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Stress influences mating preferences in humans.

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General Abstract

Stress is a common phenomenon for animals living in the wild, but also for humans in modern societies. Originally, the body's stress response is an adaptive reaction to a possibly life-threatening situation, and it has been shown to impact on energy distribution and metabolism, thereby increasing the chance of survival. However, stress has also been shown to impact on mating behaviour and reproductive strategies in animals and humans.

This work deals with the effect of stress on reproductive *behavior*. Up to now, research has only focused on the effects of stress on reproduction in general. The effects of stress on reproduction may be looked at from two points of view. First, stress affects reproductive *functioning* by endocrine (e.g. glucocorticoid) actions on the reproductive system. However, stress can also influence reproductive *behavior*, i.e. mate choice and mating preferences. Animals and humans do not mate randomly, but exhibit preferences towards mating partners. One factor by which animals and humans choose their mating partners is similarity vs. dissimilarity: Similar mates usually carry more of one's own genes and the cooperation between similar mates is, at least theoretically, less hampered by expressing diverse behaviors. By mating with dissimilar mates on the other hand one may acquire new qualities for oneself, but also for one's offspring, useful to cope with environmental challenge. In humans we usually find a preference for similar mates. Due to the high costs of breeding, variables like cooperation and life-long partnerships may play a greater role than the acquaintance of new qualities.

The present work focuses on stress effects on mating preferences of humans and will give a first answer to the question whether stress may affect our preference for similar mates.

Stress and mating preferences are at the centre of this work. Thus, in the first Chapter I will give an introduction on stress and mating preferences and link these topics to each other. Furthermore, I will give a short summary of the studies described in Chapter II - Chapter IV and close the chapter with a general discussion of the findings and directions for further research on stress and mating preferences.

Human mating behavior is complex, and many aspects of it may not relate to biology but social conventions and education. This work will not focus on those aspects but rather on cognitive and affective processing of erotic and sexually-relevant stimuli, since we assume that these aspects of mating behaviour are likely related to psychobiological stress mechanisms. Therefore, a paradigm is needed that measures such aspects of mating preferences in humans. The studies presented in Chapter II and Chapter III were performed in order to develop such a paradigm. In these studies we show that affective startle modulation

may be used to indicate differences in sexual approach motivation to potential mating partners with different similarity levels to the participant.

In Chapter IV, I will describe a study that aimed to investigate the effects of stress on human mating preferences. We showed that stress reverses human mating preferences: While unstressed individuals show a preference for similar mates, stressed individuals seem to prefer dissimilar mates.

Overall, the studies presented in this work showed that affective startle modulation can be employed to measure mating preferences in humans and that these mating preferences are influenced by stress.

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Index of Publications

This doctoral thesis consists of three chapters (and, in addition, one chapters that represent a general introduction and overview), which are published or submitted for publication as ‘Original Articles’ in international peer-reviewed journals. The author of this dissertation is the first author of all three articles. However, other authors also contributed to the work (listed in the table). All articles are presented here in the originally published/submitted form, except for changes in formatting (i.e. figure labeling). References for all three articles are provided at the end of this work.

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Chapter II	Lass-Hennemann, J., Schulz, A., Nees, F., Blumenthal, T.D. & Schächinger, H. (2009). Direct gaze of female nudes influences startle in men. <i>International Journal of Psychophysiology</i> ,72:111-114. (Impact Factor 2008: 2.264)
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Chapter IV	Lass-Hennemann, J. Deuter, C.E. Kuehl, L.K., Schulz, A., Blumenthal, T.D. & Schächinger, H. (submitted). Does stress alter mating preferences in humans? Context-specific effects of facial self-resemblance.

Index of Abbreviations

Ag/AgCl	Silver/Silver chloride
ANOVA	Analysis of variance
bpm	Beats per minute
dB	Decibels
DBP	Dystolic blood pressure
e.g.	for example
ECG	Electrocardiogram
EMG	Electromyogram
HR	Heart rate
Hz	Hertz
IAPS	International affective picture system
i.e.	that is
M	Mean
min	Minutes
mmHg	Millimeters mercury
ms	Milliseconds
s	Seconds
SBP	Systolic blood pressure
SD	Standard deviation
SE	Standard error
SEM	Standard error of mean

Chapter I – General Rationale

Stress is a phenomenon that is common to most of us. If we have to think of situations that we find stressful, we would probably come up with situations like exams, traffic jams and money worries. However, originally stress-eliciting situations were possibly life-threatening situations such as getting chased by a predator. Stressful situations are accompanied by a cascade of biological mechanisms that redirect the physiology and the behavior of the animal/human towards survival, including a fast mobilization of energy, and a down-regulation of those processes that are not necessary for the immediate survival of the organism (Sapolsky, 1998). One of the first described effects of stress hormones was the suppression of reproductive activity (Wingfield & Sapolsky, 2003). However, now it is known that the relationship between stress and reproduction is not so simple: Originally stress-eliciting situations were possibly life-threatening situations. In evolution a fundamental goal is the passing on of one's own genes. The optimal reproductive strategy for individuals in stressful environments should be to maximize current reproduction in order to minimize the chances of lineage extinction (Stearns, 1992). Today it is known that animals and humans do not mate randomly, but rather actively choose the optimal mating partner (Halliday, 1983). Since stress has a fundamental impact on survival-directed behavior, it seems reasonable that stress also has some influence on mate choice and mating preferences. Thus, the aim of this work is to investigate the effects of stress on human mating preferences.

1.1 Stress and reproduction

When animals and humans experience stress, the body reacts to the stressor in a specific way. Stressful experiences lead to an activation of two biological stress systems: the hypothalamo-pituitary-adrenal axis and the autonomic sympathetic system. The activation of these two systems leads through intermediate steps to the release of glucocorticoids (in humans cortisol) and adrenalin (epinephrine) from the adrenal glands. The glucocorticoids directly reach the brain via the bloodstream and stimulate receptors in different brain regions, e.g. the hypothalamus. Circulating epinephrine may not cross the blood brain barrier, but can indirectly (via vagal afferents and neurons of the Nucleus of the solitary tract) induce the release of norepinephrine in the amygdala. The hypothalamo-pituitary adrenal axis is the part of the biological stress response that has been linked to reproductive activity. For instance, it is thought to inhibit the reproductive system resulting in a decrease of testosterone levels and less functional sperm (for a review see Negro-Vilar, 1993). However, glucocorticoid hormones also mobilize energy stores and may therefore actually facilitate energetically

expensive reproductive behavior (Husak & Moore, 2008). Thus, mating should be facilitated shortly after a stress-exposure, when glucocorticoid levels are high, but there is no immediate life threat. Furthermore, mortality salience, which results from exposure to possibly life-threatening situations, has been shown to enhance the desire for offspring in humans (Wisman & Goldenberg, 2005). This is in line with life-history theory (Stearns, 1992), which predicts that risky environments should facilitate reproduction in order to decrease the chance of lineage extinction. However, it is difficult to predict in what way stress should modulate mating behavior.

1.2 Mating preferences: Optimal outbreeding and the preference for similar mates

Mating and reproduction are energetically expensive behaviors. Therefore, it seems reasonable that animals and humans mate actively in order to ensure high reproductive success. Many aspects of the potential mate influence the mate choice of animals and humans, since there are differences in the quality of mates (Halliday, 1983). The potential partner should be healthy, physically attractive and highly fertile, have a high social status and valuable resources. Another important issue of mate choice that has been raised by evolutionary biologists is the problem of inbreeding versus outbreeding. Inbreeding as well as outbreeding have costs and benefits. Inbreeding, e.g. might lead to an expression of deleterious genes and the offspring of inbreeding relationships may be insufficiently variable to cope with a varying environment. Outbreeding on the other hand might lead to a loss of co-adapted gene complexes by recombination. Furthermore, the travelling into another population may be costly and dangerous (Bateson, 1983).

Consequently, it has been proposed that an optimal balance between inbreeding and outbreeding is most beneficial, that is animals and humans should mate with an individual that is slightly different from themselves (Bateson, 1983). This balance has been termed optimal outbreeding. The mechanism proposed for optimal outbreeding may be that animals are able to recognize close kin and will then choose a mate that looks, sounds or smells a bit different from close kin. This is of course based on the assumption that external appearance is a measure of genotypic similarity. In fact several studies in animals and humans have shown that individuals tend to prefer mates that slightly differ from familiar members of the other sex. For example, it has been shown that the Japanese Quail tends to avoid mating with very familiar individuals, who are likely to be siblings, but prefer birds similar to those with which they were reared (Bateson, 1980, 1982). In humans we usually find a preference for similar mates. Except of one study that showed a preference for dissimilar mates in the context of a

short term relationship (DeBruine, 2005), studies usually find that humans prefer a mate that resembles themselves in many traits, including facial characteristic (Bereczkei, Gyuris, Koves, & Bernath, 2002; Bereczkei, Gyuris, & Weisfeld, 2004; Griffiths & Kunz, 1973 ; Zajonc, Adelman, Murphy, & Niendenthal, 1987). This kind of phenotypic matching has been termed sexual imprinting (Bateson, 1978) and is one aspect by which animals and humans seem to choose their mates in order to ensure high reproductive success.

1.3 Stress and the context-dependence of mating preferences

However, mating preferences are also context-dependent. Stress has been linked to reproductive activity in general, but in particular stress has also been shown to influence mating preferences in animals. Studies in stalk-eyed flies, guppies, mice and soldier beetles have shown that stressed animals become less discriminatory in their mating preferences, when they are exposed to stress (Hingle, Fowler, & Pomiankowski, 2001; Kavaliers & Ossenkopp, 2001; McClain, 1981). However, there have been no studies investigating the effects of stress on human mating preferences.

From the described animal studies one could expect that humans also simply lose their preference for similar mates under stress. However, one may also argue that stress should increase the outbreeding tendency, because inbreeding leads to offspring that are not genetically diverse enough to deal with the varying circumstances that a risky and stressful environment imposes on an individual. Therefore one might also propose a preference for dissimilar mates in a stressful environment. In line with this life history theory (Stearns, 1992) predicts that the optimal reproductive strategy for individuals in stressful environments is to maximize current reproduction to minimize the chances of lineage extinction. Having short-term relationships instead of long-term relationships is a way of increasing current reproduction and it has been shown that individuals who experience psychosocial stress have more short-term relationships than do individuals without a history of psychosocial stress (Koehler & Chisholm, 2009). As described above, DeBruine (2005) found a preference for dissimilar mates in the context of a short-term relationship. Therefore, one might also argue that stress does not only decrease the mating preference for similar mates, but also increases mating preference for dissimilar mates.

1.4 Measurement of preferences for similar mates in humans

1.4.1 Current methods to measure mating preferences in humans

The measurement of mating preferences in animals is quite simple. The animal is either exposed to individuals of the opposite sex with different degrees of relatedness or similarity and the approach motivation to the different potential mates is measured by the time the test animal spends close to the cage of the potential mates (Bateson, 1983). Other studies measured copulation frequency with different potential mates in order to establish a measure of mating preferences (Hingle et al., 2001; Lopez, 1999)

Paradigms like these are of course not realizable in humans. However, there are numerous human studies on mating preferences that have used different methods to analyze mating preferences. Most studies used photographic portraits of romantic partners and asked judges to rate the similarity between these (Bereczkei et al., 2004; Griffiths & Kunz, 1973 ; Zajonc et al., 1987). Other studies used experimental manipulations of similarity to investigate putative mating preferences in purely experimental designs (DeBruine, 2004, 2005). These studies employed a morphing procedure (Tiddeman, Perrett, & Burt, 2001) in which the participants face is morphed into an average face of the opposite sex. By this the researchers are able to create opposite sex faces that share about 50% of the facial cues of the participants. However, the similarity is very subtle and is usually not recognized by the participants. These studies used subjective ratings of the morphed faces to evaluate mating preferences for similar vs. dissimilar mates. Subjective preference ratings are an important indicator of mating preferences. However, subjective ratings yield some problems. First, subjective ratings require introspection, which is susceptible to error, reconstruction, and inaccuracy (Nisbett & Wilson, 1977). Second, factors such as demand characteristics and social desirability may play a role in the answer tendencies.

Furthermore, the use of face stimuli alone is not optimal for analyzing mating preferences. Studies that focus on aspects of sexual approach motivation and states of sexual arousal typically use erotic pictures or film segments as stimulus material and, in addition to subjective ratings, physiological measures as dependent variables.

A well validated and widely used method to measure appetitive approach motivation is the affective startle modulation paradigm (for a review see Bradley, Cuthbert, & Lang, 1999). This paradigm does not yield the same problems as subjective ratings as will be described in the next section.

1.4.2 Measuring mating preferences with the startle reflex

1.4.2.1 The Startle Reflex

The startle reflex is a defensive reflex that occurs in all mammals and in most other species. Any abrupt sensory event will prompt a fast twitch of facial and body muscles, in particular eyelid-closure and a contraction of facial and skeletal muscles. The startle reflex is a simple brain stem mechanism, which involves only a few synapses. The startle reaction to acoustic stimuli e.g. is transmitted via three synapses, the Cochlear root neurons, the Nucleus reticularis pontis caudalis, and the Facial motor nucleus (Davis, Walker, & Lee, 1999). The startle reflex maybe easily quantified by measuring the electromyographic (EMG) activity of the musculus orbicularis oculi, the muscle that is responsible for eyelid closure (Blumenthal et al., 2005).

Reflexes have long been thought to be fixed and invariant reactions to stimuli. However, today it is known that reflexes are not fixed, but can be modulated by a variety of internal and external stimuli, e.g. the startle reflex has been shown to be modulated by attentional and emotional processes.

1.4.2.2 Affective Startle Modulation

The modulation of the startle reflex by emotional processes has been termed affective startle modulation. Numerous studies have shown that the startle reflex (elicited by a brief burst of noise) is facilitated when people view aversive pictures and inhibited when people view pleasant pictures (for a review see Bradley et al., 1999). According to Fridja (1987) emotional states are action dispositions that either prompt approach or withdrawal motivation. Pleasant, especially appetitive stimuli, lead to an approach motivation, while unpleasant, especially threatening stimuli lead to a defensive withdrawal motivation. Reflex responses have been shown to be valuable in studies of emotion because they have the potential to tap these basic action dispositions — appetitive-approach and defensive-withdrawal — that underlie positive and negative emotional states. Lang et al. (1990) have proposed a response matching explanation for the linear valence modulation effect observed for the startle reflex: Viewing of aversive pictures leads to an activation of the defensive/withdrawal system and, therefore, leads to an augmentation of the congruent defensive startle reflex. Viewing of pleasant pictures, on the other hand, engages the appetitive-approach system and leads to an inhibition of the non-congruent defensive startle reflex. Thus, affective startle modulation is not a direct measure of the physiological mechanisms underlying emotion, but rather an indirect measure of the activity of neurobiological structures involved in the processing of approach and withdrawal motivation (Bradley et al., 1999). Accumulating evidence suggests

that the amygdala and related structures mediate the startle potentiation by negative emotional states (for a review see Koch, 1999). The neurobiological structures underlying startle inhibition for pleasant appetitive pictures are not as well defined. However, the Nucleus accumbens has been suggested to play a role (Koch, Schmid, & Schnitzler, 1996).

The startle reflex as a measure of the activation of the appetitive/approach motivational system has several advantages compared to subjective ratings and other measures of emotion. First, because startle is an automatic/reflexive response, it is not primarily influenced by intentional control and is resistant to demand effects and response biases that can interfere with verbal reports and voluntary motor responses. Additionally, the neural circuit of the startle pathway is well described and higher cognitive structures that probably mediate the affective startle modulation have been identified. Therefore, affective startle modulation represents a very basic measure of approach motivation to appetitive stimuli, which indirectly measures the activity of neurobiological structures involved in approach motivation.

1.4.2.3 Startle Modulation to erotic stimuli

The strongest inhibition of the startle reflex has been found for stimuli that most strongly activate the appetitive motivational system, e.g. erotic stimuli and food (Bradley, Codispoti, Cuthbert, & Lang, 2001). In particular, the startle modulation paradigm has been frequently used to analyze sexual approach motivation to erotic pictures and film segments. Some of these studies investigated the strength of the startle inhibition to erotic pictures compared to other picture categories (Bradley, Codispoti, Cuthbert et al., 2001; Sabatinelli, Bradley, & Lang, 2001). Other studies investigated how differences between participants, e.g. sexual desire, influence startle inhibition (Janssen, Goodrich, Petrocelli, & Bancroft, 2008; Koukounas & McCabe, 2001; Prause, Janssen, & Hetrick, 2008).

One potential disadvantage of affective startle modulation compared to other measures of emotion is that the startle inhibition to erotic stimuli has been shown to be more reliable for male participants compared to female participants. This can be explained by the findings that men respond stronger to visual sexual stimuli (for a review see Rupp & Wallen, 2008).

Despite of this potential disadvantage, affective startle modulation is a widely used method in the research field of sexual arousal and sexual preferences: The obvious advantages of the affective startle modulation paradigm compared to other measures of approach and withdrawal motivation, that have been described above, might have even more relevance in this specific context, since the problem of controllability of the answers that a participant

gives might be even stronger in an erotic context, where factors like shame and embarrassment may play a role.

1.5 Effects of stress on mating preferences: Empirical Evidence

1.5.1 Startle Modulation within the category of erotic stimuli

Previous studies have investigated how erotic stimuli are modulated compared to other stimulus categories (Bradley, Codispoti, Cuthbert et al., 2001; Sabatinelli et al., 2001) and how differences between participants influence affective startle inhibition to erotic stimuli (Janssen et al., 2008; Koukounas & McCabe, 2001; Prause et al., 2008). However, there are no studies that investigated startle modulation within one category, for example how features of the erotic stimuli influence startle inhibition. To investigate the effects of stress on human mating preferences, we had to first show that startle modulation within the category of erotic pictures is possible. Additionally, gaze direction has been shown to play a role in face perception and attractiveness ratings of faces (Kampe, Frith, Dolan, & Frith, 2001; Mason, Tatkov, & Macrae, 2005). Thus, Study I was designed to investigate whether startle modulation within the category of erotic pictures is possible and whether the gaze direction of the presented stimuli has an impact on startle modulation. Two subsets of erotic photographs of female nudes (women looking directly at the observer vs. gazing away) and neutral pictures of the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 1999) were viewed by 26 male volunteers, while startle eye blink responses to binaural bursts of white noise (50 ms, 105 dB) were recorded by EMG. Erotic pictures reduced startle eyeblink magnitude as compared to neutral pictures. Participants showed a greater startle inhibition to erotic without direct gaze at the observers compared to erotic stimuli with direct gaze at the observer, indicating a higher sexual approach motivation for erotic female nudes with an indirect gaze at the observer. These data show that startle modulation within the category of erotic stimuli is possible, and importantly, that this modulation can be elicited by features of the face of the erotic female nudes. Furthermore, our data showed that the gaze direction of the erotic female nudes may influence the approach motivation to appetitive erotic female nudes and should be controlled in further studies.

1.5.2 Startle Modulation as a measure of mating preferences in humans

As described above, humans usually prefer mates that resemble themselves. This has been shown by various observational studies (Bereczkei et al., 2004; Griffiths & Kunz, 1973 ; Zajonc et al., 1987), but there is a lack of true experiments investigating the preference for self-resembling mates. The aim of this work was to analyze how stress influences men's

preferences for similar mates with the affective startle modulation paradigm as an index for mating preferences. Thus, we had to first show whether the preference for similar mates occurs in an experimental manipulation of facial self-resemblance with startle inhibition as a measure of sexual approach motivation. In Study II, male volunteers (n = 30) viewed 30 pictures of erotic female nudes and 10 neutral pictures while startle eyeblink responses were elicited by acoustic noise probes. The female nude pictures were digitally altered so that the face either resembled the male participant, another participant, or were not altered. Non-nude neutral pictures were also included. Importantly, the digital alteration was undetected by the participants. Erotic pictures were rated as being pleasant, and clearly reduced startle eyeblink magnitude as compared to neutral pictures. Participants showed greater startle inhibition to self-resembling than to other-resembling or non-manipulated female nude pictures indicating a higher sexual approach motivation to self-resembling/similar mates. Thus, our results show that the preference for similar mates can be measured with the affective startle modulation paradigm.

1.5.3 Effects of Stress on mating preferences in humans

The main aim of this work was to analyze the effects of stress on humans' preference for similar mates. In Study I and Study II we showed that affective startle modulation may be used to indicate differences in the approach motivation to different categories of erotic female nudes, and that affective startle modulation may be used to indicate men's preferences for similar mates. In Study III we investigated whether stress influences men's preference for similar mates. The procedure of Study III was similar to that of Study II except that participants first underwent a cold pressor test or a control procedure. Then, participants viewed participants pictures of erotic female nudes whose facial characteristics were computer-modified to resemble either the participant or another participant, or were not modified, and neutral pictures. Startle eyeblink responses were elicited by probes of white noise (50 ms, 105 dB) during picture viewing. Erotic pictures were rated as being pleasant, and clearly reduced startle magnitude as compared to neutral pictures. In the control group, startle magnitude was smaller during foreground presentation of photographs of self-resembling female nudes compared to other-resembling female nudes and not-manipulated female nudes, indicating a higher sexual approach motivation to self-resembling mates. In the stress group, startle magnitude was larger during foreground presentation of self-resembling female nudes compared to other-resembling female nudes and not-manipulated female nudes, indicating a higher sexual approach motivation to dissimilar mates. Our findings show that stress affects human mating preferences: While unstressed individuals showed the expected

preference for similar mates, stressed individuals express a higher sexual approach motivation pattern towards dissimilar mates.

1.6 Summary, Limitations and Concluding Remarks

This work aimed to investigate the effects of stress on human mating preferences. We were able to show that the startle reflex can be modulated within the category of erotic female nudes by facial features of the erotic female nudes. Additionally, we showed that affective startle modulation may be employed to indicate men's preferences for similar mates. And finally we provided the first evidence that men's mating preferences for similar mates are modulated by stress, i.e. that acute stress leads to a higher sexual approach motivation to dissimilar mates. However, some important questions remain unclear and should be investigated in future studies.

In our studies we solely investigated men's preferences for similar mates, because it is known that men respond more strongly to visual sexual stimuli than women (Rupp & Wallen, 2008). One aim of this work was the development of a new methodology to measure mating preferences for similar mates. The affective startle modulation seemed to be an appropriate paradigm, because it is a very basic measure of the activity of neurobiological circuits involved in approach motivation and has several advantages compared to self-report measures. To develop this new methodology we had to use a sample of which we could be sure that it reacts to the erotic nudes with startle inhibition that is heterosexual men. This is a limitation of our study, not only because we cannot generalize our findings to both sexes, but also because females tend to be the more choosy gender. Poor mating decisions may have less impact on men than they do on women, since men have a potentially faster rate of reproduction and less costs of reproduction. Therefore, they tend to be less choosy in their mate choices (Geary, Vigil, & Byrd-Craven, 2004). Thus, future studies are needed to develop a methodology to experimentally investigate mating preferences in females and to examine the effects of stress on female mating preferences.

One might also question whether affective startle modulation is the right method to investigate mating preferences. affective startle modulation indicates the activity of neurobiological circuits involved in approach motivation. One might argue that affective startle modulation is not a true measure of mating preferences, because it solely measures approach motivation to the erotic stimuli. However, studies on mating preferences in animals

incorporate a similar measure. They use the visible approach motivation (time spent near the cage of the potential mate) as an indicator of mating preferences (Bateson, 1983). Other animal-paradigms use a more direct measure of mating preferences: direct choice between different mates or number of copulations with different mates (Hingle et al., 2001; Lopez, 1999). Of course such a measure is not realizable in humans. However, one possible approach would be to use a penile/vaginal photoplethysmograph to measure changes in blood flow in the penis/vagina in order to gather a more direct measure of the sexual arousal to similar vs. dissimilar mates.

Another point which has to be addressed is the question as to which degree of similarity represents the optimal outbreeding balance. In animals a preference for first cousins has been shown (Bateson, 1982). In our studies we used 50% facial similarity between the participant and the erotic female nudes. On the first sight this resembles the degree of sibling similarity. However, we only manipulated facial similarity and no other potential mediators of similarity and we did find the expected preference for similar mates in our studies. For these reasons, it is feasible to argue that we struck the right level of similarity. Nevertheless, future studies should incorporate different levels of facial similarity in order to find the preferred degree of facial similarity between spouses.

Another limitation of our approach may be the procedure we used to create similarity. In our studies we used a morphing procedure to create facial similarity between our participants and the erotic female nudes. However, besides similarity in facial cues other potential similarity cues like hair color, eye color and body stature, but also non-visible aspects like body odor may play a role in mating preferences for similar mates. In our studies we only manipulated one of many possible cues that people might use to detect similarity. Future studies should manipulate more aspects of similarity, not only to make the similarity more ecologically valid, but also in order to investigate which aspects of similarity play the largest role in the preference for similar mates.

This work was performed to shed light on the impact that stress may have on our mating preferences. Stress is a common phenomenon in modern societies and various research has focused on the impact that stress has on our emotions and cognitions. However, up to date the impact that stress may have on our mating preferences has been neglected. Mate choice is a central aspect of human life as it may have an impact on the well-being and health of ourselves and possible offspring. Despite cultural influences on mating preferences,

evolutionary mechanisms for mate choice have been evolved. Since chronic stress is widespread in modern societies, it is necessary to understand how stress might influence these long evolved mating preferences. Thus, this work can only be a starting point for a new field of research investigating the effects that acute and chronic stress may have on evolutionary adaptive mating preferences.

Chapter II: Startle Modulation within the category of erotic stimuli

Direct gaze of photographs of female nudes influences startle in men

Co-Authors: André Schulz, Frauke Nees, Terry D. Blumenthal & Hartmut Schächinger.

2.0 Abstract

Foreground presentation of photographs of opposite sex nudes lowers startle elicited by sudden acoustic stimuli. However, the impact of gaze direction of the presented nudes on this startle modulation has not been investigated. Theoretically, direct gaze of photographs of female nudes could either lead to a larger inhibition of the startle reaction due to a summing valence and arousal effect of direct eye contact, or lead to a smaller inhibition due to an attention capturing effect of the eyes. Two subsets of erotic photographs of female nudes (women looking directly at the observer vs. gazing away) and standard IAPS neutral pictures were viewed by 26 male volunteers, while startle eye blink responses to binaural bursts of white noise (50 ms, 105 dB) were recorded by EMG. Erotic pictures reduced startle eyeblink magnitude as compared to neutral pictures. Furthermore, erotic stimuli without direct gaze at the observer showed a greater startle eyeblink inhibition than erotic stimuli with direct gaze at the observer. Our data suggest that direct gaze of opposite sex nudes may direct attention to the face, thereby reducing the appetitive impact of an attractive body.

Keywords: Affective startle modulation, erotic stimuli, gaze contact

2.1 Introduction

The vast majority of men perceive attractive female faces and erotica as highly pleasant stimuli. Both elicit positive emotional reactions (Bradley, Codispoti, Sabatinelli, & Lang, 2001; Hietanen, Leppänen, Peltola, Linna-Aho, & Ruuhiala, 2008) and are experienced as rewarding (Aharon et al., 2001; Sabatinelli, Bradley, Lang, Costa, & Versace, 2007). An important modulatory effect on the perceived pleasantness and the reward value of a face is its gaze direction. Recent research has shown that when a person is seen to move their eyes to directly gaze at the observer, the person is perceived as more likeable and more attractive than when they are seen to disengage eye contact (Mason et al., 2005). Functional imaging studies support these behavioral data. Studies have shown that observing direct gaze in contrast to averted gaze activates the neural dopamine systems which are involved in the processing of reward (Aharon et al., 2001; Kampe et al., 2001). Importantly, this effect is modulated by

attractiveness. Direct gaze of an attractive face of the opposite sex is experienced as more rewarding than direct gaze of an unattractive face (Kampe et al., 2001). Therefore, it seems reasonable to assume that attractive photographs of female nudes with direct gaze at the observer would be perceived as even more pleasant and rewarding than attractive photographs of female nudes with averted gaze.

However seeing a face with direct gaze also captures the observer's attention. Evidence from functional imaging studies show that faces with direct gaze lead to enhanced activity in the fusiform area, compared to faces with averted gaze (George, Driver, & Dolan, 2001). In visual search paradigms eyes directly looking at the observer are found more efficiently than eyes gazing away (von Grunau & Anston, 1995). Furthermore, detection of peripherally presented targets is delayed when a central face stimulus is gazing ahead compared to when its gaze is directed away or the eyes are closed (Senju & Hasegawa, 2005). Considering this empirical evidence, direct gaze seems to capture attention and delay disengagement from the face stimulus (Frischen, Bayliss, & Tipper, 2007).

Therefore, it also seems reasonable to assume that the direct gaze of a photograph of a female nude may reduce the perceived pleasantness via a focussed attention on the face, which may reduce the impact of the attractive body.

In this study we tested two hypotheses, whether direct gaze influences the perceived pleasantness of photographs of female nudes by reducing or enhancing this pleasantness. We used the affective startle modulation paradigm, which is a well validated and widely used method for assessing affective valence in the laboratory, to evaluate pleasantness. Numerous studies have shown that the startle reflex is facilitated during aversive motivational states induced by affective picture presentation and inhibited during appetitive states (for a review see Bradley et al., 1999). This affective startle modulation has been shown to generalize to a variety of foreground stimuli other than pictures that modify the emotional state of the participants (Bradley et al., 1999), and eliciting the startle response during foreground presentation of different stimuli serves as a validated measure of the emotional valence of the presented stimuli. Therefore, affective startle modulation appears to be an appropriate measure to indicate differences in the affective valence of attractive photographs of female nudes with direct gaze at the observer compared to attractive photographs of female nudes gazing away from the observer.

The purpose of the present study was to test whether direct gaze has a facilitating or inhibiting effect on perceived pleasantness of erotic stimuli. Two subsets of erotic pictures (direct gaze vs. gazing away) and neutral pictures were viewed by male volunteers while

startle eyeblink responses to acoustic stimuli were recorded. We predicted that the startle response during presentation of erotic pictures would be modulated by the gaze direction of the erotica, indicating different affective valences of the two erotic picture categories.

2.2 Method

2.2.1 Participants

Participants were 30 male heterosexual students (mean age: 24.54, SD: 3.32) with normal or corrected to normal vision and no history of hearing problems. All participants received course credit and provided written informed consent. The study procedures have been approved by the local ethics committee and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2.2 Materials and Design

Experimental material consisted of 36 pictures, some of which were selected from the *International Affective Picture System* (IAPS, Lang et al 1999)¹ and some of which were selected from a picture set that was successfully utilized in other studies (Stark et al., 2005). Pictures were chosen to comprise 3 different picture contents: attractive photographs of female nudes with direct gaze at the observer, attractive photographs of female nudes with gaze directed away from the observer, and neutral pictures (household objects). The two subsets of erotic pictures (direct gaze vs. gaze away) were selected to be similar in terms of rated valence and arousal, based on published rating norms (Lang et al., 1999). Pictures consisted of full body images (at least down to the upper thighs). Photographs of female nudes had a neutral expression in all of the pictures in order to control for unsystematic effects of facial expressions. Neutral pictures were included as a baseline for the effect of affective startle modulation. Pictures were displayed on an LCD computer and picture onset was virtually instantaneous.

2.2.3 Procedure

Participants sat in a comfortable chair approximately 80 cm in front of a computer screen with a visual angle of 25°. Electrodes for electromyographic (EMG) measurement of the left musculus orbicularis oculi were attached below the left eye with an inter-electrode distance of 1.5 cm (center to center). A third electrode taped on the forehead served as reference. Electrode placement and skin preparation followed published guidelines

¹ IAPS picture numbers used in this study were 7000, 7002, 7004, 7006, 7009, 7010, 7020, 7025, 7035, 7080, 7090, 7150, 4001, 4002, 4003, 4005, 4180, 4210, 4232, 4235, 4240, 4290, 4300, 4302, 4310

(Blumenthal et al., 2005). Participants were instructed via computer screen that a series of pictures would be displayed and that each picture should be viewed for its entire duration. Participants were also asked to relax, to neither move nor speak, and to avoid long periods of eye closure. Finally, they were told that brief noises would be delivered via headphones. Six startle probes presented before the experimental session served as habituation trials. After habituation, pictures were displayed on the computer screen in a randomized order for each participant. Each picture was shown for 4 s and an acoustic startle probe was presented between 2.5 and 3.5 s after picture onset in 10 (of 12) pictures per category, for a total of 36 pictures trials. A black screen was shown for 4 s in every Inter-Picture-Interval. The acoustic startle stimulus consisted of a binaurally presented burst of white noise (105 dB, 50 ms, instantaneous rise time).

After completing the startle paradigm a sub-sample of the participants ($n = 15$) were asked to evaluate all pictures based on perceived valence and arousal using Self-Assessment-Manekin ratings ranging from 1 to 9 (1 indicates extremely negative, 5 neutral, and 9 extremely positive) (Bradley & Lang, 1994). After completing the experimental session the subjects were debriefed and thanked for their participation.

2.2.4 Physiological recordings and data analysis

The startle response was assessed as peak EMG activity of the left orbicularis oculi, and was recorded with an EMG 100C and BIOPAC MP 150 system at a sampling rate of 1000 Hz, with a notch filter of 50 Hz and a band pass filter of 28 to 500 Hz. The raw signal was rectified and integrated online with a time constant of 10 ms.

A semi-automated PC program was used to analyze EMG data. The algorithm identified response peaks in the time interval of 20-150 ms after stimulus onset and baseline was set to 50 ms prior to stimulus onset. EMG data of all participants was manually confirmed with respect to non-response (no visible startle response) and/or artifacts (i.e. voluntary or spontaneous eyeblinks coinciding with the startle stimulus, trials with excessive background noise, multiple peaks). Four participants had to be excluded for these reasons.

The startle response was defined as the difference between a stable baseline (50 ms before stimulus onset) and the maximum magnitude of the startle reflex 20-150 ms after startle stimulus onset. If responses were not visible at the typical response latency of a particular subject response magnitude was set to zero. Zero response magnitude data were included in the averaging procedure, with startle response magnitude as the output measure. Raw data were T-scored using all blinks of each subject as the standard distribution in order

to minimize between-subject variability in the absolute size of the startle response (Blumenthal, Elden, & Flaten, 2004).

A repeated measure analysis of variance (critical α level = .05) was used to analyze the effect of picture content on startle magnitude. Furthermore, a multivariate analyses of variance (critical α level = .05) with picture content as the within subject factor and valence and arousal ratings as dependent variables was conducted. We applied the Greenhouse-Geisser-adjustment whenever necessary, indicated in the corrected degrees of freedom. Effect sizes are reported as partial eta-squared values.

2.3 Results

2.3.1 *Blink magnitude*

As expected, startle response magnitude was affected by picture content, ($F(2, 50) = 11.32$; $p < .001$, $\eta^2 = .312$) (see Figure 1). Startle probes elicited larger blink responses during foreground presentation of neutral pictures compared to erotic pictures with direct gaze at the observer ($F(1, 25) = 6.41$, $p < .018$, $\eta^2 = .204$) and compared to erotic pictures with gaze directed away from the observer ($F(1, 25) = 22.21$, $p < .001$, $\eta^2 = .470$), showing the expected startle inhibition for appetitive pictures. Also, startle responses during foreground presentation of the two erotic photograph categories differed significantly from each other. Foreground presentation of erotic pictures with the gaze directed away from the observer led to a larger inhibition of the startle reflex compared to erotic pictures with direct gaze at the observer ($F(1, 25) = 4.93$; $p = .036$, $\eta^2 = .165$).

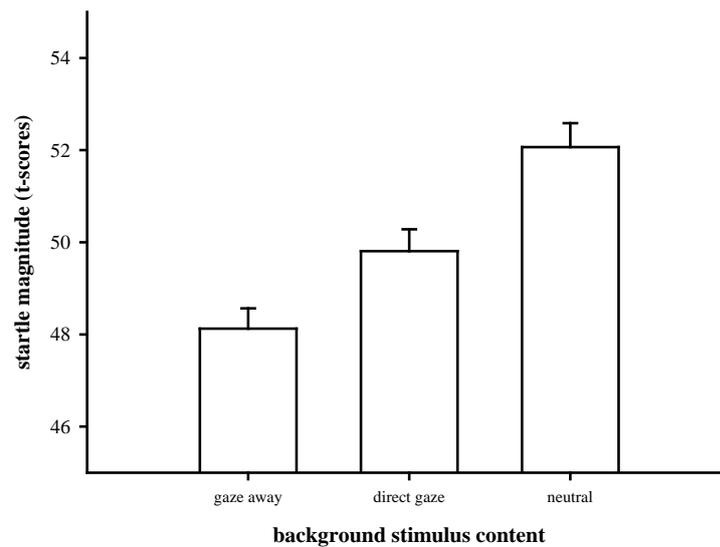


Figure 1 Blink magnitude to startle stimuli during foreground presentation of three different picture contents: (a) photographs of female nudes gazing away from the observer, (b) photographs of female nudes with direct gaze at the observer and (c) neutral pictures. Data are reported as T-scores. Error bars indicate one standard error.

2.3.2 Self-report valence and arousal ratings

Analysis of picture valence ratings revealed a main effect of content ($F(2,26) = 75.53$, $p < .001$, $\eta^2 = .85$). Neutral pictures ($M = 4.61$ $SD = .38$) were rated as less pleasant than both subsets of erotic pictures ($p < .001$). However, there was no difference in valence ratings between the two erotic categories ($p = .45$). Photographs of female nudes with both direct gaze ($M = 7.15$ $SD = .91$) and gaze directed away ($M = 7.43$ $SD = .96$) were rated as highly pleasant. Analysis of arousal ratings revealed a main effect in the same direction ($F(2,26) = 151.33$, $p < .001$, $\eta^2 = .91$). Both erotic subsets were rated as more arousing than neutral pictures ($p < .001$), but there was no significant difference between the two erotic subsets ($p = .35$).

2.4 Discussion

The purpose of the present study was to investigate whether direct gaze has an influence on the perceived pleasantness of erotic pictures. We predicted that direct gaze should either lead to reduced pleasantness due to the attention capturing effect of direct gaze or lead to enhanced pleasantness due to the summing valence and reward effect of direct gaze and attractive body. Although self-reported ratings of the pictures were not sensitive to the direction of gaze, startle response magnitude was larger during foreground presentation of photographs of female nudes with direct gaze compared to photographs of female nudes with averted gaze. This indicates that direct gaze reduced the valence of an attractive nude, even

when those nudes are not subjectively rated as less attractive. This result is in line with the hypothesis that direct gaze directs the attention to the face and, therefore, reduces the impact of the attractive body.

The dissociation between affective startle modulation and subjective ratings may be explained by the different processes underlying startle modulation and evaluation of picture content. While evaluation is a conscious mechanism, which may be confounded with person variables such as social desirability and demand characteristics, startle modulation is independent of conscious intentional control. The attention-capturing effect of direct gaze may disappear if a person is explicitly asked to evaluate the picture. Participants will most likely try to consciously evaluate the whole picture and, therefore, direct their attention to both face and body.

In addition to the attention capturing effect of direct gaze there are other explanations that may account for the different startle response magnitudes observed in this study. First, prolonged eye contact (stare) may also be perceived as an aggressive approach signal. There are many studies showing that animals respond to staring eyes with signs of fear and submission (Beausoleil, Stafford, & Mellor, 2006; Schwab & Huber, 2006) and there is also some evidence for this from human studies (for a review see Kleinke, 1986). Emery (2000) explained this effect from an evolutionary point of view: the ability to discriminate between direct and averted gaze may have evolved because direct gaze may signal that a predator is attending. Therefore, one might argue that direct gaze of photographs of female nudes could also reduce the perceived pleasantness via this mechanism. However, eye contact has diverse effects on the judgement of other persons, ranging from liking and attraction to dominance and aggression (for a review see Frischen et al., 2007). The interpretation of gaze contact depends upon the situation in which direct gaze is experienced. Researchers have shown that direct gaze is experienced as an aggressive and dominant signal in situations with aggression and anger (Ellsworth & Carlsmith, 1973) and during defence of personal space (Hughes & Goldmann, 1978). It is unlikely that the erotic context depicting female nudes with high valence and arousal ratings in the present study is comparable to either of the situations described above.

A further possible limitation of the present study is that it did not examine the role of facial expression in perceived pleasantness. We intended to control for facial expression by using neutral expressions in both erotic picture sets. However recent research has shown that there is an interaction between facial expression and gaze direction. Jones (2006) found that faces looking at the observer are perceived to be more attractive when smiling than when

holding a neutral expression, while faces gazing away from the observer are less attractive when smiling than when holding a neutral expression. Thus, our intention to control for the effects of facial expression by keeping it constant might have been inappropriate, because there are differences in perceived pleasantness of neutral faces depending on their gaze direction that may account for the differences in affective valence.

Another limitation of the present study is the fact that the direct and indirect gaze pictures varied according to gaze, but also were pictures of different people, rather than pictures of the same person looking at or away from the participant. The problem with using pictures of the same person with different gaze directions is that the second time the participant sees the person in a picture, their responses may be affected by familiarity rather than just gaze direction. This could be evaluated by testing for interactions between gaze direction and order of presentation effects, and a subsequent study should evaluate this question. The present study did not do so, for the sake of testing the gaze direction question in its simplest form in this first startle study to look at this issue. We also decided to test this question using pictures that have been used in other startle modulation studies (Bradley et al., 1999; Stark et al., 2005) to facilitate comparisons with previous research.

Finally, replicating this study with the addition of a measure of eye tracking would be an interesting next step. This would allow for a direct test of the hypothesis that direction of gaze modifies the extent to which an attractive nude is viewed.

A study which controls for these confounding factors will shed further light on the mechanisms underlying the impact of gaze direction on startle modulation. Such a study should evaluate the contribution, if any, of variations in the facial expression of erotic females. In order to minimize the possibility that eye contact may be perceived as an aggressive approach signal it may be reasonable to use short film clips instead of pictures in which gaze direction is manipulated, and thereby use gaze shifts towards or away from the observer. Gaze shifts towards a person have also been associated with attraction (Mason et al., 2005) and the movement of the eyes may prevent the gaze from being perceived as a stare. Furthermore such a study should include other physiological measures like skin conductance and heart rate to allow a multidimensional assessment of emotional engagement.

Despite these legitimate criticisms, this study is the first, to our knowledge, to show that gaze direction influences the appetitive valence of erotic nudes. Thus, our data serve as further support of the impact of gaze direction on social perception and emotion.

Chapter III: Startle Modulation as a measure of mating preferences in humans

Do humans prefer similar or dissimilar mates? Facial self-resemblance influences physiological reactions but not subjective ratings to erotic stimuli

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3.0 Abstract

Cues of kinship are predicted to increase prosocial behavior due to the benefits of inclusive fitness, but to decrease sexual approach motivation due to the potential costs of inbreeding. Previous studies have shown that facial resemblance, a putative cue of kinship, increases prosocial behavior. However, the effects of facial resemblance on mating preferences are equivocal, with some studies finding that facial resemblance decreases sexual attractiveness ratings, while other studies show that individuals choose mates partly on the basis of similarity. To further investigate this question, a psychophysiological measure of affective processing, the startle response, was used in this study, assuming that differences in sexual approach motivation to erotic pictures will modulate startle. Male volunteers (n = 30) viewed 30 pictures of erotic female nudes while startle eyeblink responses were elicited by acoustic noise probes. The female nude pictures were digitally altered so that the face either resembled the male participant, another participant, or were not altered. Non-nude neutral pictures were also included. Importantly, the digital alteration was undetected by the participants. Erotic pictures were rated as being pleasant, and clearly reduced startle eyeblink magnitude as compared to neutral pictures. Participants showed greater startle inhibition to self-resembling than to other-resembling or non-manipulated female nude pictures, but subjective pleasure and arousal ratings did not differ between the three erotic picture categories. Our data suggest that visual facial resemblance of opposite-sex nudes increases sexual approach motivation in men, and that this effect is not due to their conscious evaluation of the erotic stimuli.

Keywords: Facial self-resemblance, kin recognition, inbreeding avoidance, erotic stimuli, Affective startle modulation

3.1 Introduction

Humans and many other vertebrates are able to recognize their kin. Experimental evidence shows that humans are able to recognize genetic similarity based on shared olfactory and visual cues (Oda, Matsumoto-Oda, & Kurashima, 2006; Wedekind, 2007; Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003). Kin recognition is important, because organisms can increase their fitness by recognizing and responding appropriately to kin. Such responses are said to be context dependent, because the fitness-enhancing response to kin is different in the context of nepotism and mate choice: Cues of kinship are predicted to increase non-sexual prosocial regard owing to the benefits of inclusive fitness (Hamilton, 1964) while decreasing sexual approach motivation owing to the costs of inbreeding (Bateson, 1983; Bittles & Neel, 1994). Indeed, several studies have shown that experimentally induced facial resemblance, a putative cue of kinship, increases prosocial attributions like trusting behavior (DeBruine, 2002), self-reported preference for children (DeBruine, 2004b; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003), and the attractiveness of same-sex faces (DeBruine, 2004).

While there is considerable evidence for increased prosocial attributions for self-resembling faces, the evidence for the effects of kinship cues on mating preferences is less clear. Experimental manipulations of facial resemblance have shown that self-resembling opposite-sex faces (putative mating partners) are not rated to be more attractive than control faces (DeBruine, 2004). Extending these findings, DeBruine (2005) showed that self-resemblance increased attributions of trustworthiness to opposite-sex face images, but had no effect on attractiveness in the context of a long-term relationship, and decreased attractiveness in the context of a short-term (sexual) relationship. These findings support the notion that cues of kinship (facial similarity) decrease sexual approach motivation.

On the other hand, observational studies have shown that human romantic partners tend to resemble each other in many traits, including facial characteristics (Berezkei et al., 2002; Berezkei et al., 2004). Imprinting-like mechanisms have been suggested to account for this effect (Berezkei et al., 2002; Daly, 1989): Cross-fostering studies with animals and adoption studies with humans have revealed that animals and humans prefer sexual partners that are similar to the opposite sex-parent that reared them (Immelmann, Pröve, Lassek, & Bischof, 1991; Oetting, Pröve, & Bischof, 1995). This is believed to be due to a fixation to a set of family characteristics that later shape mate preferences during adulthood.

Thus, there is a lack of consensus as to whether facial similarity decreases the sexual approach motivation to potential mating partners or increases it. One problem inherent in the

previously described studies is that their designs are solely based on subjective ratings of faces, which might not be the optimal method for analyzing mating preferences, e.g. sexual approach motivation to potential mates. The validity of subjective ratings as a measure of emotional and motivational status is problematic for several reasons. First, subjective ratings require introspection, which is susceptible to error, reconstruction, and inaccuracy (Nisbett & Wilson, 1977). Second, factors such as demand characteristics and social desirability may play a role in the answer tendencies. Third, there is often a considerable time gap between the affective process itself (for example, during viewing of the picture) and the retrieving of the affective process (since the subjective ratings are usually given after picture viewing) during which the impression of the target can decay or be influenced by new input. Furthermore, the use of face stimuli alone is not optimal for analyzing mating preferences. Studies that focus on aspects of sexual approach motivation and states of sexual arousal typically use erotic pictures or film segments as stimulus material and, in addition to subjective ratings, use physiological measures as dependent variables.

One well validated and widely used physiological method for assessing affective valence in the laboratory is the affective startle modulation paradigm. Numerous studies have shown that the startle reflex (elicited by a brief burst of noise) is facilitated when people view aversive pictures and inhibited when people view pleasant pictures (for a review see Bradley et al., 1999). Viewing of aversive pictures leads to an activation of the defensive system and, therefore, leads to an augmentation of the congruent defensive startle reflex. Viewing of pleasant pictures, on the other hand, engages the appetitive/approach system and leads to an inhibition of the non-congruent defensive startle reflex. Thus, affective startle modulation is not a direct measure of the physiological mechanisms underlying emotion, but rather an indirect measure of the activity of neurobiological structures involved in the processing of approach and withdrawal motivation. The inhibition of the startle reflex while viewing pleasant pictures reflects the activity of neurobiological circuits involved in approach motivation.

Affective startle modulation has been shown to generalize to a variety of foreground stimuli other than pictures that modify the emotional state of the participants (Bradley et al., 1999), and eliciting the startle response during foreground presentation of different stimuli serves as a validated measure of the affective valence of the presented stimuli. In particular, the startle modulation paradigm has been frequently used to analyze sexual approach motivation to erotic pictures and film segments (Koukounas & McCabe, 2001; Koukounas &

Over, 2000; Lass-Hennemann, Schulz, Nees, Blumenthal, & Schachinger, 2009; Prause et al., 2008).

The utility of startle over self-report in studying sexual approach motivation is based on the fact that the affective startle modulation paradigm is not hampered by the same problems as subjective ratings are. Affective startle modulation is largely independent of instructions and does not require an introspective focus. It is not a conscious or controlled process and there is a very short time gap between the affective process itself and the measurement of the affective process. Therefore, affective startle modulation appears to be an appropriate measure to evaluate differences in the sexual attractiveness of, and sexual approach motivation to, photographs of erotic female nudes who resemble the participant compared to photographs of erotic female nudes who do not resemble the participant.

In the present study, we investigated whether the extent to which computer manipulated pictures of erotic female nudes that resembled the participant influenced the perceived attractiveness (via subjective ratings) and the sexual approach motivation (via affective startle modulation) of the participant. Participants viewed pictures of erotic female nudes whose facial characteristics were either computer-modified to resemble themselves, or made to resemble another person, or were not manipulated, as well as viewing neutral pictures. We predicted that the startle response in the presence of erotic pictures would be influenced by facial self-resemblance, indicating differences in the activity of neurobiological structures involved in approach motivation.

3.2 Methods

3.2.1 Participants

Participants were 40 male heterosexual students at the University of Trier, Germany, who responded to notices offering 20 € for taking part in two different experiments. Participation was limited to heterosexual Caucasian students without beards, piercings, or tattoos in the facial region. Furthermore, only participants with normal or corrected to normal vision and no history of hearing problems were included in the study. Exclusion criteria were determined by a telephone screening interview. All participants signed a written informed consent and were given a small financial compensation (5 € for the photograph acquisition, 15 € for the actual experiment) for taking part in the experiment. Study procedures were approved by the local ethics committee.

3.2.2 Materials and Design

Experimental material consisted of 40 pictures, 30 of which showed erotic female nudes with a completely visible face (i.e. no hair covering parts of the face), a direct gaze at the observer, and a neutral facial expression. The other 10 pictures were neutral pictures selected from the International Affective Picture System² (household objects) (Lang et al., 1999).

We used computer imaging techniques to manipulate facial resemblance between pictures of the face of each participant and the faces of the pictures of the erotic female nudes. The pictures of the erotic female nudes formed the basis for the morphing procedure, in which the face of the participant was morphed into the face of the erotic female nude (see Figure 2). Templates were created that specified the contours and certain landmarks on each face. The morphing routine itself comprises two processes: a shape-morph averages the distance between the features of both faces that were specified in the template and a color morph averages the colors of each pixel. These processes result in two different output images, and the color morph was used as a layer on top of the shape morph. To ensure that the resulting female nude pictures still looked attractive and feminine, transparency was added to the color morph layer to a 30% degree. That means that the morphed picture shared 50% of the shape of the participants' face, but only 30% of the color information. By doing this, a composite face was created which was in favour of the women's features, i.e. the face was still primarily female and fitted to the body of the erotic female nude, even though it had a subtle resemblance to the participant. For further details on the underlying technology see Tiddeman, Perrett and Burt (2001). No participants reported detecting the nature of the experiment, suggesting that the morphing did not result in conscious recognition of their own face by any participant.

The 30 pictures of the erotic female nudes were randomly assigned to three subsets that consisted of 10 erotic female nudes each. For each participant, one of the three subsets was morphed with his own face and formed the “self-resembling” erotic female nude picture set, so that ten pictures had a subtle resemblance to the participant. Ten other photos of erotic female nudes were morphed with the face of a different participant and formed the “other-resembling” erotic female nude picture set. The remaining ten female nude pictures remained in their original state and were used as the “not manipulated” erotic female nude picture set. For the assignment of the picture sets to the participants we employed a cross-over design:

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Pairs of two participants were presented with the same version of the picture sets, so that the picture set that formed the self-resembling erotic female nude picture set for participant A formed the other-resembling erotic female nude picture set for participant B and vice versa. That is, every morphed picture set functioned once as the self-resembling erotic female nude picture set and once as the other-resembling erotic female nude picture set.

We included the not manipulated erotic female nude pictures as a control condition to test whether morphed erotic female nude pictures led to a comparable startle inhibition as not manipulated erotic female nude pictures. Furthermore, we included neutral pictures as a control to illustrate the effect of affective startle modulation. Pictures were displayed on an LCD computer and picture onset was virtually instantaneous.

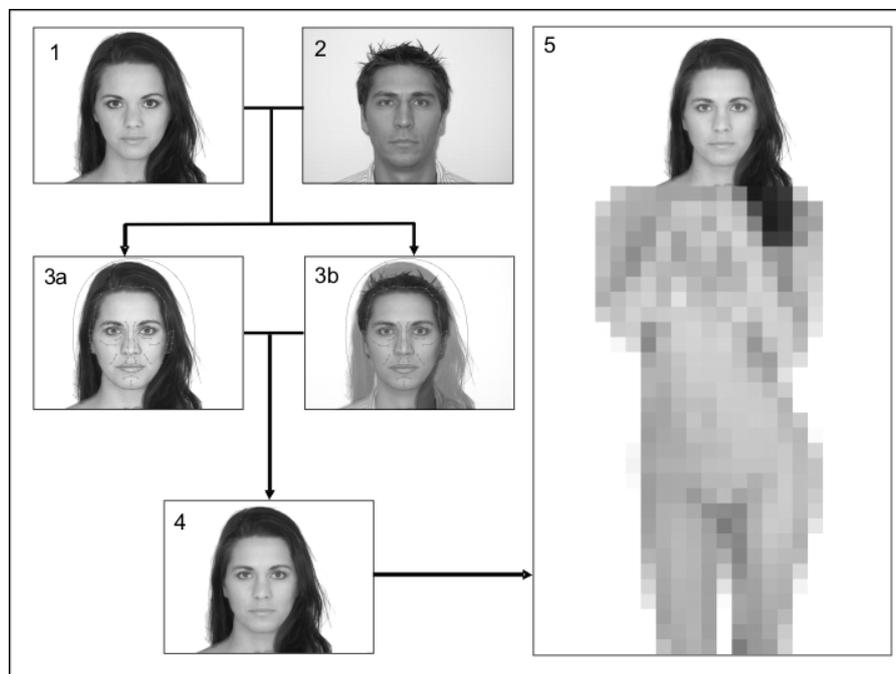


Figure 2 Image editing procedure: The nude woman's detailed face (1) was morphed with the portrait picture of the participant (2). The morphing software produces two output images, a shape-only morph (3a) and a combined shape-color morph (3b). In a second step the shape-color morph is used as a semi-transparent layer on top of the shape-only morph. All artefacts of the morphing procedure are eliminated. The resulting image (4) was photo-mounted on the woman's body in a last step (5). The resulting image was used as a stimulus (the image was not masked in the experiment).

3.2.3 Cover Story

To be able to morph the participants faces into the faces of the erotic female nudes, we had to gather a standardized photograph of each participant's face. For the nature of the experiment it was necessary that participants did not know about the true purpose of the experiment. To assure this, we used the following cover story: Participants were told that for a payment of 20 € they could participate in two unrelated studies in our lab: The experimenter

told participants that the first study was to establish a new emotional face data base that would be used for psychophysiological research in our lab. The second study would analyze emotional and physiological reactions to erotic pictures. Furthermore, the experimenter explained that both studies were run together for economic reasons.

3.2.4 Procedure

Photograph Acquisition. If the participant met the criteria in the telephone interview he was invited to our laboratory to take the photographs of his face. After arriving at the laboratory the experimenter asked the participant to sign an informed consent in which the participant approved the scientific usage of the photographs of his face.

The experimenter instructed the participant to look into the camera with a neutral facial expression. Then the experimenter took the portrait photographs with a digital camera from a distance of 80 cm in a fully lit room.

Startle Pretest. Directly after the photographs were taken, participants underwent a brief startle paradigm. The experimenter explained to the participants that the reaction to startle probes was the main dependent measure in the second study and that some people do not respond to these startle probes. Furthermore, he explained that only those people who showed a reliable startle reaction to the stimuli would be able to participate in the second study. The experimenter attached electrodes for electromyographic (EMG) measurement of the left musculus orbicularis oculi below the left eye of the participant with an inter-electrode distance of 1.5 cm (center to center). A third electrode taped on the forehead served as a reference. Electrode placement and skin preparation followed published guidelines (Blumenthal et al., 2005). Ten startle probes (105 dB, 50 ms, instantaneous rise time) were presented to each participant and the EMG response to the startle probes were recorded.

After finishing the startle pretest, an appointment for the second part of the study was made with the participants. 10 participants showed less than 70% measurable startle responses and were therefore not invited to the second part of the study. Every participant received 5 Euros for participation and left the laboratory.

Affective Startle Modulation Paradigm. Participants arrived for the second appointment about one week after the pictures were taken. During this week participants' pictures were morphed with one subset of the erotic female nude pictures.

When participants arrived at our laboratory, the experimenter asked them to sit in a comfortable chair approximately 80 cm in front of a computer screen with a visual angle of 25°. The experimenter attached electrodes for electromyographic (EMG) measurement (as described in Startle Pretest). Participants were instructed via computer screen that a series of

pictures would be displayed and that each picture should be viewed for its entire duration. Participants were also asked to relax, to neither move nor speak, and to avoid long periods of eye closure. Finally, they were told that brief noises would be delivered via headphones. Six startle probes presented before the experimental session served as habituation trials. Then the previously described pictures (self-resembling erotic female nudes, other resembling erotic female nudes, not manipulated erotic female nudes, and neutral pictures) were displayed on the computer screen in a randomized order for each participant. Each picture was shown for 5 s and an acoustic startle probe was presented between 2.5 and 3.5 s after picture onset in 8 (of 10) pictures per category, for a total of 40 pictures trials. A black screen was shown for 4 s in every Inter-Picture-Interval. The acoustic startle stimulus consisted of a binaurally presented burst of white noise (105 dB, 50 ms, instantaneous rise time).

Pleasure and Arousal Ratings. After completing the affective startle modulation paradigm the participants were asked to evaluate each picture for perceived pleasure and arousal using Self-Assessment-Manikin ratings ranging from 1 to 9 (1 indicates very low pleasure and arousal, and 9 very high pleasure and arousal) (Bradley & Lang, 1994).

After completing the affective startle modulation paradigm and the pleasure and arousal ratings participants filled out a small questionnaire about their opinion about the purpose of the experiment: They were asked if they found anything to be special about the pictures of the erotic female nudes. None of the participants correctly detected that the pictures were digitally altered. After completing the questionnaire the participants received 15 Euros and were thanked for their participation.

Debriefing. We did not inform participants about the true purpose of the experiment until we finished the data acquisition of all participants, because we wanted to avoid participants speaking about the experiment with other potential participants. After we finished data acquisition we contacted each participant and explained the purpose of the experiment. Participants were encouraged to contact the experimenter at any time if they had further questions.

3.2.5 Physiological recordings and data analysis

The startle response was assessed as peak EMG activity of the left orbicularis oculi, and was recorded with a BIOPAC MP 150 system and an EMG 100C amplifier at a sampling rate of 1000 Hz, with a notch filter of 50 Hz and a band pass filter of 28 to 500 Hz. The raw signal was rectified and integrated online with a time constant of 10 ms.

A semi-automated PC program was used to analyze EMG data. The algorithm identified response peaks in the time interval of 20-150 ms after stimulus onset and baseline

was set to 50 ms prior to stimulus onset. EMG data of all participants was manually confirmed with respect to non-response (no visible startle response) and/or artifacts (i.e. voluntary or spontaneous eyeblinks coinciding with the startle stimulus, trials with excessive background noise, multiple peaks).

The startle response was defined as the difference between a stable baseline (50 ms before stimulus onset) and the maximum magnitude of the EMG 20-150 ms after startle stimulus onset. If responses were not visible at the typical response latency of a particular participant response magnitude was set to zero. Zero response magnitude data were included in the averaging procedure, with startle response magnitude as the output measure. Raw data were T-scored using all blinks of each participant as the standard distribution in order to minimize between-participant variability in the absolute size of the startle response (Blumenthal et al., 2004).

A repeated measure analysis of variance (critical α level = .05) was used to analyze the effect of picture content (4 levels: self-resembling erotic female nudes, other-resembling erotic female nudes, not manipulated erotic female nudes, and neutral) on startle magnitude. Furthermore, a multivariate analyses of variance (critical α level = .05) with picture content as the within participant factor and pleasure and arousal ratings as dependent variables was conducted. Effect sizes are reported as partial eta-squared values.

3.3 Results

3.3.1 Startle Magnitude

To analyze the difference in sexual approach motivation to the different erotic picture categories, we had to first show that affective startle modulation actually took place. As expected, startle response magnitude was affected by picture content ($F(3, 87) = 15.989, p < .001, \eta^2 = .355$). Startle probes elicited larger blink responses during foreground presentation of neutral pictures compared to self-resembling erotic female nudes ($p < .001$), other-resembling erotic female nudes ($p < .01$), and not manipulated erotic female nudes ($p < .01$), showing the expected startle inhibition for appetitive pictures.

The experimental findings of central importance tested the hypothesis that the startle activity was different in the presence of pictures of self-resembling erotic female nudes compared to other-resembling erotic female nudes and not manipulated erotic female nudes. As expected, startle responses during foreground presentation of the three erotic photograph categories differed significantly from each other. Foreground presentation of pictures of self-resembling erotic female nudes led to a larger inhibition of the startle reflex compared to

other-resembling erotic female nudes ($p < .05$) and not manipulated erotic female nudes ($p < .05$), indicating a higher sexual approach motivation to these pictures (Figure 3).

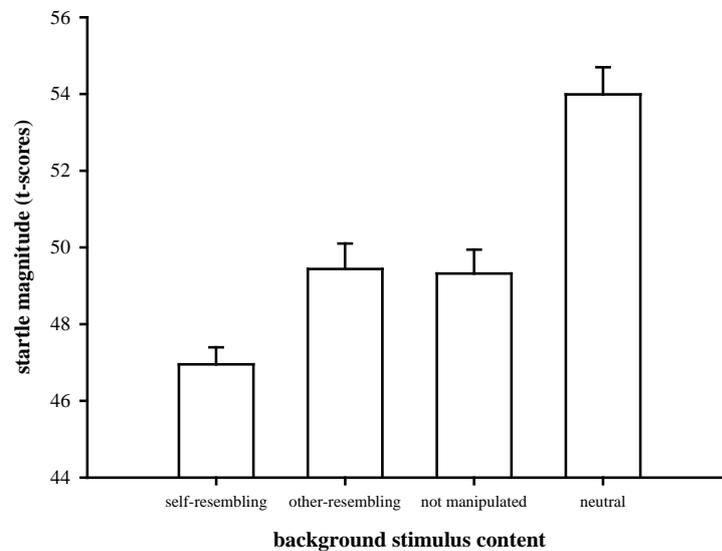


Figure 3 Blink magnitude to startle stimuli during foreground presentation of four different picture contents (a) photographs of erotic female nudes with manipulated facial similarity to the participant (self-resembling), (b) photographs of erotic female nudes with manipulated facial similarity to another participant (other-resembling), (c) photographs of erotic female nudes whose facial characteristics were not manipulated (not manipulated), and (d) neutral pictures. Data are reported as T-Scores. Error bars indicate one standard error.

3.3.2 Self-report Pleasure and Arousal ratings

Analysis of picture valence ratings revealed a main effect of content ($F(3,87) = 47.02$, $p < .001$, $\eta^2 = .62$). All three erotic picture categories were rated to be more pleasant than the neutral pictures ($p < .001$). However, there was no difference in valence ratings between the three erotic categories. Ratings of pictures of self-resembling erotic female nudes did not differ significantly from that for pictures of other resembling erotic female nudes ($p = 1.00$) or not manipulated erotic female nudes ($p = 1.00$). Analysis of arousal ratings revealed a main effect in the same direction ($F(3,87) = 96.203$, $p < .001$, $\eta^2 = .77$). All three erotic subsets were rated as more arousing than neutral pictures ($p < .001$), but there was no significant difference in arousal ratings between self-resembling pictures of erotic female nudes and other-resembling pictures of erotic female nudes ($p = 1.00$), and there was also no significant difference between ratings for self-resembling erotic pictures and not manipulated erotic pictures ($p = .298$). These findings indicate that participants experienced all three erotic categories to be equally pleasant and arousing. Means and standard deviations are presented in Table 1.

Table 1 Mean reports of rated pleasure and arousal when viewing self-resembling erotic pictures, other-resembling erotic pictures, not manipulated erotic pictures, and neutral pictures.

Dependent measure	Self-resembling erotica		Other-resembling erotica		Not manipulated erotica		Neutral pictures	
	M	SD	M	SD	M	SD	M	SD
Pleasure ratings (1-9)	6.57 ± .73 ^a		6.46 ± .65 ^a		6.75 ± .93 ^a		4.85 ± .72	
Arousal ratings (1-9)	5.76 ± 1.29 ^a		5.70 ± 1.25 ^a		6.03 ± 1.43 ^a		2.64 ± 1.31	

Note. ^aDifference from neutral pictures is significant

3.4 Discussion

The purpose of the present study was to investigate whether facial self-resemblance has an influence on attractiveness ratings of pictures of erotic female nudes and sexual approach motivation to these pictures. In addition to subjective ratings, we used affective startle modulation to investigate the activity of neurobiological circuits involved in approach motivation. We predicted that facial self-resemblance should influence affective startle modulation to, and subjective ratings of, pictures of erotic female nudes. We showed that startle response magnitude was smaller during foreground presentation of photographs of self-resembling female nudes compared to other-resembling female nudes and not-manipulated female nudes. This indicates that facial self-resemblance increases the activity of neurobiological structures involved in approach motivation, suggesting that similar mates lead to a larger sexual approach motivation and, thus, to a larger sexual attractiveness than dissimilar mates. Although our results are based on a pre-attentive measure of approach motivation, the startle response, these results are in line with the findings that humans tend to prefer similar mates over dissimilar mates.

However, this effect was not found for subjective pleasure and arousal ratings, which did not differ from each other in the three erotic female nude picture categories. Thus, there is a dissociation between our two indicators of sexual attractiveness: Affective startle modulation and subjective ratings. This dissociation has been shown before (Lass-Hennemann et al., 2009; Levenston, Patrick, Bradley, & Lang, 2000) and may be explained by the different processes underlying startle modulation and subjective ratings of picture content. As described above, subjective ratings are a voluntarily controllable measure, one that may be confounded by person variables such as social desirability and demand characteristics. Startle modulation, on the other hand, is not dependent on conscious intentional control. Therefore, affective startle modulation might be a more valid measure of sexual approach motivation, especially in this specific context, since the problem of

controllability of the answers that a participant gives might be even stronger in an erotic context, where factors like shame and embarrassment may play a role.

The dissociation between subjective ratings and affective startle modulation may also be explained by the opponent process theory of emotion (Solomon & Corbit, 1974). According to this theory, emotional and motivational states are modulated by opposing reactions, the a and b processes. The a process is the initial reaction to an emotion-eliciting stimulus (in our case, the pictures of the erotic female nudes). The b process is a lagging compensatory reaction that tends to return the system to equilibrium, thereby modulating the affective experience. The affective valence of the b process is opposite to that of the a process. In our paradigm, affective startle modulation took place during picture viewing, whereas the subjective ratings were assessed at the end of the session, shortly after picture viewing. Therefore, the b process might already have been dominant during picture rating, explaining the absence of a difference in subjective ratings between self-resembling, other-resembling, and not-manipulated pictures.

One important methodological advantage of our study is that we employed a cross-over design, using the same erotic pictures for pairs of two participants, with the other-resembling erotic pictures for the one participant serving as the self-resembling pictures for the other participant. This indicates that the inhibition of startle reactions in the presence of the pictures of self-resembling erotic female nudes was based on the degree of self-resemblance with the participant, and not on some other characteristic of the pictures.

Two different processes could lead to the greater startle inhibition during pictures of self-resembling erotic female nudes compared to the other erotic picture categories. One explanation proposes an additive effect of the similar face and the attractive body. The similar face might be perceived as more attractive than the dissimilar faces and, therefore, enhances the affective valence of the erotic female nude by an additive effect of the similar, more attractive face, and the attractive body. Another explanation proposes that the similar face is more familiar to the participant and does not capture as much attention as the dissimilar faces. This could lead to a shift of attention from the face to the attractive body, leading to an enhanced startle inhibition. A replication of this study with a measure of eye-tracking would be an appropriate next step to test the hypothesis that facial similarity modulates the extent to which the face and attractive body of erotic female nude pictures are viewed. However, it must be remembered that, when we speak of perception, familiarity, and attention in these explanations, the participants did not consciously realize that the self-resembling face actually

included aspects of their own features. That is, the participants were not consciously aware of the manipulation of self-resemblance.

Our results are in line with the findings that human romantic partners tend to resemble each other, indicating a preference for similar mates (Bereczkei et al., 2002; Bereczkei et al., 2004). However, our results are not compatible with the findings of DeBruine (2005), who showed that facial-self-resemblance decreased attractiveness in the context of a short-term relationship and had no effect on attractiveness in the context of a long-term relationship. However, DeBruine's study and our study differ significantly from each other in several ways. For example, DeBruine used a forced-choice paradigm in which participants viewed pairs of facial stimuli, which may have led to an artificially forced attractiveness decision which might not represent a participant's true opinion about the facial stimuli.

Another difference between our design and that of DeBruine is that we used male participants only. We decided to use men because research has shown that men respond more to visual sexual stimuli than females (for a review see Rupp & Wallen, 2008). However, poor mating decisions may have less impact on men than they do on women, since men have a potential faster rate of reproduction and less costs of reproduction, and therefore tend to be less choosy in their mate choices (Geary et al., 2004). Therefore, facial self-resemblance as a potential cue for inbreeding might be more relevant to women than to men, which might be tested by replicating the present study with women as participants. Future studies might also include other physiological measures, such as skin conductance and heart rate, to allow for a more detailed assessment of emotional engagement.

In spite of these limitations, our results are in line with many studies showing that romantic partners tend to resemble each other. The advantage of our study is that it is, to our knowledge, the first experimental manipulation of facial resemblance that yields this result. Furthermore our study is the first to use a sensitive, well-studied measure of sexual attractiveness (startle reactivity) and approach motivation that is not directly under the voluntary control of the participant. Thus, our findings not only serve to further support facial similarity as a modulator of the attractiveness of, and sexual approach motivation to, potential mates, but it also shows that these effects can be found in the modulation of the startle reflex, a response that may represent a very basic measure of sexual approach motivation.

Chapter IV: Effects of Stress on mating preferences in humans

Effects of stress on human mating preferences: Stressed individuals prefer dissimilar mates

Co-Authors: Christian E. Deuter, Linn K. Kuehl, André Schulz, Terry D. Blumenthal & Hartmut Schächinger.

4.0 Abstract

Humans usually prefer mates that resemble themselves. However, mating preferences are also context dependent. Stress has been shown to alter mating preferences in animals, but the effects of stress on human mating preferences are unknown. Here, we investigated whether stress alters men's preference for self-resembling mates. Participants first underwent a cold pressor test or a control procedure. Afterwards participants viewed pictures of erotic female nudes whose facial characteristics were computer-modified to resemble either the participant or another participant, or were not modified, and neutral pictures, while startle eyeblink responses were elicited by noise probes. Erotic pictures were rated as being pleasant, and reduced startle magnitude as compared to neutral pictures. In the control group startle magnitude was smaller during foreground presentation of photographs of self-resembling female nudes compared to other-resembling female nudes and not-manipulated erotic female nudes, indicating a higher sexual approach motivation to self-resembling mates. In the stress group, startle magnitude was larger during foreground presentation of self-resembling female nudes compared to other resembling female nudes and not manipulated female nudes, indicating a higher sexual approach motivation to dissimilar mates. Our findings show that stress affects human mating preferences: While unstressed individuals showed the expected preference for similar mates, stressed individuals seem to prefer dissimilar mates.

Keywords: Mate choice, facial self-resemblance, stress, cold pressor test

4.1 Introduction

Mating is a central aspect of human and animal life, and many studies have investigated how humans and animals choose their mating partners. In humans one of the most frequently investigated topic is the preference for similar vs. dissimilar mates. Studies have shown that human romantic partners tend to resemble each other in many traits, including facial characteristics (Bereczkei et al., 2002; Bereczkei et al., 2004; Griffiths & Kunz, 1973 ; Zajonc et al., 1987). Recently, we also showed a preference for similar mates in an experimental manipulation of facial resemblance (Lass-Hennemann et al., submitted). Overall, experimental evidence indicates a preference for self-resembling mates, even though there is one study that showed a preference for dissimilar mates specifically for short-term relationship (DeBruine, 2005).

However, mating preferences are also context-dependent, and one factor that has repeatedly been found to alter mate choice in animals is stress. Stress is an adaptive response that is typically thought to enhance the probability of survival in the face of threat, but it is becoming apparent that stress is also associated with sexual behavior and mate choice. For example, corticosterone (a hormone released in response to stress) has been shown to reduce male odor preferences in female mice (Kavaliers & Ossenkopp, 2001). Furthermore, research has shown that stress alters the mating preference of stalk-eyed flies , showing less preference for more attractive mates and a willingness to mate with less attractive mates than are non-stressed animals (Hingle et al., 2001; Lopez, 1999). These studies seem to indicate that stressed animals lose their "normal" mating preferences.

However, the effects of stress on human mating preferences have not been investigated yet. From the described animal studies one could expect that humans also simply lose their preference for similar mates under stress. However, life history theory (Stearns, 1992) predicts that the optimal reproductive strategy for individuals in stressful environments is to maximize current reproduction to minimize the chances of lineage extinction. Having short-term relationships instead of long-term relationships is a way of increasing current reproduction and it has been shown that individuals who experience psychosocial stress have more short-term relationships than do individuals without a history of psychosocial stress (Koehler & Chisholm, 2009). As described above, Debruine (2005) found a preference for dissimilar mates in the context of a short-term relationship. Therefore, one might also argue that stress does not only decrease the mating preference for similar mates, but also increases mating preference for dissimilar mates.

To investigate the effects of stress on men's preferences for similar vs. dissimilar mates we used a set of erotic pictures of female nudes that were computer-modified to resemble either the participant or another participant. We employed two independent methods to measure men's sexual attraction to the different erotic picture categories, subjective valence and arousal ratings of the erotic pictures, and affective startle modulation. Affective startle modulation is a well validated and widely used method for assessing affective valence in the laboratory (Bradley et al., 1999). Numerous studies have shown that the startle reflex (elicited by a brief burst of noise) is facilitated when people view aversive pictures and inhibited when people view pleasant (especially erotic) pictures (Bradley, Codispoti, Cuthbert et al., 2001). Viewing of aversive pictures leads to an activation of the defensive system and, therefore, leads to an augmentation of the congruent defensive startle reflex. Viewing of pleasant pictures, on the other hand, engages the appetitive/approach system and leads to an inhibition of the non-congruent defensive startle reflex. Thus, affective startle modulation is not a direct measure of the physiological mechanisms underlying emotion, but rather an indirect measure of the activity of neurobiological structures involved in the processing of approach and withdrawal motivation. The inhibition of the startle reflex while viewing pleasant pictures reflects the activity of neurobiological circuits involved in approach motivation.

Affective startle modulation has been shown to generalize to a variety of foreground stimuli other than pictures that modify the emotional state of the participants (Bradley et al., 1999), and eliciting the startle response during foreground presentation of different stimuli serves as a validated measure of the affective valence of the presented stimuli. In particular, the startle modulation paradigm has been frequently used to analyze sexual approach motivation to erotic pictures and film segments (Koukounas & McCabe, 2001; Koukounas & Over, 2000; Lass-Hennemann et al., submitted; Lass-Hennemann et al., 2009; Prause et al., 2008). Therefore, affective startle modulation appears to be an appropriate measure to evaluate how stress influences the sexual attractiveness of, and sexual approach motivation to, photographs of erotic female nudes. We used the affective startle modulation paradigm in addition to subjective ratings, because in previous studies it has served as a more sensitive measure for approach and withdrawal motivation than subjective ratings (Lass-Hennemann et al., submitted; Lass-Hennemann et al., 2009; Levenston et al., 2000). Subjective ratings are a voluntarily controllable measure, one that may be confounded by person variables such as social desirability and demand characteristics, while the startle response is a pre-attentive measure of approach motivation, that is not easily controllable by the participant.

In our study, participants first underwent a stressful procedure or a non-stressful control procedure. Then participants viewed pictures of erotic female nudes whose facial characteristics were either computer-modified to resemble the participant, or made to resemble another person, or were not manipulated, as well as viewing neutral pictures.

Based on previous research (Lass-Hennemann et al., submitted), we predicted that non-stressed participants would show a preference for similar mates, as indicated by decreased startle magnitude in the presence of pictures of self-resembling erotic female nudes. We predicted that stressed participants would not show the usual preference for similar mates, but instead a preference for dissimilar mates as indicated by an inhibition of startle magnitude in the presence of pictures of other-resembling female nudes and not manipulated female nudes.

4.2 Methods

4.2.1 Participants

Participants were 50 male heterosexual students at the University of Trier, Germany, who responded to notices offering 25 € for taking part in two different experiments. Participation was limited to heterosexual Caucasian students without beards, piercings, or tattoos in the facial region. Furthermore, only participants with normal or corrected to normal vision and no history of hearing problems were included in the study. Participation was also limited to healthy non-smokers with body mass index in the normal range of between 20 and 25 kg/m². Exclusion criteria were determined by a telephone screening interview that the respondent completed before being invited to take part. We also required participants to refrain from physical exercise, alcohol, caffeinated drinks, and meals within 3 hours prior to each of the two experimental sessions. The research was approved by the responsible local ethics committee, and all participants gave their written informed consent.

4.2.2 Materials and Design

Experimental material consisted of 40 pictures, 30 of which showed erotic female nudes with a completely visible face (i.e. no hair covering parts of the face), a direct gaze at the observer, and a neutral facial expression. The other 10 pictures were neutral pictures selected from the International Affective Picture System³ (household objects) (Lang et al., 1999).

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We used computer imaging techniques to manipulate facial resemblance between pictures of the face of each participant and the faces of the pictures of the erotic female nudes. The pictures of the erotic female nudes formed the basis for the morphing procedure, in which the face of the participant was morphed into the face of the erotic female nude (see Figure 4). Templates were created that specified the contours and certain landmarks on each face. The morphing routine itself comprises two processes: a shape-morph averages the distance between the features of both faces that were specified in the template and a color morph averages the colors of each pixel. These processes result in two different output images, and the color morph was used as a layer on top of the shape morph. To ensure that the resulting female nude pictures still looked attractive and feminine, transparency was added to the color morph layer to a 30% degree. That means that the morphed picture shared 50% of the shape of the participants' face, but only 30% of the color information. By doing this, a composite face was created which was in favour of the women's features, i.e. the face was still primarily female and fitted to the body of the erotic female nude, even though it had a subtle resemblance to the participant. For further details on the underlying technology see Tiddeman, Perrett and Burt (2001). No participants reported detecting the nature of the experiment, suggesting that the morphing did not result in conscious recognition of their own face by any participant.

The 30 pictures of the erotic female nudes were randomly assigned to three subsets that consisted of 10 erotic female nudes each. For each participant, one of the three subsets was morphed with his own face and formed the “self-resembling” erotic female nude picture set, so that ten pictures had a subtle resemblance to the participant. Ten other photos of erotic female nudes were morphed with the face of a different participant and formed the “other-resembling” erotic female nude picture set. The remaining ten female nude pictures remained in their original state and were used as the “not manipulated” erotic female nude picture set. For the assignment of the picture sets to the participants we employed a cross-over design: Pairs of two participants were presented with the same version of the picture sets, so that the picture set that formed the self-resembling erotic female nude picture set for participant A formed the other-resembling erotic female nude picture set for participant B and vice versa. That is, every morphed picture set functioned once as the self-resembling erotic female nude picture set and once as the other-resembling erotic female nude picture set.

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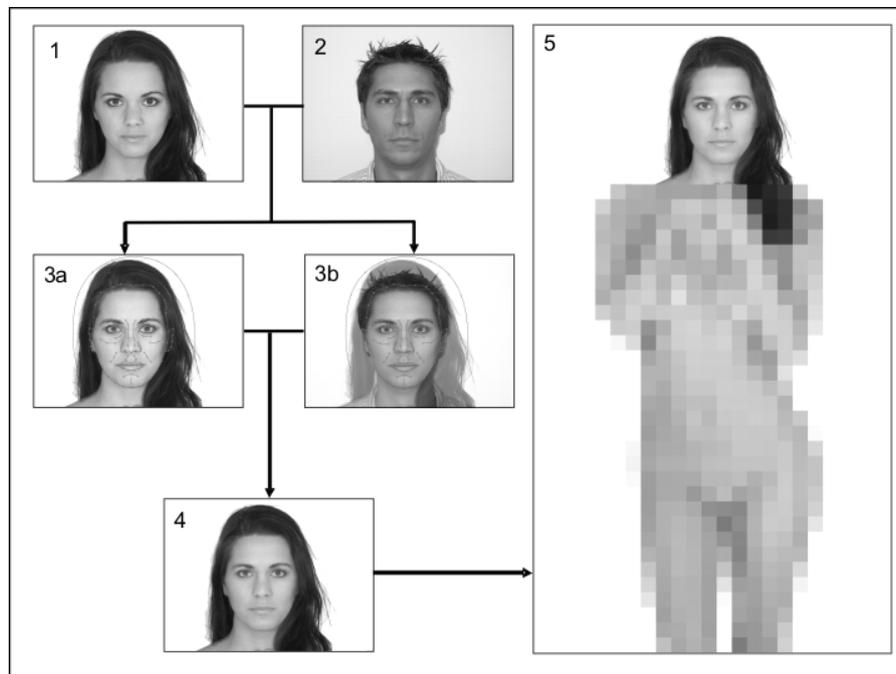


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4.2.3 Cover Story

To be able to morph the participants' faces into the faces of the erotic female nudes, we had to obtain a standardized photograph of each participant's face. For the nature of the experiment it was necessary that participants did not know about the true purpose of the experiment. To assure this, we used the following cover story: Participants were told that for a payment of 25 € they could participate in two unrelated studies in our lab: The experimenter told participants that the first study was to establish a new emotional face data base that would be used for psychophysiological research in our lab. The second study would analyze the influence of acute pain on emotional and physiological reactions to erotic pictures. Furthermore, the experimenter explained that both studies were run together for economic reasons.

4.2.4 Procedure

Photograph Acquisition. If the participant met the criteria in the telephone interview he was invited to our laboratory to take the photographs of his face. After arriving at the laboratory the experimenter asked the participant to sign an informed consent in which the participant approved the scientific usage of the photographs of his face.

The experimenter instructed the participant to look into the camera with a neutral facial expression. Then the experimenter took the portrait photographs with a digital camera from a distance of 80 cm in a fully lit room.

Startle Pretest. Directly after the photographs were taken, participants underwent a brief startle paradigm. The experimenter explained to the participants that the reaction to startle probes was the main dependent measure in the second study and that some people do not respond to these startle probes. Furthermore, he explained that only those people who showed a reliable startle reaction to the stimuli would be able to participate in the second study. The experimenter attached electrodes for electromyographic (EMG) measurement of the left musculus orbicularis oculi below the left eye of the participant with an inter-electrode distance of 1.5 cm (center to center). A third electrode taped on the forehead served as a reference. Electrode placement and skin preparation followed published guidelines (Blumenthal et al., 2005). Ten startle probes (105 dB broadband noise, 50 ms, instantaneous rise time) were presented to each participant and the EMG responses to the startle probes were recorded.

After finishing the startle pretest, an appointment for the second part of the study was made with the participants. Six participants showed less than 70% measurable startle responses and were therefore not invited to the second part of the study. Every participant received 5 Euros for participation and left the laboratory.

Electrode Placement and Pre-Measurement. Participants arrived for the second appointment about one week after the pictures were taken. During this week participants' pictures were morphed with one subset of the erotic female nude pictures.

Experimental sessions were run between 14:00 and 17:00 to control for diurnal cycle of cortisol. When participants arrived at our laboratory, they were asked to sit in a comfortable chair approximately 80 cm in front of a computer screen with a visual angle of 25°. Then the experimenter attached electrodes for electromyographic (EMG) measurement (as described above in Startle Pretest) and electrodes for electrocardiographic (ECG) measurement according to a standard lead II configuration. Furthermore, to measure continuous blood pressure a cuff was placed around the middle finger of the left hand of each

participant. After the electrode placement, ECG and blood pressure were recorded for 3 minutes (pre measurement). After the pre measurement a saliva sample was collected using Salivette tubes (Sarstedt). The participant first placed a cotton swab provided with each Salivette tube in his mouth and gently chewed on it for about a minute. The swab was then placed back in the Salivette tube. Tubes were stored at room temperature until completion of the experimental session and were then kept at -20° C until analysis.

Assignment to stress or non-stress conditions. After we gathered the saliva sample, we assigned participants randomly to either a cold water stress condition or a warm water non-stress condition.

Stress condition. Cold pressor test. The experimenter then informed participants assigned to the stress condition that they would be immersing their hand in ice water for as long as they could tolerate, that the procedure was potentially painful, and that their performance would be videotaped so that the researchers could analyze their facial expressions. The cold pressor (ice-water) test is a frequently used and well validated laboratory pain stressor (for a review see Lovallo, 1975) and has been shown to activate both biological stress systems: the hypothalamo-pituitary-adrenal axis and the autonomic nervous system (Schwabe, Haddad, & Schachinger, 2008). Then the experimenter asked participants to immerse their right hand up to the wrist into a cold water bath maintained at 0-4° C, while keeping the computer screen in view to see additional instructions. A female experimenter watched the participants during the cold water stress task. After 3 min the computer screen told participants to remove their hand from the water. All participants kept their hand in the ice water for the full 3 min.

Non-stress condition. Warm water test. The experimenter asked participants in the non-stress condition to place their right hand including the wrist into a tub of warm water, which was maintained at normal body temperature (35-37° Celsius), and to keep the computer screen in view. The experimenter then left the room. After 3 min the computer screen told participants to remove their hand from the water. All participants kept their hand in the warm water for the full 3 min.

Ratings of Stress, Pain, and Unpleasantness. Immediately after the participants took their hand out of the cold or warm water the computer screen prompted them to rate separately on scales ranging from 0 ("not at all") to 100 ("very much") in 10-point increments, first how "stressful" the previous hand immersion had been, then how "unpleasant" it had been, and then how "painful" it had been.

Post measurement. Immediately after the stress, pain, and unpleasantness ratings, another saliva sample was collected and participants' heart rate and blood pressure were measured again for 3 minutes (post measurement).

Affective Startle Modulation Paradigm. After the post-measurement, participants were instructed via computer screen that a series of pictures would be displayed on the computer screen and that each picture should be viewed for its entire duration. Participants were also asked to relax, to neither move nor speak, and to avoid long periods of eye closure. Finally, they were told that brief noises would be delivered via headphones. Six startle probes presented before the experimental session served as habituation trials. Then the previously described pictures (self-resembling erotic female nudes, other resembling erotic female nudes, not manipulated erotic female nudes, and neutral pictures) were displayed on the computer screen in a randomized order for each participant. Each picture was shown for 6 s and an acoustic startle probe was presented between 3 and 5 s after picture onset in 8 (of 10) pictures per category, for a total of 40 pictures trials. A black screen was shown for 4 s in every Inter-Picture-Interval. After completing the affective startle modulation paradigm (about 15 minutes after the stress manipulation) the computer screen prompted participants to collect another saliva sample.

Pleasure and Arousal Ratings. After completing the affective startle modulation paradigm the participants were asked to evaluate each picture for perceived pleasure and arousal using Self-Assessment-Manikin ratings ranging from 1 to 9 (1 indicates very low pleasure and arousal, and 9 very high pleasure and arousal) (Bradley & Lang, 1994).

After completing the affective startle modulation paradigm and the pleasure and arousal ratings (about 30 minutes after the stress manipulation) participants provided another saliva sample. Then the experimenter led participants to a nearby room and instructed them to collect additional saliva samples at 45 and 60 min after the stress or non-stress (cold or warm water) procedure. After the last saliva sample was collected, participants filled out a small questionnaire about their opinion about the purpose of the experiment: They were asked if they found anything to be special about the pictures of the erotic female nudes. None of the participants correctly detected that the pictures were digitally altered. After completing the questionnaire the participants received 20 Euros and were thanked for their participation.

Debriefing. We did not inform participants about the true purpose of the experiment until we finished the data acquisition of all participants, because we wanted to avoid participants speaking about the experiment with other potential participants. After we finished data acquisition we contacted each participant and explained the purpose of the experiment.

Participants were encouraged to contact the experimenter at any time if they had further questions.

4.2.5 Physiological recordings and data analysis

Startle Magnitude Data. The startle response was assessed as peak EMG activity of the left orbicularis oculi, and was recorded with a BIOPAC MP 150 system and an EMG 100C amplifier at a sampling rate of 1000 Hz, with a notch filter of 50 Hz and a band pass filter of 28 to 500 Hz. The raw signal was rectified and integrated online with a time constant of 10 ms. A semi-automated PC program was used to analyze EMG data. The algorithm identified response peaks in the time interval of 20-150 ms after stimulus onset and baseline was set to 50 ms prior to stimulus onset. EMG data of all participants was manually confirmed with respect to non-response (no visible startle response) and/or artifacts (i.e. voluntary or spontaneous eyeblinks coinciding with the startle stimulus, trials with excessive background noise, multiple peaks).

The startle response was defined as the difference between a stable baseline (50 ms before stimulus onset) and the maximum magnitude of the EMG 20-150 ms after startle stimulus onset. If a response was not visible within the typical response latency range of a particular participant response magnitude was set to zero. Zero response magnitude data were included in the averaging procedure, with startle response magnitude as the output measure. There are wide interindividual differences in the absolute size of the startle magnitude that are often unrelated to the experimental phenomena of interest. To test whether this was the case for our experiment, we compared startle magnitude for the stress and the control group using neutral pictures as the reference category. Startle magnitude for neutral pictures differed non-significantly between the two groups. To eliminate the impact of these differences we standardized the raw data with intraindividual T-Scores using all blinks of each participant as the standard distribution, as recommended by Blumenthal et al. (2005).

Cardiovascular Data. The ECG signal was high-pass filtered (Biopac ECG100; HPF: 0.5 Hz) and stored to disk (1 kHz), and heart rate was derived from the ECG measure. Beat detection and artifact control was performed offline with WinCPRS (Absolute Aliens, Oy, Turku, Finland).

Continuous blood pressure was recorded using the Finapres System (Ohmeda, Englewood, CO; USA). Beat to beat systolic and diastolic blood pressure were determined offline by WinCPRS software. Due to technical problems during data acquisition the cardiovascular data of one participant in the warm water non-stress group and the cardiovascular data of two participants in the cold water stress group were missing.

Saliva. After thawing the saliva samples for biochemical analysis, the fraction of free cortisol in saliva was determined using a time-resolved immunoassay with fluorometric detection, as described in detail elsewhere (Dressendorfer and Kirschbaum, 1992). The saliva of one participant in the warm water non-stress condition was missing.

4.2.6 Statistical Analysis

Data were analyzed by repeated measures or mixed design ANOVA as appropriate, with the alpha level set at $p < .05$. Effect sizes are reported as partial η^2 .

4.3 Results

4.3.1 Manipulation Checks

In order to analyze the effects of stress on men's preference for similar mates, it was important to show that the cold water stress procedure actually stressed participants in contrast to the warm water non-stress procedure. This requirement was met, as follows:

Stress induction: Cortisol response. The results for cortisol, which indicate activity of the hypothalamo-pituitary-adrenal-axis, supported the effectiveness of the stress manipulation. Participants' cortisol responses are displayed in Figure 5, by Stress Condition and Saliva Sample Occasion. A mixed 2 (Stress Condition: cold water stress, warm water non-stress) x 6 (Saliva Sample Occasion: -1 (pre-manipulation), +1 (post-manipulation), +15, +30, +45, +60) ANOVA with repeated measures on the Saliva Sample Occasion factor found, as expected, that the Stress Condition x Saliva Sample Occasion interaction was significant, $F(5, 205) = 10.424$, $p < .001$, $\eta^2 = .24$). This significant interaction, together with pattern evident in Figure 2, shows that after the stress manipulation, cortisol levels were significantly increased by the cold water stress task but not by the warm water non-stress task.

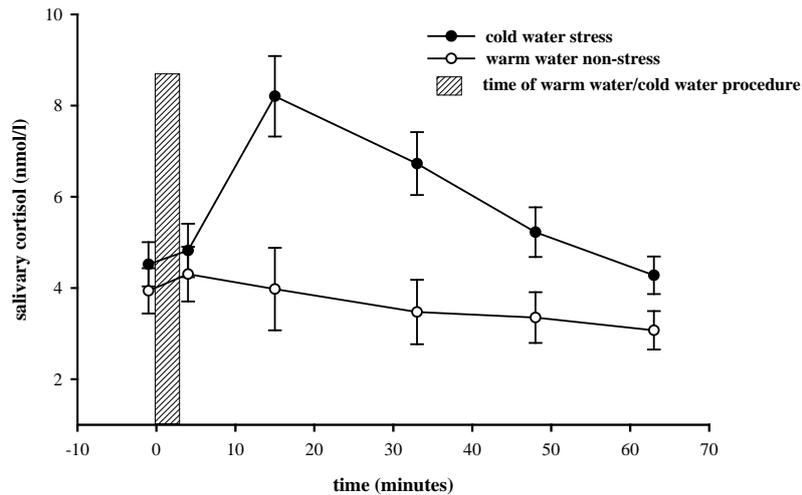


Figure 5 Salivary Cortisol in nanomoles per liter at several time points across the experiment. The bar represents the time of the stress and the non-stress manipulation, respectively. Error bars indicate one standard error.

Stress induction: subjective stress ratings. The subjective and cardiovascular stress indices are shown in Table 1, separately for the cold water stress and warm water non-stress conditions. The upper section of Table 1 presents the mean subjective stress, pain, and unpleasantness ratings. Participants in the cold water stress condition experienced the hand immersion as significantly more stressful, $F(1, 42) = 38.65$, $p < .001$, $\eta^2 = .48$, painful, $F(1, 42) = 168.79$, $p < .001$, $\eta^2 = .81$, and unpleasant, $F(1, 42) = 79.47$, $p < .001$, $\eta^2 = .65$, than did participants in the warm water non-stress condition.

Stress induction: Systolic blood pressure. Participants' mean systolic blood pressure, by Stress Condition and Assessment Occasion, are shown in the second section of Table 2. The stress induction procedure elevated systolic blood pressure in the cold water stress condition compared to the warm water non-stress condition, as shown by a 2 (Stress Condition: cold water stress, warm water non-stress) x 3 (Assessment Occasion: before, during, and after hand immersion) mixed ANOVA that found the interaction between factors significant, $F(2, 78) = 35.56$, $p < .001$, $\eta^2 = .47$. Post-hoc analyses of intergroup differences at each of the three assessment occasions revealed a significant difference in systolic blood pressure only during hand immersion in the water, $F(1, 39) = 33.63$, $p < .001$, $\eta^2 = .46$.

Stress induction: Diastolic blood pressure. Comparable results were obtained for diastolic blood pressure, the means of which are displayed by Stress Condition and Assessment Occasion in the third section of Table 1. A mixed 2 x 3 ANOVA of these means found that the interaction was significant, $F(2, 78) = 21.20$, $p < .001$, $\eta^2 = .35$, and post-hoc

analyses of these means further revealed a significant difference between the stress and non-stress groups only during hand immersion in the water, $F(1, 39) = 19.53$, $p < .001$, $\eta^2 = .334$.

Stress induction: Heart rate. The mean heart rates of participants in each of the two stress conditions, by Assessment Occasion, are shown in the last section of Table 1. The Stress Condition x Assessment Occasions interaction was also significant, $F(2, 78) = 13.82$, $p = .42$, and post-hoc analyses of these means again found a significant difference between groups only during hand immersion, $F(1, 39) = 4.40$, $p < .04$, $\eta^2 = .10$.

Table 2 Heart rate (beats per minute) and systolic and diastolic blood pressure (mmHg) before (pre), during, and after (post) hand immersion in warm or cold water as well as subjective stress ratings in the two treatment groups.

	Warm Water Test	Cold Pressor Test
heart rate (bpm)		
pre	73.02 ± 11.90	73.14 ± 11.14
during	73.27 ± 10.55	79.98 ± 9.89**
post	73.01 ± 9.87	70.86 ± 11.51
systolic blood pressure (mmHg)		
pre	130.15 ± 9.34	127.15 ± 10.79
during	139.46 ± 15.91	172.52 ± 20.41**
post	132.53 ± 15.28	135.05 ± 13.91
diastolic blood pressure (mmHg)		
pre	71.65 ± 9.27	71.19 ± 15.14
during	78.04 ± 12.54	99.15 ± 17.72*
post	74.98 ± 13.77	78.41 ± 17.52
subjective stress ratings (0-100)		
unpleasant	1.90 ± 5.12	58.57 ± 30.04**
stressful	5.24 ± 11.67	41.42 ± 25.74**
painful	.476 ± 2.18	64.29 ± 22.71**

Note. * $p < .05$, ** $p < .001$ compared to warm water test. Data represent $M \pm SEM$.

4.3.2 Startle Magnitude

To analyze the effects of stress on sexual approach motivation to similar and dissimilar mates, we employed a mixed design analysis of variance with the between subject factor Stress Condition (cold water stress, warm water non-stress) and the within-subject factor Picture Content (4 levels: self-resembling, other resembling, not manipulated, and neutral). To be able to analyze the effects of stress on sexual approach motivation to similar and dissimilar mates we had to first show that affective startle modulation actually took place. As expected, startle response magnitude was affected by picture content ($F(3, 126) = 17.55, p < .001, \eta^2 = .30$). Startle probes elicited larger blink responses during foreground presentation of neutral pictures than during presentation of self-resembling erotic female nudes ($p < .001$), other-resembling erotic female nudes ($p < .001$), and not manipulated erotic female nudes ($p < .001$), showing the expected startle inhibition for appetitive pictures.

The experimental findings of central importance tested the hypothesis that the startle activity in the different erotic picture categories differed between the cold water stress and the warm water control group. The interaction between Stress Condition (cold water stress, warm water non-stress) and picture content (self-resembling, other-resembling, not manipulated and neutral) for startle magnitude was significant ($F(3, 126) = 6.796, p < .001, \eta^2 = .132$). Replicating earlier findings (Lass-Hennemann et al., submitted), in the warm water non stress group foreground presentation of pictures of self-resembling erotic female nudes led to a larger inhibition of the startle reflex compared to other-resembling erotic female nudes ($p < .05$) and not manipulated erotic female nudes ($p < .01$), indicating a higher sexual approach motivation to self-resembling erotic pictures. In the cold water stress group, however, self-resembling erotic female nudes led to less inhibition of the startle reflex compared to other resembling ($p < .05$) and not manipulated erotic female nudes ($p < .05$), indicating a higher sexual approach motivation to other resembling and not manipulated erotic pictures.

Furthermore, independent T-tests showed significant differences between the two groups for self-resembling erotic pictures ($T(42) = 5.776, p < .001$), other resembling erotic pictures ($T(42) = -1.871, p < .05$) and not manipulated erotic pictures ($T(42) = -2.134, p < .05$), but not for neutral pictures ($T(42) = .014, p = .989$). Overall these results indicate that acute stress leads to a reduction of sexual approach motivation to self-resembling erotic female nudes (see Figure 6).

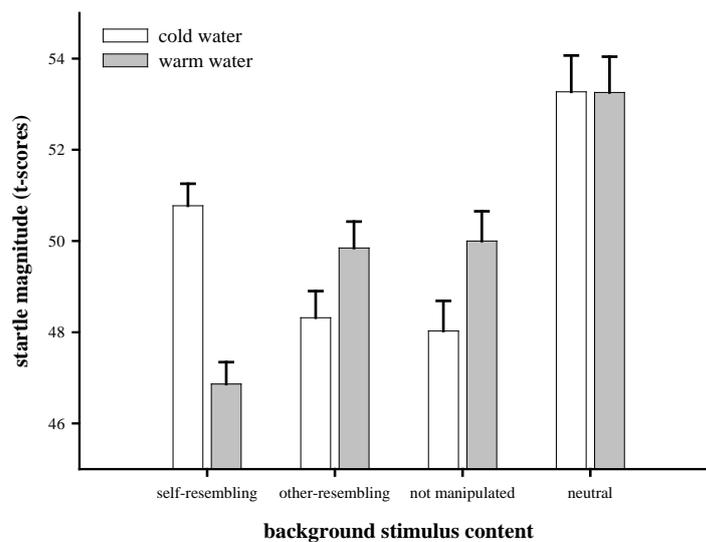


Figure 6 Blink magnitude to startle stimuli during foreground presentation of 4 different picture contents: (a) photographs of erotic female nudes with manipulated facial similarity to the participant (self-resembling), (b) photographs of erotic female nudes with manipulated facial similarity to another participant (other-resembling), (c) photographs of erotic female nudes whose facial characteristics were not manipulated (not manipulated), and (d) neutral pictures in the stress and the control group. Data are reported as T-Scores. Error bars indicate one standard error.

4.3.3 Self-report Pleasure and Arousal ratings

Analysis of picture valence ratings revealed a main effect of content ($F(3,126) = 54.68, p < .001, \eta^2 = .56$). All three erotic picture categories were rated to be more pleasant than the neutral pictures (all p s $< .001$). A significant Stress Condition \times Picture Content interaction showed that the stress and the control group differed in their valence ratings for the four picture categories. Post hoc tests showed that participants in the cold water stress group rated self-resembling female nudes to be less pleasant than other-resembling ($p < .05$) or not manipulated erotic female nudes ($p < .05$) ($F(3.63) = 29.09, p < .001, \eta^2 = .58$), while participants in the warm water non-stress group rated self-resembling erotic female nudes to be more pleasant than other-resembling female nudes ($p < .001$) and not manipulated female nudes ($p < .001$) ($F(3.63) = 36.55, p < .001, \eta^2 = .63$). Both groups rated all erotic picture categories to be more pleasant than neutral pictures (all p s $< .001$). Independent t-tests showed that the difference in valence ratings for self-resembling female nudes between the two groups was significant ($T(42) = -3.897, p < .001$).

Analysis of arousal ratings also revealed a main effect of Picture Content ($F(3,126) = 165.02, p < .001, \eta^2 = .79$). All three erotic subsets were rated to be more arousing than neutral pictures ($p < .001$). However, there was no interaction between Stress Condition and

Picture Content ($F(3, 126) = 1.93, p = .13$). Both groups' arousal ratings for the four picture categories were comparable to each other. Overall, these findings indicate that participants in the stress group experienced self-resembling erotic pictures as less pleasant than participants in the control group. Both groups experienced all three erotic categories to be equally arousing. Means and standard deviations are presented in Table 3.

Table 3 Mean reports of rated pleasure and arousal of the cold water stress and the warm water non-stress group when viewing self-resembling erotic pictures, other-resembling erotic pictures, not manipulated erotic pictures and neutral pictures.

	Warm Water Test	Cold Pressor Test
Self-resembling erotica		
Pleasure ratings (1-9)	7.60 ± 1.10	6.26 ± 1.19
Arousal ratings (1-9)	5.84 ± 1.52	5.62 ± 1.17
Other-resembling erotica		
Pleasure ratings (1-9)	6.57 ± 1.21	6.82 ± .92
Arousal ratings (1-9)	5.77 ± 1.59	6.14 ± 1.21
Not manipulated erotica		
Pleasure ratings (1-9)	6.25 ± 1.19	7.02 ± 1.09
Arousal ratings (1-9)	5.82 ± 1.71	5.60 ± 1.11
Neutral pictures		
Pleasure ratings (1-9)	5.00 ± .75	5.00 ± .63
Arousal ratings (1-9)	2.54 ± 1.42	1.99 ± .85

Note. Data represent Mean ± Standard Deviation

4.4 Discussion

Humans usually prefer similar mates. However, mating preferences in animals have been shown to be influenced by stress. In this study we asked the question whether stress influences men's preference for similar mates. To test this we employed two independent methods to measure sexual attraction: subjective valence and arousal ratings, and affective modulation of startle. We predicted that stress would modulate affective startle inhibition in the presence of pictures of self-resembling erotic female nudes. For non-stressed participants we replicated earlier findings showing that the startle response magnitude was smaller during foreground presentation of photographs of self-resembling female nudes compared to other-

resembling female nudes and not-manipulated female nudes. In the stress group we observed the opposite pattern: Startle response magnitude was larger during foreground presentation of self-resembling female nudes compared to other resembling female nudes and not manipulated female nudes. The results for subjective valence ratings were in the same direction: Participants in the cold water stress group rated self-resembling erotic female nudes to be less pleasant than other resembling female nudes and not manipulated female nudes, while participants in the warm water non-stress group rated self-resembling pictures to be more pleasant than other resembling and not manipulated female nudes. However, this effect was not found for arousal ratings: Arousal ratings for the three erotic picture categories did not differ between the stress and the control group. Importantly, none of our participants detected the digital alteration of the erotic female nudes. Therefore, we succeeded in creating pictures of erotic female nudes with a subtle and undetected resemblance with the participant.

Our findings indicate that under non-stressful circumstances facial self-resemblance increases the attractiveness ratings and the activity of neurobiological structures involved in approach motivation, suggesting that similar mates lead to greater sexual approach motivation and, thus, to higher sexual attractiveness than dissimilar mates. Under stressful conditions, however, these mating preferences seem to be reversed. Our findings indicate greater sexual approach motivation to other-resembling female nudes and not manipulated female nudes under stressful circumstances, and thus to higher sexual attractiveness of dissimilar mates compared to similar mates. Importantly, this result was not only found for subjective ratings, but also for modulation of startle magnitude. Subjective ratings are a voluntarily controllable measure, one that may be confounded by person variables such as social desirability and demand characteristics. Startle magnitude, on the other hand, is well validated measure of the activity of neurobiological circuits involved in approach motivation that is not directly under the voluntarily control of the participant.

Our results are in line with animal studies showing that stress reduces preference for those mates that are preferred under non-stressful circumstances (Hingle et al., 2001; Kavaliers & Ossenkopp, 2001). Recent studies have shown that humans tend to prefer similar mates (Bereczkei et al., 2002; Bereczkei et al., 2004; Griffiths & Kunz, 1973 ; Zajonc et al., 1987). This is remarkable, because optimal outbreeding theory (Bateson, 1983) proposes that individuals would show a preference mates that are not similar to oneself, because of the costs of inbreeding. This prediction is in line with human and animal genetic mate choice studies that show a preference for major histocompatibility complex-dissimilarity in potential partners (for a review see Havlicek & Roberts, 2009). However, theoretically heritable

benefits are more important in short-term mates (Gangestad & Simpson, 2000) and preferences for potential cues of genetic quality have been found to be stronger in short-term than in long-term contexts (Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak et al., 2003). When men pursue long-term mating strategies, they usually invest in their children: because paternity is often uncertain for men, in a long-term relationship men place greater value on characteristics such as trustworthiness and sexual loyalty (Buss & Schmitt, 1993). Research has shown that people tend to find self-resembling faces to be more trustworthy than dissimilar faces (DeBruine, 2002, 2005) . Therefore, it seems likely that men who pursue a long-term relationship should prefer self-resembling mates.

As described above, life history theory predicts that the optimal reproductive strategy for individuals in stressful environments is to maximize current reproduction to minimize the chances of lineage extinction (Stearns, 1992). A way to maximize current reproduction is to have short-term relationships instead of long-term relationships, and it has been shown that individuals who experienced psychosocial stress have more short-term relationships than individuals without a history of psychosocial stress (Koehler & Chisholm, 2009). Therefore, it seems likely that, in our study, stress altered men's mating preference by making positive features of possible short-term mates (dissimilarity) more attractive than positive features of possible long-term mates (trustworthiness).

Our results provide further support for facial self-resemblance as a potential modulator of sexual attractiveness. Furthermore, our study is the first study to show that stress influences human mating preferences, and serves as a further support for the influence of stress on mate choice and sexual behavior.

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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbst verfasst und keine anderen als die angegebenen Hilfsmittel verwendet habe. Zudem wurde die Arbeit an keiner anderen Universität zum Erlangen eines wissenschaftlichen Grades eingereicht.

Trier, den 05.01.2010

Johanna Lass-Hennemann