PSYCHOLOGY MISCELLANY

No.113 - November 2018

Evolutionary Psychology

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ISSN: 1754-2200

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An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

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CONTENTS

1. INTRODUCTION

In 1906 the president of the American Psychological Association talked of the possibility of "functional psychology" (evolutionary psychology today), but Gangestad and Tybur (2016) noted that it was not until the 1960s onwards that theories (eg: reciprocal altruism; Trivers 1971) allowed for its development. "From its inception, evolutionary psychology was heralded as a new meta-theory that could bridge gaps between cognitive, developmental, social, and other areas of psychology while simultaneously inspiring new and unique theory" (Gangestad and Tybur 2016 pvi).

Gangestad and Tybur (2016) continued: "Although not developed by psychologists per se, many of these theories had direct implications for understanding psychological processes (related to, eg: parenting, mate selection, co-operativeness, risk-taking, competitiveness, development). A productive psychology that stood 'cheek by jowl' with general biology was finally born, and christened 'evolutionary psychology'" (ppv-vi).

2. FUNDAMENTAL MOTIVES

Life history their is an evolutionary viewpoint which focuses on three interlinked ideas that are linked to expected pay-off for a species(Kenrick and Griskevicius 2015):

i) Survival from birth and the speed of the organism to sexual maturity ("somatic effort");

ii) Finding a mate and whether to have hundreds of offspring or just a few ("mating effort");

iii) The presence of maternal, paternal, parental, or no care of offspring ("parenting effort" or parental investment [1]).

Animals exist, then, on a continuum from "fast"

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[1] Parental investment was defined by Trivers (1972) as "any investment by the parent in the offspring that increases the offspring's chance of survival (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (quoted in Hedges et al 2016). Put simply, parents have less offspring because they spent more time and effort raising the current child(ren). But parents will "strategically focus investment into children with the greatest (perceived) returns in the long-term" (Hedges et al 2016 p144) (ie: first-born), according to evolutionary models.

Formal schooling is a parental investment in rural societies as it is "costly to parents, both directly, through expenditure on school fees and supplies, and indirectly, because it reduces children's ability to offset their costs through economic contributions to their household" (Hedges et al 2016 p143).

(swift maturity; many offspring; little parental care) (eg: fish) to "slow" (slow maturity; few offspring; high parental care) (eg: mammals) (Kenrick and Griskevicius 2015).

There will also be differences in these "efforts" between males and females of a species. For example, female mammals invest more in a limited number of eggs and so choosing "good genes" is important, while males in 95% of mammalian species invest nothing in their offspring beyond the sperm (Kenrick and Griskevicius 2015).

The different "efforts" have been called "fundamental motives" (or fundamental motivational systems), and follow a particular order (Kenrick et al 2010). Somatic effort first (ie: surviving to sexual maturity), then mating effort. "Female humans must mature to the point where their bodies are capable of carrying a foetus and nursing a large-brained but physically immobile child; males must mature to the point where they can demonstrate either superior physical capacities or wisdom sufficient to generate resources" (Kenrick and Griskevicius 2015 p41). Subsequently, parental effort.

Kenrick and Griskevicius (2015) argued that "fundamental motivational systems are intrinsically linked to ongoing changes in cognition, physiology, and behaviour, which are in turn linked to acute and chronic environmental inputs" (p41). These researchers talked of different behaviours in response to different fundamental motives. For example, when self-protecting motivation (related to somatic effort) is primed in experiments, men and women show similar behaviours (eg: enhanced ingroup favouritism and outgroup discrimination; greater concern with economic losses than gains) (Kenrick and Griskevicius 2015).

But if mating motives are primed, Maner et al (2005), for example, found that men "'project' sexual feelings onto attractive members of the opposite sex, women do not" (Kenrick and Griskevicius 2015 p41).

Mating motives may produce different behaviours in different men. Drawing from studies of a fish species like the arctic charr, where larger males defend territories and try to monopolise females and smaller males engage in "sneak copulation" (Sigurjonsdottir and Gunnarsson 1989), human males may show equivalent differences (Kenrick and Griskevicius 2015). Some males have an "unrestricted" mating strategy (many casual sexual relationships and low emotional commitment), while others have a "restricted" strategy (ie: monogamy) (Gangestad and Simpson 2000). Activating mating mtovies leads "unrestricted" men to engage in showy conspicuous consumption, but not "restricted" men (Sundie et al 2011).

2.1. SPECIALISED CALIBRATION MECHANISMS

A popular explanation for the evolutionary basis of individual differences (ie: "relatively stable differences among individuals in a population") is "specialised species-typical calibration mechanisms, evolved to optimise the level of the trait to relevant contextual factors. These factors may be other characteristics of the individual, early environmental conditions, or stable aspects of the current environment" (Zietsch 2016 p71) [2]. Specialised calibration mechanisms have been proposed for personality traits, mate preferences, and attachment styles, for instance.

Zietsch (2016) provided evidence against specialised calibration mechanisms. For example, in the case of individual differences in women's preference for masculine faces in men, a large twin study found that related contextual factors accounted for little of the variation between individuals (Zietsch et al 2015).

Zietsch (2016) believed that "specialised mechanisms are uncommon, and explain very little of the stable behavioural variation between individuals" (p72). For instance, specialised mechanisms as an explanation is "less parsimonious, simple and feasible than pervasive genetic 'noise' originating as mutations" (Zietsch 2016 p72).

2.2. ADAPTIVE WORKAROUNDS

EP talks of "adaptation" to refer to "a feature of an organism that emerged via natural selection", and "the human mind contains many mental adaptations, each designed to produce thoughts, feelings, or behaviours that would have been functional in humans' evolutionary past" (Eastwick and Durante 2015 p92).

But more than one mental adaptation may be relevant at one time, even producing conflict as in a man's long-term commitment to the mother of their child versus the opportunity of sexual relations with a young female. "Adaptive workaround" is a concept used to deal with such conflicts. They are "features that evolved relatively recently in an organism's evolutionary history and function to mitigate or manage some maladaptive element of a pre-existing adaptation" (Eastwick and Durante 2015 p92).

A classic evolutionary example is the narrowing of the birth canal as hominids became bipedal, which limited

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[2] Other terms used include facultative calibration, adaptive calibration, adaptive plasticity, and reactive trait (Zietsch 2016).

the baby's head size. An adaptive workaround that evolved was cranial growth after birth. "This shift allowed early Homo to grow large adult brains without compromising the ability of newborn heads to fit through the narrow birth canal" (Eastwick and Durante 2015 p92).

Eastwick and Durante (2015) outlined three adaptive workarounds that appeared in recent hominid evolution, which "muted" or "refocused" older evolutionary urges:

i) Attachment or pair-bonding to aid in the care of helpless infants (versus mating with multiple partners) - eg: male circulating testosterone is lowered in pair-bonds (Eastwick and Durante 2015).

ii) The ability to distinguish ingroup and outgroup members, and focusing mating on the former (less dangerous in ancestral environments) (versus mating with anybody) - eg: men find women's voices more attractive when the women are in the fertile period of the menstrual cycle, and only for ingroup members (eg: same ethnicity) (Tidwell 2014 quoted in Eastwick and Durante 2015).

iii) Self-control to conform to group norms (versus mating with anybody) - eg: individuals high in self-control are less interested in opportunities to meet and flirt with attractive opposite-sex individuals (Pronk et al 2011) (appendix A).

Eastwick and Durante (2015) concluded their review: "Part of the human mating psyche derives from our shared ancestry with other primates, and many of these mechanisms have been honed by natural selection over millions of years. But other mating-relevant adaptations evolved more recently in the hominid lineage, and some might even be unique to our species" (p95).

3. HUMAN SEXUAL SELECTION

Strong selection pressures on a species lead to large differences between the sexes (sexual dimorphism), and/or exaggerated traits, particularly in males, that are favoured by mates.

It is argued by some (eg: Hyde 2005) that sexual selection has been "relatively weak" in human evolutionary history as sexual dimorphism is small, males lack large canines (seen in primates with high male-male competition, like baboons). "Moreover, humans exhibit biparental care and social monogamy, which tend to occur in species with low levels of male mating competition. Concealed ovulation also hinders men's ability to monopolise women during the fertile phase of their cycles" (Puts 2016 p28).

Puts (2016) disagreed - sexual dimorphism occurs in facial shape, facial and body hair, and vocal characteristics, for instance. While women show sexual dimorphism in body fat which aids the gestation and nursing of high-energy demanding offspring. Puts (2016) summed up: "sexual selection has probably been weaker in women than in men, but stronger than in most female primates. Sexual selection has probably been somewhat stronger among men than among many – perhaps most – male primates, but weaker than in the most sexually dimorphic primates, such as gorillas, orang-utans, and Hamadryas baboons" (p29).

Puts (2016) outlined the mechanisms of sexual selection in humans:

1. Among men - "contest competition" ("the use of force or threat of force to exclude same-sex competitors from mates") was most important. Larger muscle mass, aggression, use of weapons, and signals of threat (eg: deep voices) lead to dominance, which favoured by females. Gildersleeve et al's (2014) meta-analysis, for example, found a stronger preference for male dominant and contest-related traits by women during the fertile phase of the ovulatory cycle.

2. Among women - Mate choice and selectivity was key here, which led to the evolution of signs of fertility.

3.1. MATE QUALITY

Humour is a signal of "mate quality", and for social interactions. In the former case, more physically attractive men are rated as funnier (humour production) than less attractive individuals by both men and women (Cowan and Little 2013). "Having a good sense of humour is also associated with having more socially desirable traits, such as friendliness and co-operativeness" (Cowan et al 2016). This is the "interest indicator theory" (Li et al 2009). Thus, the preference for humorous individuals generally in social interactions.

Cowan et al (2016) investigated humour appreciation with the hypothesis that "dominant men would express a stronger preference for jokes told by their dominant peers". Ninety-eight undergraduates at the University of Stirling in Scotland listened to recordings of "one-liner" jokes by male and female voices. The pitch of the voices was artificially changed to lower (more masculine) or higher (feminine). After rating the jokes for funniness, the participants completed a dominance questionnaire.

Male participants showed a positive correlation between their own dominance score and their preference for jokes by male voices in a lower pitch. There was no difference for female voices, nor for female participants.

Cowan et al (2016) explained the findings in terms of male alliances - "group cohesion is thought to have been particularly important for male fitness over evolutionary history..., aiding males in reducing the costs of conflict between groups... Humour can help to defuse conflict and demonstrate shared knowledge and attitudes..., and while shared appreciation of culture can promote affiliation, its effects on altruistic behaviour appear to be specific to the shared appreciation of humorous content" (p102).

Choosing a mate does not focus on one characteristic, but "requires paying attention to multiple, potentially competing, signals" (Schacht and Grote 2015 p456).

Two approaches are distinguished here (Schacht and Grote 2015):

a) Prioritised traits - Independent relevant traits of a potential partner are viewed as a hierarchy of importance (eg: waist-to-hip ratio, physical attractiveness, social status).

b) Integrated traits - Traits are inter-related and so the combination is important (eg: physical attractiveness and health).

"Additionally, organisms have to make decisions under uncertainty, as individual traits may not be reliable signals of underlying quality or the condition of a potential mate... Because of this uncertainty, several traits, each related to underlying condition but likely only offering partial information, may need to be attended to. Thus variation in trait priorities, or in how preferences for different traits are combined, may arise due to individual and contextual factors" (Schacht and Grote 2015 p457).

Schacht and Grote (2015) investigated the two approaches with the Makushi people living in Guyana, South America. Partner traits were operationalised into ten items (eg: financial resources, physical attractiveness), and 148 men and 152 women from eight communities rated the importance of each item on a five-point scale.

Overall, men rated "physical attractiveness" as "very important" in a partner more than women, and opposite for "financial resources" and "strength of family bonds".

Statistical analysis of the data suggested support for the integrated traits approach. Furthermore, Schacht and Grote (2015) stated: "Changes in social and ecological environments, as well as uncertainty about traits that accurately signal partner quality, may prompt individuals choosing a mate to use different combinations of traits in different contexts" (p465).

3.2. SEXUAL COERCION THREAT MANAGEMENT

"A threat-management perspective (Neuberg et al 2011) suggests that humans are equipped with psychological systems for coping with adaptive challenges to biological fitness. Such systems are thought to be characterised by a suite of mechanisms adaptively tuned to perceptual cues in the environment that increase or decrease the risk of harm to the individual, as well as to individual characteristics that make an individual more or less vulnerable to such threats" (McDonald et al 2015 p438).

One example of this threat management system is women avoiding situations of potential sexual coercion (eg: threats to female reproductive choice from outgroup men) (McDonald et al 2015). "A psychological system for protecting reproductive choice should be attuned not only to time periods when sexual coercion is most costly (ie: peak conception risk), but also when the likelihood of sexual coercion increases. Throughout human history, intergroup conflict has provided greater affordances for sexual violence to be perpetrated against women, especially by men of the invading group" (McDonald et al 2015 p439).

McDonald et al (2015) tested this theory with a study of responses to dating requests among 350 US undergraduates. Participants were allocated to arbitrary groups (red, yellow or blue) before supposedly interacting online. A confederate, in fact, followed a standard script which ended in a dating request - "Do you want to hang out with me sometime this week?". The confederate was presented as the opposite sex (and physically attractive based on a photograph), and either from the same or a different arbitrary group. Female participants also completed a questionnaire about their conception risk (ie: menstrual cycle), and their perceived vulnerability to sexual coercion (eg: "I'm afraid of being sexually assaulted").

Overall, 61% of participants agreed to the dating request, but this hid a gender difference of 91% of men and 51% of women. There was no difference in acceptance or refusal of dating request based on ingroup or outgroup member asking. But, concentrating of women who reported high perceived vulnerability to sexual coercion and high conception risk, they were significantly more likely to refuse a dating request from an outgroup member than other female participants.

McDonald et al (2015) concluded: "These findings are consistent with the notion that women may be equipped with a psychological system that functions to protect reproductive choice by promoting the avoidance of individuals perceived to pose an elevated threat of sexual coercion. Further, we also provide evidence that the mechanisms of the system are calibrated to produce more avoidance when threats to reproductive choice are most costly (ie: when they are most likely to result in conception) and when they are most likely (eg: when women appraise themselves as more vulnerable to such threats)" (p443).

3.3. LIFE HISTORY STRATEGY

Life history theory focuses on two decisions - to reproduce now or later, and how much to invest in each offspring (Stearns 1992). Though humans tend to have a "slow" strategy (reproduce at later age and invest more in each offspring), the environment can influence the strategy.

A "fast" life history species will reach sexual maturity quickly, and invest little in each offspring (eg: no parental care). "Conversely, individuals at the slower end of the continuum maximise long-term reproductive success... and will produce fewer offspring, provide greater nurturing, show high parental effort, and exert low mating effort" (van Brummen-Girigori and Buunk 2016 p135).

In an unstable environment, a faster strategy is optimal, compared to a slower one in a stable environment.

van Brummen-Girigori and Buunk (2016) used the example of "father absent girls" (ie: no father physically present as the girls grow) - an unstable environment and thus a faster life history. "Therefore, such girls would be more interested in attracting a partner at a young age, especially for short-term mating. As a consequence, father-absent girls will be intrasexually more competitive and engage more often in non-verbal seduction to defeat other girls in attracting males" (van Brummen-Girigori and Buunk 2016 p135).

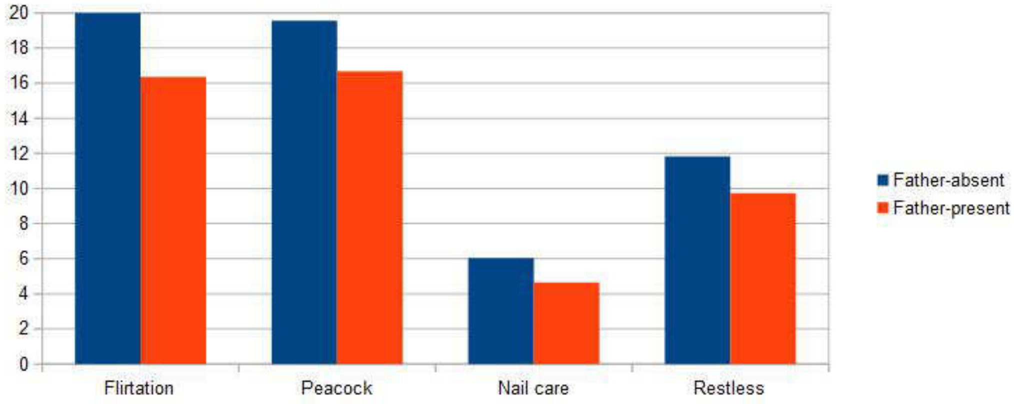
Observing father-absent female teenagers on the Caribbean island of Curacao, van Brummen-Girigori and Buunk (2016) noted non-verbal seduction strategies including flirtatious behaviour, and wearing more jewellery and make-up. A list of forty such behaviours was compiled, which was reduced to nine categories:

- "Direct flirtation" - eg: "laughs constantly when she is communicating with males".

- "Peacock behaviour" - eg: "wears bright lipstick".
- "Restless and active behaviour" - eg: "laughs out loud".
- "Sweet temptation" - eg: "wears high heels".
- "Use of hairstyles with waves and make-up" - eg: "wears excessive lip gloss".
- "Use of jewels and accessories".
- "Lollypop" - eg: "she walks around with a lollypop".
- "Conspicuous nail care".
- "Sexy outfit".

It was hypothesised that father-absent female teenagers (n = 47) would show more of these behaviours than father-present teenagers (n = 76). The participants were interviewed and observed in a social situation. The data supported the hypothesis (figure 1).

The study did not assess the motivations of the participants in terms of their use of the seductive non-verbal behaviours, nor the age of father-absence.



(Data from van Brummen-Girigori and Buunk 2016 table 3 p138)

Figure 1 - Mean scores on four statistically significant seductive non-verbal behaviours.

3.4. FEMALE SEXUAL FLUIDITY

Kanazawa (2017) began: "It has long been known that women's sexuality is more plastic and malleable than men's" (p1252). "Sexual fluidity" is the term used, and it can refer to self-identified labels or sexual behaviour and feelings (Kanazawa 2017). For example, analysis of data from the US National Longitudinal Study of Adolescent Health (Add Health) by this researcher found that women were more likely to describe themselves with non-exclusive labels (eg: "mostly straight" vs "100% straight") than men, and are more likely to change their sexual orientation over time.

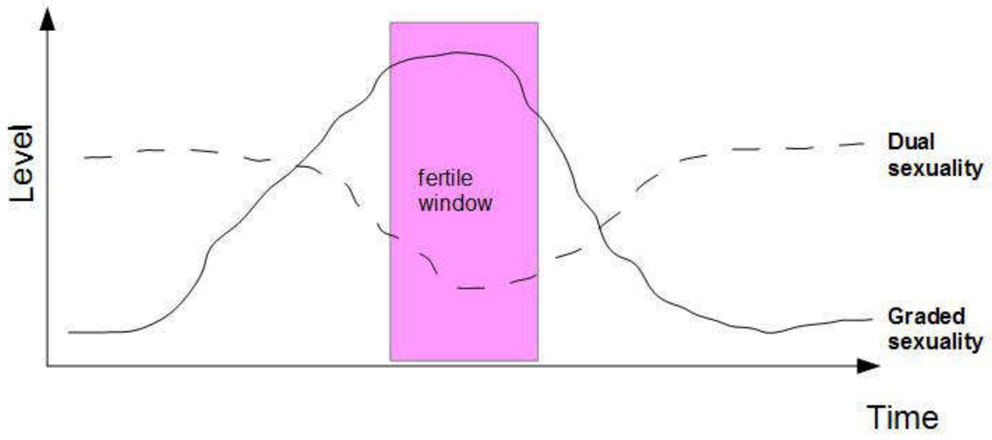
Diamond (2008) proposed an evolutionary explanation of female sexual fluidity based on her ten-year study of 100 women. She distinguished between two types of sexual desire - proceptivity (the motivation to initiate sexual content - ie: libido) and arousability ("the capacity to become sexually aroused to sexual stimuli"; Kanazawa 2017). The former is based on sexual orientation, but the latter is more flexible. "Because men can reproduce at all time, their proceptivity dominates arousability in their sexual desire. As a result, they constantly pursue sexual contact with desired partners. So heterosexual men consistently pursue sex with women, and homosexual men consistently pursue sex with men. In sharp contrast, women are reproductive only for a few days of the month during ovulation. Proceptivity dominates women’s sexual desire during ovulation, but for the rest of the time the more flexible arousability dominates. As a result, women are capable of being aroused by either men or women during the time when their arousability dominates their proceptivity" (Kanazawa 2017 p1252).

Kanazawa (2017) proposed an alternative evolutionary explanation for female sexual fluidity. It was argued that "women may have been evolutionarily selected to be sexually fluid in order to allow them to have sex with their co-wives in polygynous marriage. Even though humans have been mildly polygynous throughout evolutionary history, polygynous marriages are often characterised by conflict and tension among co-wives... [Kanazawa] propose that occasional sex among co-wives may have reduced such conflict and tension, and increased their reproductive success. Female sexual fluidity may have evolved as an adaptation to facilitate it" (Kanazawa 2017 p1253).

3.5. GRADED OR DUAL SEXUALITY

Most female mammals have a period of "heat" (ie: sexual receptivity) when sex is actively sought. Humans are different in that sexual interest is not limited to this period of time. This is "dual sexuality" (figure 2), where female sexual interest occurs outside the fertile period as well as during it. In primate species, this "appears to function to confuse paternity by allowing non-dominant males sexual access. These males cannot rule out their own paternity, which might reduce their likelihood of harming a female's offspring. In humans, by contrast, extended sexuality may function to induce primary pair-bond partners to invest in women and offspring" (Gangestad and Haselton 2015 p47).

A problem is that women "leak" cues to their fertility status which men can perceive. For example, Puts et al (2013) asked men to rate the facial and vocal attractiveness of women at different stages of the menstrual cycle. Those at peak fertility were rated most attractive by the men. Male mate guarding behaviour (eg: jealousy) is also highest at this time (Gangestad and Haselton 2015).



(Graded sexuality = sexual interest limited to fertile period; Dual sexuality = non-fertile sexual interest as well)

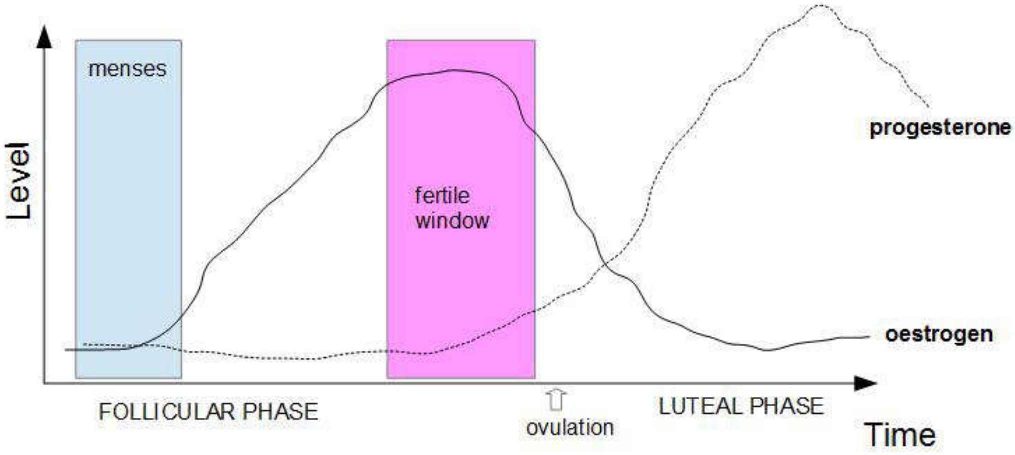
(Based on Gangestad and Haselton 2015 figure 2 p47)

Figure 2 - Level of sexual interest during menstrual cycle according to two theories.

Other studies may suggest a "graded sexuality" (ie: "a single form of sexual interests varies in intensity across the cycle"; Gangestad and Haselton 2015 p47). For example, Roney and Simmons (2013) collected regular salivary hormonal samples from 43 women over two months, and found that reported sexual drive positively correlated with oestrogen levels (highest just before ovulation - ie: "fertile window") and negatively correlated with progesterone levels (highest after ovulation) (figure 3).

The "mate retention hypothesis" suggests that women initiate sex with a long-term partner outside the fertile window when there is a low relationship investment by the partner (Thompson and Muller 2016). Grebe et al (2013) confirmed this idea in a study of fifty couples.

The research on women's skin colour changes across the ovulatory cycle is equivocal (Rowland and Burriss 2017). Redness may increase with oestrogen levels (eg: Jones et al 2015), whereas Samson et al (2011), for instance, has not found any changes. But any changes are "unlikely to be perceivable by the human visual system" (Rowland and Burriss 2017).



(Based Gangestad and Haselton 2015 figure 1 p46)

Figure 3 - Approximate levels of oestrogen and progesterone over the menstrual cycle.

Women's skin colour may darken during low fertility (and pregnancy). Rowland and Burriss (2017) were not convinced as "much of this early evidence came from women's self-reports of facial skin change, and participants were often aware of the studies' aims and hypotheses. Furthermore, these studies often lacked objective quantitative colour metrics" (p4).

The "ovulatory shift hypothesis" (Gangestad and Thornhill 1998) argued that during high fertility women are more sexually attracted to male features that signal high genetic quality (eg: facial symmetry; behavioural dominance; masculinity) (Gangestad and Haselton 2015) (appendix B) [3].

Gildersleeve et al (2014a) supported this hypothesis with a meta-analysis of over fifty studies, while Wood et al's (2014) meta-analysis did not. Gildersleeve et al (2014b) reanalysed the latter data and found support for the "ovulatory shift hypothesis". Wood and Carden (2014) continued to disagree.

3.5.1. Human Ovulation Cues

Studies tend to use "within-women comparisons" - ie: the same women at high and low fertility - in scent, appearance, or voice, for instance (Haselton and Gildersleeve 2016).

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[3] Extra-pair copulations by females have been reported in monogamous primates - varying from around 50% in lemurs to 7% in gibbons, and less than 5% in humans - while promiscuous female chimpanzees can mate with more than twenty males in a day (Thompson and Muller 2016).

- Scent - Men rated female body scents collected at high fertility more attractive than at low fertility (Gildersleeve et al 2012).

- Facial appearance - Attractiveness ratings of female faces was negatively correlated with women's progesterone level at the time of the photograph (Puts et al 2013).

- Voice - Perceived as more attractive by men when progesterone of speaker was low (Bryant and Haselton 2009).

In terms of behaviour changes:

- Women at high fertility are more likely to agree to dance with male confederates at a nightclub (Gueguen 2009).

- Analysis of mobile phone records found less calls to fathers at periods of high fertility (ie: to reduce the risk of incest), but no change with mothers (Lieberman et al 2010).

Explanations for the evolution of concealed human ovulation (compared to other primates) include (Haselton and Gildersleeve 2016):

- Biparental child-rearing - "If female ovulation is non-obvious, male partners must be near their partner throughout the cycle to be certain of their genetic relation to their children. In turn, greater paternity certainty increases the benefits to men of investing in their partner and children, further reinforcing pair bonding" (Haselton and Gildersleeve 2016 p122).

- Preserving female choice - "Current male partners cannot mate guard constantly and therefore may benefit by guarding their female partner primarily during her fertile period (when a failure to do so could result in her conceiving with another male). Thus, the concealment of cues of ovulation might have enhanced females' freedom to choose the genetic fathers of their offspring" (Haselton and Gildersleeve 2016 p122).

- Avoiding female aggression - Female-female aggression in different species is highest at times of highest fertility.

3.5.2. Cosmetics

Women wearing cosmetics have been perceived as higher status in studies (eg: company director vs cleaner; Nash et al 2006). But is this down to dominance (ie: using force, coercion, or intimidation to achieve one's goals") or prestige ("in which people will freely bestow high status to an individual due to their exceptional abilities and qualities") (Mileva et al 2016)?

Mileva et al (2016) investigated this question in two experiments.

Experiment 1 - The researchers produced ninety face images (composites of photographs) of women wearing cosmetics typical of a "night out" or no cosmetics. Then 128 students at a Scottish university rated a sample of faces for attractiveness, dominance, and prestige (each on a 100-point scale).

The with-cosmetics faces were rated as significantly more attractive by both sexes, higher on dominance by female participants, and higher on prestige by male participants.

Experiment 2 - This experiment involved 48 female undergraduates at the same Scottish university, who viewed the faces as before. The participants were also asked the question, "how jealous would you feel if this woman were to interact with your partner?". They were also asked which faces "men would find more attractive".

The participants reported being more jealous of faces with cosmetics, which were perceived as more attractive to men.

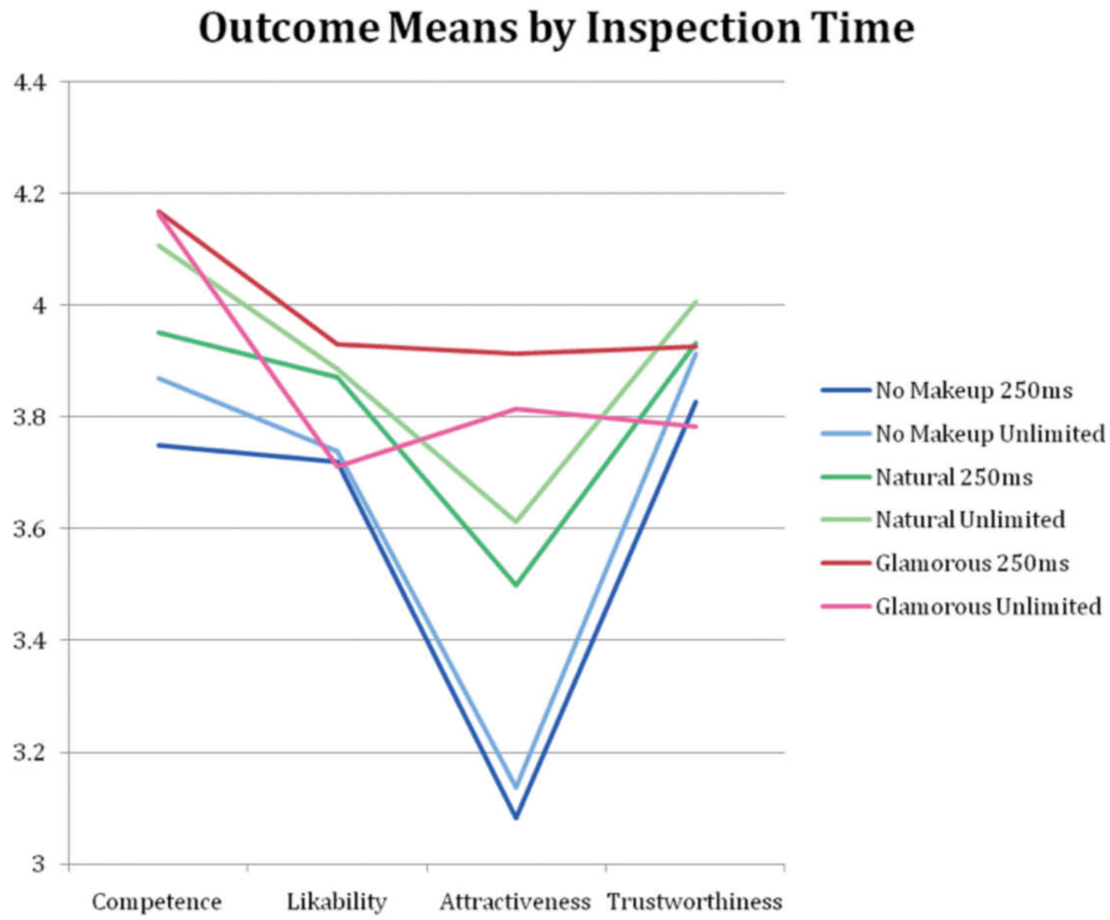
Mileva et al (2016) offered the explanation that "cosmetics may serve to directly increase the perceived competitive value of women. Women with more feminine faces are ranked as being more of a threat to individuals' mating success, and this perceived threat seems to increase linearly with increasing femininity... Since cosmetics exaggerate cues to femininity..., this is a very likely explanation for why women view faces with cosmetics as more socially dominant and attractive to men. Additionally, as more feminine women are perceived as more attractive..., it is likely men will hold facial femininity in high regard (ie: conferring it higher prestige), which may be a possible reason for men rating faces with cosmetics as having higher prestige" (p1178).

So, cosmetics can be seen as an "extended human phenotype" (Dawkins 1989). This refers to "any effect of the genes beyond the organism's body. The spider's web, the hermit crab's shell, the bowerbird's bower and the beaver's dam are all considered examples of the extended phenotype. Among human artefacts, clothing, make-up and other forms of body adornment are considered phenotypic extensions. They are found universally and presumed to enhance perceived biological fitness (Etcoff et al 2011 p2).

Etcoff et al (2011) presented female faces with minimal make-up ("natural"), moderate ("professional") or "dramatic" ("glamorous) levels (and a no-make-up control condition) (figure 4) to 149 adults for 250 ms each and 119 adults with no time limit. It was found that "make-up had significant positive effects on ratings of female facial attractiveness at brief and longer inspection times" (Etcoff et al 2018 p8), particularly competence (figure 5).

(Source: Etcoff et al 2011 figure 1)

Figure 4 - Examples of female faces with different levels of make-up - none, minimal, moderate, and dramatic.



(Source: Etcoff et al 2011 figure 2)

Figure 5 - Mean ratings of four traits for three different levels of make-up based on viewing time.

4. COGNITION

In environments that are harsh and unpredictable [4], individuals are more vigilant, more impulsive, and discount the future more (ie: present-oriented) (Frankenhuis et al 2016). This orientation is seen as a biological adaptation - ie: "increased reproductive success in ancestral environments" (Frankenhuis et al 2016 p77). But the behaviour may not be adaptive today. For example, violent offenders are often impulsive, with the risk of physical injury and early death, but they have more sexual partners (Frankenhuis et al 2016).

In terms of research, female students who recalled more early life stress had their first sexual intercourse at a younger age, and were more present-oriented

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[4] Harshness refers "to the rates of mortality and morbidity caused by factors an individual cannot control (eg: high rates of infectious disease)" (Frankenhuis et al 2016 p76).

(Chisholm 1999). While individuals who experienced more close bereavements preferred a small amount of money now than twice as much in the future (known as future financial discounting) (Pepper and Nettle 2013).

Mittal et al (2015) found evidence for the "enhanced shifting effect" (the ability to switch efficiently between tasks) among individuals who grew up in unpredictable conditions and when tested under conditions of uncertainty. Frankenhuis and de Weerth (2013) proposed that "people who grew up in stressful conditions show enhanced cognition for solving problems that they have developmentally adapted to" (Frankenhuis et al 2016 p78).

4.1. INTERNAL REGULATORY VARIABLES

A "welfare trade-off" involves "pitting personal welfare against the welfare of someone else" (Delton and Robertson 2016 p12), and varies from helping another person on a small task versus doing something for self, to jumping into a river to save a drowning child.

The process of these decisions involves "internal regulatory variables" (IRVs) (Tooby et al 2008), which are "quantitative representations that encode features of the self and others (eg: relatedness, value as a co-operation partner) and are used in decision making" (Delton and Robertson 2016 p12). The final decision (or integration of information) is a "welfare trade-off ratio" (WTR), and is based on (Delton and Robertson 2016):

- IRVs encoding features of people - eg: kinship; reciprocity.

- IRVs encoding features of situations - eg: who is watching; how much is at stake.

Emotions also play a part in terms of evolutionary design". "Anger, for instance, appears designed to raise other people's welfare trade-off ratios toward the self. To do this, the mind must estimate another person's welfare trade-off ratio toward the self and compare it to an expectation of what it should be. If the actual welfare trade-off ratio is too low, then anger is activated, which causes bargaining for better treatment, such as by threatening withdrawal of co-operation (eg: lowering your own welfare trade-off ratio toward them)" (Delton and Robertson 2016 p15).

WTRs tend to be studied in co-operative games in the laboratory (eg: Kirkpatrick et al 2015). An individual is given a choice of options to share money with another person - for example: (i) £5 to self and £10 to other person, or (ii) both £10, or (iii) £15 to self and £10 to other. The nature of the relationship can be varied (eg: friend, relative, stranger). "By systematically varying the amounts at stake, researchers can estimate a subject's welfare trade-off ratio toward their friend by looking for 'switch points', the choices where subjects stop favouring their friend and start favouring themselves. For instance, a welfare trade-off ratio of 0.25 toward a friend implies you would pass up anything less than $2.50 to give them $10 (eg: 0.25 x $10 >$2.25)" (Delton and Robertson 2016 p14).

5. CROSS-CULTURAL EVOLUTIONARY PSYCHOLOGY AND CULTURAL EVOLUTION

"Cross-cultural evolutionary psychology" is interested in "identifying evolved psychological mechanisms that respond plastically to environmental conditions" (Apicella and Barrett 2016 p92). For example, Apicella et al (2007) found that "the preference for statistically average faces (appendix C) appears to be universal, but experience in the local environment defines the average shape for a given population and this leads to different preferences between groups" (Apicella and Barrett 2016 p92).

Universality of behaviour or trait is thus not required by evolutionary psychologists. "'Human nature' does not imply strict phenotypic uniformity but rather a shared set of evolved developmental resources, which are responsible for building psychological phenotypes that may vary depending on the local developmental environment. Thus, the observation that substantial psychological variation exists across the globe should not be misinterpreted as evidence against a pan-human nature; instead it should be viewed as a promising opportunity for testing evolutionary hypotheses" (Apicella and Barrett 2016 p92).

One example is human "co-operative" parenting. Sear (2016) stated: "Co-operative child-rearing may be a human universal, but the behavioural flexibility of our species, including variation in subsistence, marriage and residence patterns, and relying heavily on social learning, means that the nature of parenting (from mothers and others) varies within and between societies" (p98). This is a model proposed by LeVine et al (2008).

Though the mother is the primary caregiver, "vital to the infant's survival at least until the infant was capable of surviving without breast-milk", alloparenting is important (eg: care by other family members), and LeVine (2014) has criticised "models of mother–infant attachment that rely too heavily on cultural norms of parenting as observed in the Western middle classes around the middle of the 20th century, the period when influential theories about parenting were developed" (Sear 2016 p98). For example, among the Aka people of the Central African Republic, fathers, grandmothers, siblings, and other individuals are involved in childcare as required (Meehan 2005).

5.1. CULTURAL EVOLUTION

"Cultural evolution" "represents a body of theory and findings premised on the notions that... human cultural change constitutes a Darwinian evolutionary process that shares key characteristics with (but is not identical in details to) genetic evolution..." (Mesoudi 2016 p17). Social learning is key here.

Mesoudi (2016) continued: "A full understanding of the evolutionary basis of human psychology therefore requires an understanding of these mechanisms and pathways of social learning, and how these in turn generate and guide the cumulative cultural evolution of technology, institutions, knowledge and practices. According to this view, humans uniquely inhabit not just a cognitive niche, but also a 'cultural niche' [Boyd et al 2011]. We are not just intelligent, we are 'culturally' intelligent [Hermann et al 2007]" (p17).

"Cultural micro-evolution" is a term used, and it "comprises the details of who people learn from, how they learn from others, how they transform traits as they are learned, and other socio-cognitive processes that cause changes in cultural traits within populations over time" (Mesoudi 2016 p18). These processes include (Mesoudi 2016):

- Content biases - certain behaviours are more likely to be learned (eg: related to social interactions).

- Model-based biases - learning is more likely from skilled or successful models, high status individuals, and ingroup members.

- Frequency-dependent biases - copying of the most common behaviours in the group (ie: "conformity").

- Guided variation - the passing on of behaviour with some modification.

Among ethno-linguistic groups (ie: those that share language and cultural identity) cultural transmission occurs in three ways (Ross and Atkinson 2016):

- Vertical transmission - new (breakaway) groups "inherit" cultural traits from a parent group.

- Horizontal transmission - groups living nearby share learning/cultural traits.

- Independent innovation - groups living in similar environments independently converge on similar "solutions" to problems.

Ross and Atkinson (2016) applied these processes to a study of Arctic folktales among eighteen groups living in the Arctic (covering Siberia, Alaska, Canada, and Greenland). The tales showed evidence of horizontal transmission (based on trade, and friendly and hostile relations), and vertical transmission (with a shared cultural ancestry of the Eskimo-Aleut language family 5000 years ago).

Ross and Atkinson (2016) saw the findings as applicable to early human hunter-gatherer groups without writing systems where folktales were used to transmit the culture and learning of the group. The researchers referred to this as "high bandwidth" social or cultural learning (ie: greater than within the small group), "which may help explain how complex cultural traditions can develop and be retained in ostensibly small groups" (Ross and Atkinson 2016 p47).

A key social learning strategy is "conformist transmission" (Boyd and Richerson 1985), where "individuals are disproportionately inclined to copy the most common trait in their sample of the population (eg: individuals have a 90% probability of copying a trait that 60% of people possess)" (Muthukrishna et al 2016 p11). The opposite is "unbiased transmission", "whereby individuals copy a trait at the frequency found in the population (eg: individuals have a 60% probability of copying a trait that 60% of people possess)" (Muthukrishna et al 2016 p11).

Muthukrishna et al (2016) explored conformist transmission in two experiments with the same seventy-four Canadian undergraduates. Individuals were shown a selection of lines for three seconds, and had to say which was the longest. This was done ten times (asocial decision condition), then another ten times with details of another person's guess (social decision condition). One dollar was earned for every correct answer. In Experiment 1, conformity to the other person's guess increased with the number of lines presented.

Experiment 2 varied the reward for correct answers between 0 and 2 dollars, and told the participants that sometimes the social information would be false (eg: 40% of the time). Conformity was higher for higher rewards, and where the social information was guaranteed as correct (high fidelity). "Conformist transmission is string when fidelity is higher than 60%, but at 60% it's only slightly above unbiased transmission" (Muthukrishna et al 2016 p17).

Put simply, there is a tendency towards conforming when the information provided by others is believed to be correct, and the rewards for success are higher.

Schillinger et al (2015) compared the processes of imitation and emulation in an experiment to make an ancient hand axe. Imitation is where "the social learner copies the precise details and sequences of behavioural actions employed by a 'model", while emulation is "whereby only the outcome of an individual's behaviour on an object or objects is copied by another, but not necessarily the exact actions used by the demonstrator" (Schillinger et al 2015 p447).

Sixty students at an English university either watched a video of the process of making the axe (without seeing the final form) (imitation condition) or saw the end product (emulation condition). The participants were videotaped during their attempts to make the axe. Participants in the imitation condition made significantly less errors in the shape of the axe. The experiment showed the importance of imitation in cultural transmission of tools ("material culture").

Schillinger et al (2015) ended: "It is not simply the case that imitation allows manufacturing techniques to be transmitted with greater ease culturally; but rather, that imitation, when incorporated into the cultural learning process, acts directly as a mutation-reducing 'repair' mechanism, actively countermanding the effect of copying errors that are also – inevitably – part of cultural processes over the longer term" (p454).

5.1.1. Supernatural Beings and Co-operation

Explaining co-operation between non-kin and without direct reciprocity, and on a large-scale is a challenge to evolutionary psychology. One theory is the "supernatural punishment hypothesis" (SPH) (Johnson and Kruger 2004), which proposes that "it becomes impossible to monitor every action and punish every transgression of group members in large groups. However, the idea of a supernatural monitor who oversees every human action and is capable of punishing every transgression can keep everyone in line. Thus, it is plausible that the idea of supernatural punishment (meted out through a supernatural agent like God) evolved to allow large scale co-operation in human societies" (Yilmaz and Bahcekapili 2016 p79).

This hypothesis makes the assumption that individuals will co-operate if they believe a supernatural agent is watching and monitoring their behaviour. For example, Randolph-Seng and Nielsen (2007) found less cheating in a game after religious priming (ie: words related to religion presented subliminally). This study is actually more supportive of the "supernatural monitoring hypothesis" (SMH) (Norenzayan and Shariff 2008), which describes the monitoring of the supernatural being as similar to that of other people, whereas SPH places more emphasis on punishment.

So is monitoring or punishment more important in promoting co-operation? Yilmaz and Bahcekapili (2016) investigated this question in two studies.

In Study 1, 161 undergraduates in Turkey firstly solved anagrams that produced one of five sets of words:

- "Punishing secular" - eg: police, judge.
- "Non-punishing secular" - eg: democracy, civilisation.
- "Punishing religious" - eg: hell, sin.
- "Non-punishing religious" - eg: heaven, mercy.
- Neutral.

After this priming, the participants completed a questionnaire about pro-social behaviour (eg: giving blood, donating money to charity). Higher pro-social behaviour scores occurred in the two "punishing" conditions, which supported the SPH.

In Study 2, ninety-four more Turkish undergraduates read either a passage from the Quran (emphasising punishment or mercy) or a neutral paragraph before completing the pro-social behaviour questionnaire. Pro-social behaviour scores were higher after reading the punishment passage. Again support for the SPH.

Yilmaz and Bahcekapili (2016) concluded: "It appears that the idea of being watched by agents or institutions capable of punishing norm violations lies at the heart of the evolution and maintenance of a co-operative, harmonious society" (pp83-84).

6. AGGRESSION-RELATED BEHAVIOURS, AND PREJUDICES

Sell et al (2016) began: "An organism can often benefit its own reproduction at the expense of another's. These conflicts of interest can be solved in one organism's favour if it can prevent the other from acting. One way of preventing another organism from acting is to 'break' them, ie: to introduce chaotic elements into their body that prevent the full functioning of their behavioural systems. This is aggression" (p105).

Aggression, however, can be costly, and so animals have evolved means to assess opponents, which reduce actual fighting (eg: displays; assessment of probability of winning). "Assessment mechanisms" (ie: cognitive and perceptual abilities) take account of stable (or semi-stable) variables like fighting ability, and fluctuating ones like need for food. For example, "when fighting over food, animals will be more likely to persist when they have been starved..., but they are also less likely to persist if there are perceptible cues that their opponent has been starved" (Sell et al 2016 p105). Hansen (1986) found that bald eagles assessed the distention of the opponent's stomach and ceded food to hungrier individuals.

Among stable social groups, the assessments become structured in dominance hierarchies. The position in the hierarchy is based on "bargaining power" - ie: "the ability to impose costs, deny benefits or otherwise exert control over the actions of another" (Sell et al 2016 pp105-106). Individuals with more bargaining power can gain higher "welfare trade-off ratios" from others (ie: gain their own way in the future).

Applying these ideas to humans, Sell et al (2016) referred to "aggressive bargaining" to sum up feelings of entitlement, frequent use of aggression, and belief in the usefulness of aggression. "In short, those with more bargaining power should demand better treatment and more commonly threaten or deploy aggression against others. Furthermore, those individuals with bargaining power should believe that aggression is a more appropriate and efficient strategy than those without bargaining power. Finally, because bargaining power can be used to protect individuals against exploitation, those with bargaining power should anticipate that they are more protected from the consequences of aggressive behaviour" (Sell et al 2016 p106).

Sell et al (2016) investigated these ideas with data from the Zurich Project on the Social Development of Children and Youth (z-proso), a longitudinal study begun in 2004 with 1447 Swiss individuals, who were adolescents at this point.

Measures were taken of fighting ability (self-rated and bicep circumference), coalitional strength (membership of groups), and "mate value" (self-perceived attractiveness) [5] as well as of aggression.

The following hypotheses were tested and supported by the data:

1 - Fighting ability will correlate with aggressive

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[5] Bargaining power comes from fighting ability, coalitional strength, and mate or co-operative value (Sell et al 2016).

bargaining among males.

2 - Fighting ability will correlate less with aggressive bargaining among females.

3 - Coalitional strength will correlate with aggressive bargaining among males.

4 - Coalitional strength will not correlate with aggressive bargaining among females.

5 - Mate value with correlate with aggressive bargaining among males.

6 - Mate value with correlate with aggressive bargaining among females.

Overall, more bargaining power goes with aggressive bargaining (use and belief in aggression), and fighting ability, coalitional strength, and mate value link to bargaining power, particularly for males.

6.1. FACIAL STRUCTURE

Facial width-to-height ratio (FWHR) is technically defined as "the distance between the left and right zygomatic bone and dividing that distance by the distance between upper lip and mid-brow" (Welker et al 2015 p423). A high FWHR (or wider face) could be an indicator of physical dominance, as it is linked to more testosterone (Welker et al 2015).

Studies are divided over the link between FWHR and dominance behaviours, like aggression. This may be because relative social status is a mediator (Welker et al 2015). Goetz et al (2013), for instance, found a positive correlation between FWHR and reactive aggression, but only for men with low subjective social status. This fits with risk-sensitivity theory, which proposes that "when faced with the option of adopting a risky strategy (one with high variance in outcome) or a less risky strategy, one's state of need will determine which to adopt" (Welker et al 2015 p424). Put simply, low status individuals will take more risks than high status individuals (appendix D).

Welker et al (2015) found support for Goertz et al's (2013) findings in a competitive video game study. One hundred and sixty-five male US students played a volleyball video game that they were randomly assigned to win or lose. Individuals with high FWHR and low perceived social status (which was operationalised as losing) took more risks in subsequent competitive video games.

6.2. PREJUDICES

An evolutionary explanation of prejudices focuses on "psychological adaptations 'designed' by natural selection to manage threats and opportunities that had implications for reproductive fitness within the ecologies that characterised much of human (and pre-human) evolutionary history" (Neuberg and Schaller 2016 p1).

Co-operation with others helped early human survival, but maintaining close proximity to people is also risky (eg: violence, disease, free-riders). "These threats imposed selection pressures that shaped the evolution of social cognition. Individuals who more successfully identified those who posed fitness-relevant threats, and responded in ways that minimised those threats, were more likely to survive and reproduce. Therefore, as a companion to evolved mechanisms for sociality, there would also have evolved affordance-management systems comprising psychological mechanisms that facilitated learning of cues connoting specific forms of threat, use of these cues to identify conspecifics who potentially posed specific forms of threat, and cue-based affective, cognitive and behavioural responses that — within ancestral ecologies — mitigated specific forms of threat" (Neuberg and Schaller 2016 p1).

However, these "threat-detection systems" can produce "false alarms", and because such systems "operate on the heuristic of 'better safe than sorry', people discriminate against those who may, in fact, pose no threat at all" (Neuberg and Schaller 2016 p2).

There are a number of models under the general umbrella of threat-management. In different ways they describe how "anxiety-eliciting stimuli prompt anxiety-reducing responses" (known as "fluid compensation") (Holbrook 2016 p82).

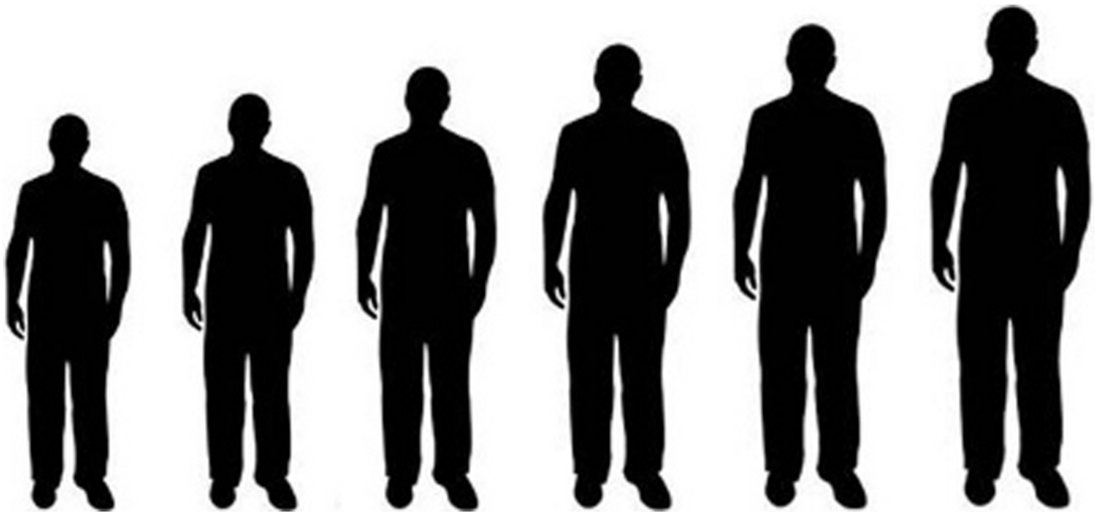
For example, the "group-based control model" (Fritsche et al 2013) suggests that "threats to personal control over events motivate group identification and bias in order to gain the perceived effectance of collective action" (Holbrook 2016 p83).

Another adaptation is to spot physical dominance, and to defer to it. According to the "formidability representation hypothesis" (Fessler et al 2012), "mental representations of prospective foes become either larger or smaller, and more or less muscular, contingent on cues of the potential to inflict harm" (Holbrook et al 2016 p68).

Humans also represent and respond similarly to prestige-based status (Holbrook et al 2016).

Heuristic summary representations (ie: cognitive short-cuts) are used to save time, like stereotypes, and sensitivity to ingroup and outgroup members is also relevant here. Holbrook et al (2016) used the example of race/ethnicity in the USA in their three studies. It was hypothesised that individuals from outgroups stereotyped as threatening will be perceived as more physically formidable.

In Study 1, 300 US participants, mostly White, recruited online read a short story about a fictional man with a stereotypically "White name" (eg: Wyatt) or "Black name" (eg: Jamal) before choosing a silhouette body size for the character in the story (figure 5). Larger body sizes were chosen for individuals with stereotypically "Black names". Studies 2 and 3 replicated the findings, including using stereotypical Hispanic and Asian names.



(Source: Fessler et al 2012 figure 1)

Figure 5 - Silhouettes of body size similar to those used by Holbrook et al (2016).

6.3. PAROCHIAL ALTRUISM

"Parochial altruism" (PA) (eg: Choi and Bowles 2007) refers to "the human inclination toward costly intra-group co-operation and inter-group aggression without expectations of future returns" (Yamagishi and Mifune 2016 p39). Other explanations of altruism based on direct and indirect reciprocity emphasise actual or expected future rewards for altruism. PA is a group selection model, and "the nature of co-operative behaviour predicted by group selection is unconditional, because what matters is the behaviour's effect on the group, not on the actors themselves" (Yamagishi and Mifune 2016 p39).

Another prediction of PA is "the non-instrumental nature of inter-group aggression; whenever there is a chance to increase the inter-group differences in fitness by reducing another group's overall fitness level, group members should aggress against the other group despite a loss in their individual fitness" (Yamagishi and Mifune 2016 p39) (ie: inter-group aggression is offensive rather than defensive).

Yamagishi and Mifune (2016) considered the evidence for the two predictions of PA:

i) Unconditional intra-group co-operation - Tafjel et al's (1971) work on minimal groups is taken as evidence for this prediction, as individuals showed ingroup favouritism even when there is no interaction or contact with other ingroup members (appendix E).

Subsequent research with minimal groups has shown that "the seemingly unconditional in-group-favouring resource allocation is actually contingent upon expectations of hidden indirect reciprocity, that is, by the expectation that most group members would treat their fellow members including the participants favourably" (Yamagishi and Mifune 2016 p40) (eg: Karp et al 1993). A meta-analysis supported this interpretation (Balliet et al 2014).

ii) Offensive inter-group aggression (or non-instrumental, non-retaliatory (or unprovoked) and costly (NNC) aggression) - Little evidence for this prediction. For example, Halevy et al (2008) offered three choices to players in a sharing game - keep all money for self, share with ingroup members only, or share with ingroup members and deprive outgroup members. The last option is predicted by PA, but it was chosen only around 5% of the time (table 1).

Option	Self	Ingroup members	Outgroup members
No sharing	All money	None	None
Ingroup only	None	All	None
PA	None	All	Take from

(Based on Yamagishi and Mifune 2016 table 1 p41)

Table 1 - Options in Halevy et al (2008) study.

Yamagishi and Mifune (2016) concluded that the evidence is "insufficient to demonstrate the legacy of evolution of co-operation through parochial altruism in modern human psychology" (p42).

Chiang and Wu (2015) used the same school class as the ingroup and a different class as the outgroup in their sharing game with children from four to fifteen years old in Taiwan. Each of the 541 participants had ten stickers to allocate, and the average was 4.92 to ingroup members and 2.89 to outgroup members.

A sub-group of the participants (n = 331) were given information supposedly on what other ingroup members had done - eg: 0 stickers to outgroup (and 10 to ingroup), or eight stickers to outgroup (and 2 to ingroup). The remainder of the participants were the control group, who were told that previous ingroup members had allocated five stickers to outgroup and five to ingroup.

Participants adjusted their giving of stickers to the outgroup based on the social information received beforehand. In particular, parochial altruism was reduced (by around 30%) when positive social influence was exerted from the ingroup (ie: giving the outgroup eight stickers).

Bohm et al (2016) argued for defence intergroup aggression - "protecting the ingroup from potential outgroup threat. Such defence preparedness, eg: conquering territories strategically in order to reach an advantageous position against possible attacks, or pre-emptive strikes against potential aggressors..." (p29).

These researchers examined pre-emptive and retaliatory intergroup aggression in an experiment game situation. The players shared points between their group and another group. The three options were keep points for self ("kept strategy"), share with ingroup and extra points added to everybody in that group ("within strategy"), or as within but outgroup has points deducted ("between strategy"). The "between strategy" was the operationalisation of intergroup aggression.

The participants were 216 German students who were randomly assigned to groups and conditions. The game was played alone on a computer, and the researchers varied the behaviour of "other" players - using the "between strategy" to induce retaliation, or the threat of it to induce pre-emptive aggression.

Not surprisingly, participants used the "between strategy" after experiencing it from the outgroup (retaliation), but also used it first when there was the threat that the outgroup would use the "between strategy" in the future (pre-emptive aggression). The perception of vulnerability was important here.

Efferson et al (2016) found that, in an experimental game situation, co-operative players, given a choice of partners, sorted themselves into "relatively co-operative neighbourhoods". Though players did not know how other partners would play (co-operate or not), "moving away from unco-operative behaviour has the potential to significantly reduce or eliminate the force of individual selection against co-operation" (Efferson et al 2016 p7).

6.4. SIDE-TAKING HYPOTHESIS

DeScioli and Kurzban (2013) argued that moral judgments (ie: taking sides in a moral argument) can be a way of limiting fighting ("side-taking hypothesis"). DeScioli (2016) explained: "Observers morally judge the actions of each disputant and then side against the person who chose the most morally wrong action. If a majority of observers use this strategy, and also share the same moral rules, then they will take the same side, such as opposing a liar, thief, or blasphemer. Choosing the same side reduces observers’ fighting costs by avoiding evenly- matched, escalating disputes. Observers benefit by taking the same side because they coordinate their choices to avoid an evenly-matched and costly fight. Moreover, observers achieve coordination without empowering high-status individuals to exploit them in the future. That is, moral side-takers achieve dynamic coordination: They take the same side without always siding with the same people because their choices are based on actions rather than identities" (p25).

6.5. DECEPTION

Deception is an issue with signals. "When the interest of the individual who generates the signal conflicts with the interest of the receiver, selection will favour deceptive signals that decrease the fitness of receivers unless such deceptive signals entail sufficient cost to deter defection" (Boyd and Mathew 2015 p475).

Deceptive signalling is a risk with human language because of its flexibility. When two individuals interact, detecting lies is not easy, particularly if the interaction is a one-off. But social groups have third-party monitoring and punishment. This is where other individuals observe the interaction and can report lies. In this situation, dishonesty becomes costly and honest signals dominate (Boyd and Mathew 2015).

6.6. THE ALTERNATIVE - ALTRUISM

Warneken (2016) proposed the idea of a "biological predisposition for human altruism" - ie: "social norms build upon and refine pre-existing sentiments that very young children — and even some other apes — already exhibit" (p51). The alternative is that children are "initially insensitive to the needs of others, and it is only due to a human-unique constellation of social norms and extensive child rearing that altruism is inculcated over development" (Warneken 2016 p51).

Basic helping behaviour has been reported at fourteen months old as infants spontaneously pick up an object that an adult unsuccessfully cannot reach and give it to them, for instance (Warneken and Tomasello 2007).

What motivates such helping (Warneken 2016):

a) Not reputation as children under five years do not seem concerned by observers of their altruism or not.

b) Not concrete rewards as most studies do not provide those for helping.

c) Not "an adult-like moral value system".

Warneken (2016) argued that the lack of these factors was evidence for a predisposition for altruistic behaviour.

7. INBREEDING AND KIN

The ability to recognise close kin is positive in the sense of who to help (inclusive fitness gains), and negative in who to avoid mating with (inbreeding depression). Thus, the evolution of kin detection systems (Lieberman and Billingsley 2016).

Lieberman and Billingsley (2016) concentrated on siblings, specifically strong sexual aversions between opposite-sex siblings in adulthood (known as the "Westermarck effect" [6]). But how does this work?

One answer is "childhood co-residence duration" (CCD) - ie: "the mind might track sleeping location, bathing, or frequency of shared meals" (Lieberman and Billingsley 2016 p57). Alternatively, older siblings see the younger ones being breast-fed, and this maternal-infant perinatal association (MPA) is the cue to siblingship (Lieberman and Billingsley 2016).

Lieberman et al (2007) found evidence for both of these cues. CCD did not predict sibling sexual aversion for older siblings (ie: with MPA), but did for younger siblings (ie: no MPA). This study used a survey, whereas De Smet et al (2014) replcated the findings with facial electromyography and Belgian female undergraduates. This measured facial muscles involved in disgust when asked to think about sexual behaviour with a brother (Lieberman and Billingsley 2016).

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[6] Named after Edward Westermarck who raised this issue first in the 1890s.

8. FACES GENERALLY

The "co-operative eye hypothesis" (Tomasello et al 2007) [7] proposed that the uniquely human visible white sclera (ie: the opaque white outer coat enclosing the eyeball) evolved "to facilitate communication via joint attention and signalling of gaze direction" (Segal et al 2016 p35).

Tracking the gaze orientation of others has been shown experimentally in chimpanzees, for example (eg: Tomasello et al 1999), but this seems to rely on head direction as much as the eyes (Segal et al 2016).

Humans show a preference for faces from an early age as well as for large eyes. Segal et al (2016) presented pictures of stuffed animals with the eyes varied in size and colour, and with or without sclera. Four to eight year-old children and adults had a preference for toy animals with visible white sclera, but children with autism spectrum disorder had no preference. Segal et al (2016) stated that "because autism spectrum disorder (ASD) individuals have impaired social cognition and show gaze aversion, we... hypothesised that ASD children would show no consistent preference for eyes with visible white sclera" (p35).

Infant facial cues are important for adult-child interactions, and women are better than men at discriminating between high- and low-cuteness versions of infant faces (DeBruine et al 2016). Using a standard lever-press task, Yamamoto et al (2009) found that "women were willing to expend more effort to view images of infant faces in which cuteness had been increased than they were to view images of infant faces in which cuteness had been decreased" (DeBruine et al 2016 p88). Whether these behaviours vary with hormonal levels over the menstrual cycle is contradictory in the research literature (DeBruine et al 2016).

Another aspect of infant faces is "kinship cues" (ie: resemblance to parent(s)). Because maternity is never in doubt, but paternity could be, there would be an evolutionary advantage for babies to look like the father to elicit care from the father. The results of studies have mixed conclusions (DeBruine et al 2016). For example, matching pictures of 24 one year-olds to pictures of mothers and pictures of fathers. Christenfeld and Hill (1995) found the matching more accurate for fathers and babies than mothers and babies, but other studies have not replicated this finding (eg: Bredart and

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[7] Segal et al (2016) prefer the term "communicative eye hypothesis", "given that the visible white sclera allows individuals to deceive as well as co-operate with others" (p39).

French 1999).

8.1. SKIN COLOUR AND FACE SHAPE

Studies on the relationship between masculine faces and ratings of attractiveness are varied, and de Lurdes Carrito et al (2016) argued that "most research to date has failed to address the possible independent effects of sexual dimorphism in facial shape and facial skin colour on attractiveness perception" (p125).

The choice of a masculine face shape is based on the "immunocompetence handicap hypothesis". Masculine facial appearance involves high levels of testosterone, "since only males with relatively high genetic quality are able to sustain the immunosuppression associated with high levels of testosterone and remain healthy, masculinity may therefore signal mate value" (de Lurdes Carrito et al 2016 p125). Alternatively, facial masculinity signals dominance, and that will be attractive to females. But high masculinity partners may invest less in parental care. According to the "trade-off theory", the benefits of "good genes" are weighed against poor male parental care by the woman. "Less attractive women may prefer a male with a more feminine face for a long-term relationship because such a man may invest more in the relationship and be less likely to desert... Conversely, attractive women may prefer more masculine male faces because they can cope with their lower parental ability and may even persuade them to invest more" (de Lurdes Carrito et al 2016 p126).

Skin colour of the face may be a more reliable signal of health than face shape. de Lurdes Carrito et al's (2016) experiments investigated these two elements of male faces. In the first experiment, 142 students in Scotland chose between pairs of "average" male and female faces where the face colour was manipulated. There was a preference for more masculine colour in make faces (ie: darker) compared to female faces.

In the second experiment, the shape and colour of the faces presented were manipulated for sixty-one female participants. Masculine colour was preferred, but a more feminine shape for male faces. A replication with fifty-two female students in Portugal confirmed the findings.

8.2. PUPIL DILATION

Pupil dilation (or enlargement) is:

a) An honest signal of an individual's sexual arousal - eg: heterosexual men's pupils dilated to pictures of nude women more than nude men, and vice versa for gay men (Hess et al 1965).

The participants were five heterosexual men and five homosexual men at the University of Chicago, who looked at fifteen slides of photographs and paintings of male and female nudes (and included five controls - abstract paintings). A magnification of the diameter of the pupil size of the viewers was measured with a ruler after each slide. The average change in pupil size for male and female photographs was calculated, and converted into a continuum (figure 6).

Negative score: Pupil size larger for pictures of men	0 No difference	Positive score: Pupil size larger for pictures of women
↑ Homosexual participants - mean change 10%		↑ Heterosexual participants - mean change 25%

Figure 6 - Average change in pupil size in response to stimuli in Hess et al (1965).

b) Individuals perceive pupillary information - eg: participants preferred to work with an individual with artificially dilated pupils (Stass and Willis 1967).

Male and female participants, who were students in Kansas city, met two confederates of the experimenters of the opposite sex, one of whom had drug-induced dilated pupils and the other not. Two-thirds of the male participants chose to work with the female confederate with dilated pupils, and over 80% of the female participants chose the male confederate with dilated pupils (table 2).

Participants	Dilated pupils confederate	Undilated pupils confederate	Chi-square significant level
Male	36 (67%)	18 (33%)	p<0.02
Female	21 (81%)	5 (19%)	p<0.01

Table 2 - Choice of confederate in Stass and Willis (1967).

Lick et al (2016) studied the perception of pupillary information specifically for sexual arousal signals. Initially, in the classification phase of the study, thirty-eight US undergraduates rated 700 pairs of men's and women's faces for who looked more sexually aroused. The number of pairs were reduced to 38 aroused and 38 unaroused, which were presented to two groups of

Internet users (using a nine-point scale) (validation phase of the study) (table 3). In the analysis phase, the pupil size and luminance were measured for each photograph.

PHASE	MEASUREMENT
Classification	Pair of faces: "Which face looks more sexually aroused? Left or right?"
Validation	Individual face (9-point scale): 1 = "not at all sexually aroused" 9 = "very sexually aroused"

Table 3 - Rating of faces in Lick et al (2016).

Images rated as sexually aroused had significantly larger pupils than non-aroused images, and they were also significantly darker. "Pupil dilation therefore appears to be an external cue that reliably and validly differentiates perceivers' mental representations of sexually interested vs. sexually disinterested others" (Lick et al 2016 p122).

Lick et al (2016) ended: "In summary, poets and philosophers have long claimed that the eyes are the windows to the soul. After imaging perceivers' mental representations of sexually interested and disinterested men and women, we offer an extension of this statement. On the basis of current evidence, we contend that the pupils in particular act as windows to others' sexuality" (p123).

8.3. FACE AS SIGNALLING SYSTEM

McCullough and Reed (2016) began: "There is intuitive appeal to the idea that facial displays exist in order to reveal the displayer's inner state, but evolutionary signalling theories insist that the function of a facial display – to the extent that it has a function at all – must be in the interests of both the individual making the display and the individual who can comprehend its meaning" (p110).

So, McCullough and Reed (2016) asked if facial displays, particularly concentrating on smiles and angry expressions, are signals. Scott-Phillips (2008) defined a signal as "any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the act or structure" (quoted in McCullough and Reed 2016).

This is distinct from a "cue", which is a "feature of another individual that can be used by an animal as a guide to future actions" (McCullough and Reed 2016 p111). Signalling is also different from "coercion", that is a "form of exploitation in which displayer creates a sensory stimulus that changes the behaviour of a stimulus-perceiver, consequently a fitness benefit for the displayer, but not for the perceiver" (McCullough and Reed 2016 p111).

Altogether, an act evolves as a signal because it benefits both the signaller and the receiver on average. "Otherwise, signal recipients will evolve to ignore them, and signal users will consequently evolve to stop using them" (McCullough and Reed 2016 p111).

Carazo and Font (2014) outlined four evolutionary processes involved in the reliability (honesty) of an act as a signal (McCullough and Reed 2016):

i) Indexing - The signal is impossible to fake.

ii) Handicap - Individuals of high-quality will produce acts that are costly to show their quality.

iii) Receiver-dependent responses - The receiver must believe that the signal is honest. For example, angry facial displays must be perceived by the receiver as having the backing to carry out aggression if the signaller is not heeded.

iv) Common interests - When signallers and receivers have common interests, honest signals will evolve, but when there are no common interests, an evolutionary arms race will develop "seeking to innovate the means to deceive signal receivers (thus turning their signals into uninformative 'cheap talk') and signal receivers seek to acquire the capacity to 'mind-read' the inner states of signallers" (McCullough and Reed 2016 pp112-113).

McCullough and Reed (2016) saw smiles and angry expressions as evolving as honest signals in co-operative tasks. A smile to confirm and reward co-operation by the other, and an angry expression when there is no co-operation or not enough (free-riding).

9. DEATH

Anderson et al (2018) used the term "evolutionary thanatology" to describe an evolutionary perspective on the study of death and dying. They stated:

> Major changes in human funerary activities can be traced not only over thousands of years, but also within much shorter time frames; examples include

> an increasing distance from the experience of death and funerary treatment of the corpse, by way, for example, of the increasing outsourcing of funeral services, smaller funeral gatherings, and new ways of disposing of corpses as a result of increasing urbanisation and industrialisation. The use of online social media has played an increasing role in the dissemination of death notices and expressions of condolences and commemoration, essentially a digitalisation of funerary activity, and in the USA some drive-through funeral parlours are even tailored to allow mourners to pay their respects without leaving their car. Funerals and memorial events for dead non-human animals (not only pets) are becoming increasingly popular in various countries, and in Japan this extends to defunct ("dead") robotic dogs, whose parts ("organs") may be removed and donated to other defective robots (p2).

An evolutionary approach to the treatment of the dead, however, requires a survey of non-human responses, "including corpse avoidance and disposal mechanisms in social insects, exploratory interactions with deceased companions in corvids, and caretaking responses to dying and dead individuals in mammals including cetaceans and primates" (Anderson et al 2018 p2).

Firstly, there is the cognitive and sensory bases for detecting life and death in own and other species. Eusocial insects use olfactory cues, for instance, which includes behaviours like "necrophobia (avoiding the corpse), necrophoresis (removal of the corpse from the colony), intraspecific necrophagy (cannibalism) and entombment (burial, elsewhere referred to as necroclaustralisation)" (Anderson et al 2018 p3).

Goncalves and Biro (2018) argued that vertebrates retain "notions of the animacy of the deceased, albeit in the absence of any signs of animacy" (Anderson et al 2018), which they called "animacy detection malfunction", and this is the basis of responses to the dead.

Swift and Marzluff (2018) (appendix F) presented wild American crows with taxidermy-prepared specimens in various postures. Tactile contact was rare, and alarm calls suggested a recognition of the specimens as dead. But there were also aggressive and sexual responses towards the corpses depending on the posture, which "may derive from an inability to mediate between conflicting stimuli" (Anderson et al 2018 p3).

In terms of the concept of death, Anderson (2018) reported that chimpanzees may have such an idea (similar to human children younger than ten years old) based on cessation of function. This comes "with sufficient personal experience of dangerous situations, and through witnessing injurious or fatal events in others..."

(Anderson et al 2018 p3).

10. PERSONALITY

Penke et al (2007) proposed that personality traits "seemed to be under balancing selection, where selection pressures in different directions affected the same traits at different times or in different places, in a way that no genetic variant underlying personality traits is consistently favoured over others" (Penke and Jokela 2016 p104).

This may explain why the relationship between personality and reproductive success, usually measured as number of children, is not clear-cut. Surveying twelve studies, Penke and Jokela (2016) noted that, for instance, three studies found a positive relationship between extraversion and reproductive success, five more studies for men only, two studies no relationship, and the remainder a negative relationship.

One problem is that "individuals of our species are especially good at seeking out and creating environments that suite their individual preferences, needs and capabilities. This tendency, variably called active gene–environment correlation, experience-producing drives, or niche picking and construction, can systematically lead individuals to place themselves into environments where their specific personality profiles yield the best-possible fitness pay-off. As long as environments are diverse enough for everybody to find a suitable niche (which might be much more the case in modern complex than in traditional small-scale societies), this process can stabilise balancing selection" (Penke and Jokela 2016 pp106-107).

11. APPENDICES

11.1. APPENDIX A - SELF-CONTROL

There is an evolutionary logic that organisms pursue rewarding behaviours and avoid aversive ones. "'Fitness-good', behaviours... are, generally, experienced as rewarding" (Kurzban 2016 p67).

Exerting effort or self-control is a "fitness-good" behaviour, but it is experienced as unpleasant. "The unpleasant sensation of effort drives what appear to be puzzlingly short-sighted decisions. Decisions to avoid tasks that are long-run-good – and effortful – are often made in favour of indulging in behaviours that are rewarding in the short term..." (Kurzban 2016 p67). How to explain this puzzle?

One answer is that the unpleasantness is an "aggregation of opportunity costs" (Kurzban 2016). According to this view, "when [cognitive] systems that can be used for multiple purposes are engaged in a task, the potential benefit of ending the present task in order to perform some other task is computed. This computation is the opportunity cost of persisting in whatever it is that one is doing, which increases over time. When this cost is sufficiently great, outweighing the computation of the (potentially long term benefits of persisting), the task is abandoned" (Kurzban 2016 pp68-69).

Kurzban (2016) continued: "the system or systems that compute the costs and benefits of persisting seem to be designed to favour short-term benefits" (p69). Put simply, this is a cost-benefit assessment of choices.

The main alternative is a resource model, where self-control is a resource that gets depleted with use.

The debate is mostly theoretical with a limited amount of empirical evidence (Kurzban 2016).

11.2. APPENDIX B - MEASURING "FERTILE WINDOW"

In Gildersleeve et al's (2014a) meta-analysis there were studies that found no statistically significant relationship between ovulatory cycle and attention to male fitness indicators as well as those that did and the overall effect being positive.

One explanation for mixed findings between studies could be how the ovulatory cycle is measured. Two methods are traditionally used to establish the "fertile window" (Gangestad et al 2016):

a) Luteinising hormone (LH) surge 24-36 hours prior to ovulation. Once the increased the LH is detected in the urine, say, the researchers in repeated design studies tested the female participants as the "high-fertile condition". But commercial tests that measure LH, and commonly used by researchers, are not perfect, and more expensive procedures (eg: ultrasound; daily oestradiol and progesterone levels) would be more accurate.

b) Day-of-cycle counting - Counting the onset of menstrual bleeding as Day 1, and converting the subsequent day of testing into a conception probability. Usually a range of days is defined as the fertile window.

Gangestad et al (2016) calculated the validity of counting methods as "modest, overall". Their advice was to use multiple measures of the ovulatory cycle concurrently.

11.3. APPENDIX C - FACIAL AVERAGENESS

"Facial averageness" is believed to be attractive in a mate (ie: individuals who posses more average facial features of the population) because it signals "good genes".

Using photographs of individuals from twin studies in Australia and the USA, Lee et al (2016) calculated scores for facial averageness based on the distances and angles between "landmarks" on the face (eg: nose and eyes). Undergraduates then rated the faces for attractiveness. There was a positive association between facial averageness score and attractiveness rating.

But this association could be due to "some unknown third variable that is correlated with both facial averageness and attractiveness" (Lee et al 2016). Further statistical analysis of the data found "mixed evidence with respect to the predominant theory that facial averageness is preferred for genetic benefits to offspring" (Lee et al 2016).

11.4. APPENDIX D - TYPE OF REWARD

Rosati and Hare (2016) showed that decision-making and risk-taking varied when the reward was food (primary reinforcer) compared to money (secondary reinforcer). Seventy-five participants at Duke University in the USA were offered a safe option (a small reward in a visible container) or a risky option (which involved either a large reward or nothing in a hidden container). The reward varied between independent conditions - food, money, or prizes. Participants chose the risky option significantly more often in the food (mean 69% of trials) and prize (69%) conditions, but not in the money condition (53%). "Overall, these results indicate that humans treat decisions about abstract rewards differently from decisions about concrete rewards" (Rosati and Hare 2016 p164).

11.5. APPENDIX E - RITUAL

Wen et al (2016) found that participation in a ritual increased ingroup affiliation more than no ritual among 4-11 year-olds. The ritual was an arbitrary activity created by the researchers that all members of the randomly coloured group had to perform together. Ingroup affiliation was measured by four questions about their coloured group.

This fits with other research that showed that "engaging in synchronous movement (even synchronous singing) may increase cooperation, pro-sociality, as well as self-reported feelings of connection to and trust of group members" (Wen et al 2016 p58).

Wen et al (2016) explained that "humans are psychologically prepared to engage in socially stipulated, conventional behaviour such as ritual as a means of in-group affiliation. Rituals serve four core functions that address the adaptive problems of group living by acting as social identity markers, demonstrating commitment to the group, facilitating cooperation with their coalition, and increasing group cohesion... Human psychology is thus geared to motivate individuals to engage in behaviours that increase inclusion within their social groups" (pp58-59).

11.6. APPENDIX F - SWIFT AND MARZLUFF (2018)

Swift and Marzluff (2018) performed two field experiments in Washington state, USA. in the first one, wild crows were presented with one of four taxidermy-prepared specimens in a dead position - adult crow, fledgling crow, rock pigeon, or Eastern grey squirrel. The researchers scored five behaviours - peck at specimen, touch, drag, dismember, or sexual behaviour towards it. In over 300 trials, 70% involved no contact with the specimens. In summary, the researchers said: "We observed crows engaging in all five categories of interaction with each stimulus, with the exception of sexual behaviours following presentations of the squirrel, which were never observed" (Swift and Marzluff 2018 p4).

The second experiment presented three taxidermy-prepared adult crow specimens in traditional dead posture (wings partially outstretched), dead with wings tucked close to the body, or standing. The crows did not distinguish between the two dead postures, but there was more contact and aggression towards the study specimen.

Scolding and mobbing were the most common responses to all the adult crow specimens in both experiments, which is behaviour associated with territorial defence.

"These behaviours are consistent with the danger response hypothesis and suggest that the crows correctly identified the state of the dead bird" (Swift and Marzluff 2018 p7).

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