traits that correlate with overall fitness are essentially back-up signals (CANDOLIN 2003). However, signals often do not correlate with each other (for examples see CANDOLIN 2003), rendering back-up signals less common than multiple messages (CANDOLIN 2003).

A final form of informative adaptive signals are those which arise through Fisher's runaway process. FISHER (1930) proposed that attractive traits could grow exponentially through sexual selection, provided that the magnitude of average male traits grew in accordance with female preferences over each successive generation and, that magnitude was not stabilised owing to costs incurred by inheritance. For example, female preferences for the peacock's tail could have adapted to genetic drift causing an increase in average size. As long as the fitness of progeny does not suffer as a result of a larger trait, both preference for and increase in trait size will be inherited. Fisherian traits are informative because they may have once (although possibly no longer) correlated with fitness (FISHER 1930). Moreover, the heritability of Fisherian traits and their relationship with attractiveness are adaptive since males possessing the trait are likely to mate.

ADAPTIVE UNINFORMATIVE SIGNALS

Receiver psychology posits that less reliable signals may be assessed alongside other more reliable traits (IWASA and POMIANKOWSKI 1994; reviewed by ROWE 1999b). Such signals can evolve through exploiting pre-existing sensory biases in the receiver. Rather than shape a response, signals that develop through receiver psychology hijack a response that already exists for the purpose of sexual selection (RYAN 1998). The development of red skin in fertile females, for example, has been shown to have primarily evolved through a pre-existing bias for male attraction to foraging for food such as red fruits (FERNANDEZ and MORRIS 2007). Such signals often do not indicate any indirect genetic benefits and are, therefore, termed unreliable (MØLLER and POMIANKOWSKI 1993). However, if signals are relatively cheap to produce and can attract attention to another more informative signal, then they are likely to be adaptive (ROWE 1999b). Any interaction between traits means that such signals may be less useful when studied on their own (ROWE 1999b).

The function of multiple signals in receiver psychology is proposed to enhance the detection and discrimination of a stimulus (GUILFORD and DAWKINS 1991; ROWE 1999b). Detection is defined as a signal's detectability against background noise (GUILFORD and DAWKINS 1991) and can be measured using a number of methods including reaction time, probability of detection and detection thresholds. Reaction times, for example, are proposed to be faster when two signals are presented together than when separate (MILLER 1982). This is evident when the multiple signals are presented in different modalities (MILLER 1982; RAHNE et al. 2007; VROOMEN and DE GELDER 2000) owing to inter-sensory facilitation. That is, integration between sensory modalities in the brain serves to enhance perception. This enhanced perception can occur when the auditory stimulus follows shortly after the presentation of the visual stimulus (MORRELL 1968a). While this is the case for auditory stimulus accompanying a visual signal, however, the same does not occur when reversed (MORRELL 1968b).

The presence of multiple signals also increases the probability of detection against background noise (ROWE 1999b). The purpose of some signals could be to call attention to another signal. Vocalisations, for example could serve to amplify fixed morphological traits as and when required (ROWE 1999b). Another way in which signal detection can operate is through the configuration effect (PURCELL and STEWART 1988). That is, although there is some evidence to suggest that parts of the face are processed independently (PRESS and REMINDER 2007) features of the face are more easily detected when they are in a prototypical configuration (PURCELL and STEWART 1988; YOW and CIPOLLA 1997). Detection of stimuli against background noise can also be measured through detection thresholds: the intensity with which a signal can be detected more than 50% of the time. The threshold of composite signals has a lower threshold than the constituent parts on their own (HOWARTH and TREISMAN 1958).

Signals in receiver psychology also improve the ability to discriminate (ROWE 1999b). There is evidence that multiple signals improve discrimination. Speech, for example, is more easily perceived when both visual and auditory information are available (CHEN and RAO 1998). Although acoustic signals do not aid facial recognition *per se,* it is possible that sound is used to make facial discriminations (KENDRICK et al. 1995). However, the presence of both visual and auditory signals can lead to a different response when the information is inconsistent (MCGURK and MACDONALD 1976; SAMS et al. 1991). For example, visual lip movements creating the sound 'ga' combined with the auditory sound 'ba' create the percept of 'da'. This is problematic, because if they do not correlate, opposing messages can slow down the detection of a reliable signal (MILLER 1982), particularly when the signal requires divided attention between different modalities. Where information is consistent, messages that combine to improve transmission would have more adaptive significance.

Considering a framework with which multiple signals interact is crucial for hypothesis testing (HEBETS and PAPAJ 2005). Explanations that are not mutually exclusive, however, are a particular challenge for multiple signal research (HEBETS and PAPAJ 2005). For example, multiple signals may correlate with overall fitness and yet signal different aspects of a potential mate (CANDOLIN 2003). Thus, careful scrutiny of individual signals is important and in order to elucidate their function, inclusion and manipulation of multiple signals is critical (HEBETS and PAPAJ 2005). Moreover, research should also aim to focus on both signal and receiver responses (HEBETS and PAPAJ 2005) since natural, human procreation requires both sexes. Although research tends to focus on female choice, it is of benefit to females to attract viable males. As such, investigating female signals in response to attractive males could further elucidate their role in human mate choice.

MULTIPLE SIGNALS IN HUMAN SEXUAL SELECTION

In humans, very little research has focused on the interaction between signals of putative genetic quality in sexual selection. Signals such as facial attraction (RHODES et al. 1998; RHODES et al. 2001; THORNHILL and GANGESTAD 1993; THORNHILL and GANGESTAD 1999) and voice pitch (EVANS, NEAVE and WAKELIN 2006; HUGHES, DISPENZA and GALLUP 2004; HUGHES, HARRISON and GALLUP 2002; HUGHES, PISTAZZO and GALLUP 2008) have been proposed as indicators of fitness selected for by potential partners. Given the proposed directional selection for hormone dependent traits, it is expected that females should have a preference for a masculine face and low pitched voice, and that both signals correlate in men. Conversely, males should prefer a feminine face and high voice pitch in females, both of which correlate in the individual.

FEINBERG (2008) argues that faces and voices do reflect the same underlying qualities that are used in the assessment of potential mates. Indeed, studies have found a relationship between measures of facial metric and voice pitch in females (FEINBERG et al. 2005), and correlated preferences in matched female stimuli (COLLINS and MISSING 2003). To date, two studies have also found a relationship between the attractiveness of faces and voices in males (FEINBERG et al. 2008; SAXTON, CARYL and ROBERTS 2007). However, such findings have been questioned (LANDER 2008), on the grounds that preferences were determined using a force choice paradigm, whereby participants selected between two sets of stimuli (for a discussion of comparative evaluation in relation to mate choice see BATESON and HEALY 2005). Moreover, stimuli used in the FEINBERG et al. (2008) experiment were not derived from the same source: voices were not sampled from the people whose photos were used. This indicates that a correlated preference exists for multiple signals whilst eluding the question of whether attractive males have attractive voices.

Further investigation using both static (photographs and recorded vowels sounds) and dynamic (video recordings with speech) stimuli has showed that preferences for female faces and voices do correlate (LANDER 2008). Conversely, preferences for male faces and voices only appear to be congruent when stimuli are dynamic (LANDER 2008). However, others have found no relationship between the attractiveness of voices and faces using dynamic stimuli (OGUCHI and KIKUCHI 1997; ZUCKERMAN and DRIVER 1989; ZUCKERMAN et al. 1990; ZUCKERMAN, MIYAKE and HODGINS 1991). Such inconsistencies are likely to arise from the different methods used. FEINBERG (2008) suggests that studies investigating voice pitch that failed to find a preference for masculine voices may have been confounded by regional accents or emotional content. Although an important experimental control, such variability common in vocal communication would render the function of voice pitch a relatively weak signal in the context of sexual selection. Nevertheless, these differences need to be addressed in an attempt to delineate function and importance of facial and vocal signals.

Given female cyclic preferences for masculinity (PENTON-VOAK and PERRETT 2000; PENTON-VOAK et al. 1999; PUTS 2005; PUTS 2006), and that extreme sexually dimorphic features are not preferred (RHODES et al. 2000), it appears that faces and voices are stabilised. That is, they are not under selective pressures akin to Fisher's runaway process. Evidence of a correlation between measurements of face and voice in females (FEINBERG et al. 2005), and correlated attractiveness ratings suggest that, at least in females, facial and vocal signals may transmit the same genetic message: they could be back-up signals indicating levels of oestrogen. Whilst this indicates that both faces and voices together may provide males with a more accurate picture of genetic fitness in females, the lack of consistent findings in males suggests a differential selective pressure.

However, it is possible that back-up signal hypothesis regarding the integration of voice and face signals in males is reconcilable. Voice pitch is likely to have developed as a signal of dominance and aggression through intra-sexual selection pressures (CLUTTON-BROCK and ALBON 1979; PUTS et al. 2006; PUTS et al. 2007). Cheaters are likely to pay the costs by contesting with dominant males (BERGLUND, BISAZZA and PILASTRO 1996; CLUTTON-BROCK and ALBON 1979), therefore, the signal is likely to be at least honest. Females who select for dominant males using this signal are more likely to mate with high quality males (BERGLUND et al. 1996). Indeed, a number of studies of various species have found that signals of status in intra-sexual competition are attractive (reviewed in BERGLUND et al. 1996). However, since it is more costly to fake in male-male contests than in the contest of sexual selection, males are more likely to be sensitive to cheaters than women (BERGLUND et al. 1996). This has important implications for the study of voice pitch in relation to back-up signals used by females. If voices are more honest in male-male contests, females would benefit from assessing males in the company of other males rather than in isolation, in order to gain a more accurate estimate of overall quality.

Evidence that males modulate their voice pitch in different contexts (DUNN, WELLS and BAGULEY, in prep; MILLOT and BRAND 2001; PUTS 2005), however, indicates the potential unreliability of vocal signals. As such, visual and auditory signals in males may not be back-up signals but transmit different (multiple) messages. One intriguing finding is that, despite little evidence of a significant correlation between ratings using dynamic stimuli (OGUCHI and KIKUCHI 1997; ZUCKERMAN and DRIVER 1989; ZUCKERMAN, HODGINS and MIYAKE 1990; ZUCKERMAN, MIYAKE and HODGINS 1991 – although see LANDER 2008), both faces and voices contribute toward attractiveness, although visual attractiveness had a more pronounced effect (ZUCKERMAN, MIYAKE and HODGINS 1991). Moreover, there is some suggestion that the effects may be independent (OGUCHI and KIKUCHI 1997).

One potential explanation for the independent effects of attraction on faces and voices is the attribution of personality. Studies have shown that voices can influence the perception of an individual's character (OGUCHI and KIKUCHI 1997; ZUCKERMAN and DRIVER 1989; ZUCKERMAN, HODGINS and MIYAKE 1990). Interpersonal attraction is likely to be influenced by selecting for partners that display such characteristics evident in vocal parameters. Variance in aspects of personality preference could be related to environmental or ecological aspects therefore representing a selective trade-off (NETTLE 2006). For example, extraverts are prosocial and are more likely to experience increased social support (FRANKEN, GIBSON and MOHAN 1990). However, prosocial qualities are also associated with increased number of sexual partners and, therefore, potential disruption to family stability (NETTLE 2006) through extra-pair copulation. Whilst facial characteristics are perhaps more likely to reflect inherent genetic fitness, voices could portray social information such as personality characteristics that could differentially benefit a mate.

Although voices and faces have been shown to influence attraction, it remains unclear whether the voice, by itself, is a strong selective criterion. Relaying social information through auditory perception could be adaptive despite having no effect in isolation (receiver psychology). Studies have shown that the plasticity of the brain allows for multimodal regions to facilitate sensory transduction (MILLER 1982; RAHNE et al. 2007; VROOMEN and DE GELDER 2000). That is, sensory biases in the human brain serve to process information much faster when presented in more than one modality. For example, studies have shown that there is a pre-existing bias for visual stimuli with sharp edges to be associated with harsh sounds, whilst stimuli with soft edges are associated with soft sounds (MAURER, PATHMAN and MONDLOCH 2006). Moreover, it has been shown that such examples of intersensory facilitation aid object recognition (AMEDI et al. 2005; BEAUCHAMP et al. 2004; MOLHOLM et al. 2004). Evidence of voice pitch modulation (DUNN, WELLS and BAGULEY, in prep; MILLOT and BRAND 2001; PUTS et al. 2006) could, therefore, serve to either shape or draw attention to fixed morphological features: modulation of a low pitch could enhance a males masculinity. Conversely, modulation of a higher pitch could allow the same face to be perceived as less threatening by a female partner.

A recent study investigated the relationship between auditory and visual signals in face perception (SMITH, GRABOWECKY and SUZUKI 2007). Participants rated the masculinity or femininity of an androgynous face. When paired with a low frequency (male) or high frequency (female) pure tone, participants rated androgynous faces in accordance with the tone. However, on their own, the tones were not rated as male or female. These findings suggest that auditory signals are important for influencing face perception, although auditory signals by themselves carry little information. Voice pitch may, therefore, be an uninformative signal that has an adaptive function by improving the recognition and discrimination of male faces. Moreover, female preference for masculine face and voices alters over the course of the menstrual cycle (FEINBERG et al. 2006; JONES et al. 2008; PENTON-VOAK and PERRETT 2000; PENTON-VOAK et al. 1999; PUTS 2005; 2006). Since males can modulate their voice pitch and they would benefit from adapting to the ovulation pattern of female partners (GANGESTAD, THORNHILL and GARVER-APGAR 2005), it is possible that this could be facilitated by modulating the vocal signal.

CONCLUSION

This review has provided a comprehensive account of both facial and vocal signals. Attractive faces vary across a number of dimensions including averageness, symmetry and sexual dimorphism under sexual selection. Similarly, vocal parameters, including fundamental frequency and formant dispersion are involved in the assessments of mating characteristics. However, evidence for the role of voices is more equivocal. Although there is evidence provided for evolutionary significance in terms of sexual selection, uncertainty over their role when both are presented together is problematic for proximal causes and functional inferences.

With reference to a framework for signal interaction, this review provides a number of intriguing considerations with which to base experimentation in an effort to resolve the functional nature of multiple signals. There are a number of potential theoretical explanations that could be applied to potential findings. For example, signals may have adaptive value but may be uninformative about the source of the signal or what is being signalled. Moreover, the importance of signals may be subject to environmental or contextual effects. If the function of signals is to be elucidated, it is paramount that careful scrutiny be given to both the methods and exploration of findings. As such, considering the prevalence of traits in relation to their combined effects may well provide a more fruitful and informative approach to human mate selection.

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