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Review

Sexual selection and the evolution of behavior, morphology, neuroanatomy and genes in humans and other primates

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ABSTRACT

Explaining human evolution means developing hypotheses about the occurrence of sex differences in the brain. Neuroanatomy is significantly influenced by sexual selection, involving the cognitive domain through competition for mates and mate choice. Male neuroanatomy emphasizes subcortical brain areas and visual-spatial skills whereas that of females emphasizes the neocortex and social cognitive areas. In primate species with high degrees of male competition, areas of the brain dealing with aggression are emphasized. Females have higher mirror neuron activity scores than males. Hundreds of genes differ in expression profiles between males and females. Sexually selected differences in gene expression can produce neuroanatomical sex differences. A feedback system links genes, gene expression, hormones, morphology, social structure and behavior. Sex differences, often through female choice, can be rapidly modulated by socialization. Human evolution is a dramatic case of how a trend toward pair bonding and monogamy lowered male competition and increased female choice as a necessary step in releasing the cognitive potential of our species.

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1. Introduction

The outlandish size of the human brain has always fascinated evolutionary biologists. Explaining human evolution has in large part meant developing hypotheses about why humans have brains three times the size of their nearest primate relatives (Sherwood et al., 2008) and to what extent the brain may differ in a sex specific manner (Becker et al., 2008). Darwin (1871) developed the theory of sexual selection to explain sexual dimorphism, the differences between males and females of the same species. He proposed that behavioral differences between males and females were at the root of sexual selection. Males competed for access to females whereas the most notable female characteristic was to choose the best mate among male competitors. Darwin proposed that the large brain of humans was driven by sexual selection to its absurd and sex-dependent proportion. As with the peacock's resplendent tail, males were the sex most influenced by sexual selection, so that "*the average standard of mental power in man must be above that of women*. . .*thus man has ultimately become superior to woman*". However, whereas Darwin's simplified and ridiculous view of women is typical of the Victorian age (Birkhead, 2010), his idea that sexual selection could have a profound influence on the brain is now a lively field of inquiry also in humans (Cahill, 2006; Miller, 2011). How sexual selection – which implies behavioral flexibility, cognitive abilities and different roles between sexes – has modulated primate morphology as well as complex neuroanatomy and gene expression is just beginning to be appreciated (Dunbar, 2007, 2009; Lindenfors et al., 2007; Montgomery and Mundy, 2013). Studies now show that sexual dimorphism in neuroanatomy of primates is significantly influenced by sex-biased behavioral traits that enhance fitness in different mating systems and social structures. Sex differences in neuroanatomy are part of a feedback system linking social and mating structures, behavior, and gene expression to sexual selection. New light is being shed on the evolution of humans by our improved understanding of the processes and mechanisms of sexual selection during primate evolution (Cachel, 2006, 2009; Sherwood et al., 2008; Chapais, 2013; Fleagle, 2013).

2. Social structure and mating systems affect body sex-dimorphism

It is widely acknowledged that sexual selection is modulated by variations in social structure and the reverse, but it was not an easy task to dissect out the many contributing components. Primate social organization is highly dependent on ecological variables that influence the spatiotemporal distribution of females. It is no banal conclusion that males follow females (Altmann, 1990). Female distribution then is a major driving factor in determining variation in social and mating systems (Carnes et al., 2011; Lindenfors et al., 2004). Primates have a wide range of mating systems including unusual multimale–multifemale groups (Ostner et al., 2013). The mating systems of living primates with simplification are classified as monogamous (pairs), polygynous (one male with multiple females), polyandrous (one female with multiple males) and polygynandrous (multimale–multifemale) (Martin, 2007). Mating systems are apparently not strongly influenced by primate phylogeny (Fig. 1), but on the other hand sexual dimorphism is strongly correlated with the mating system (Fig. 2). The peak of sex-dimorphism occurs in case of the harem (one male–multifemale, i.e. gorilla) or when a male is associated with a female just for mating, as in orangutan (Fleagle, 2013).

Social and mating systems determine an incredible range of both morphological and behavioral traits. Darwin (1871) discussed sex differences in size, canine teeth as well as color, length of pelage and sexual skin in various polygamous species of primates in relation to both male fights for access to a mate and female "taste for the beautiful"; nevertheless, Darwin only vaguely connected these traits to the mating types recognized today. The degree of male competition depends on both the number of females in groups and female reproductive synchrony (Nunn, 1999). Polygynous species are the most sexually dimorphic in body and canine size while monogamous species have almost no sexual dimorphism for these armaments as well as for aesthetic traits.

Male ornaments are rare among mammals in comparison to birds where male ornaments were considered as products of male–male competition. Nevertheless, male skin coloration was interpreted as an attractive sexual signal in rhesus macaques (Waitt et al., 2003; Dubuc et al., 2014) and in mandrills (Setchell and Jean Wickings, 2005). Such coloration is status-dependent, suggesting a dual utility of armaments/ornaments in sexual selection (Berglund et al., 1996).

2.1. Female promiscuity and cryptic mate choice

Females instead of males are now the focus of many sexual selection studies, due to the key role of female mate choice. Rather than being a cooperative venture between the sexes, sexual reproduction is now viewed in terms of conflicts of interests among rivals of the same sex but also between males and females (Birkhead, 2010). Females may increase reproductive success through promiscuity, especially in multimale–multifemale groups. Darwin did not account for female promiscuity; he apparently thought that female choice was keyed to select one male, not to mate with multiple males. It was only in the last 50 years that the implication of female promiscuity became clear (Birkhead, 2010). Through promiscuity females can confound paternity, avoid infanticide and acquire genetically compatible sperm.

Females also increase their mate choice toward high quality males for critical copulation and post-copulatory mate choice. "*Cryptic female choice*" (*sensu* Eberhard 1996) can operate to maximize female choice by disguising or concealing ovulation to relax male coercion (Muller et al., 2007; Stumpf and Boesch, 2010). Even the pH of the primate vagina can determine a drastic selection of sperm (Dixson and Anderson, 2004) and primate seminal fluids must adapt to neutralize low pH. In primates these female strategies are facilitated by lengthy periods of sexual activity around ovulation.

2.2. Sperm competition and genitalia

For males the quantity and quality (vigor and speed) of sperm ejaculated into the female reproductive tract can be a crucial counter strategy to female promiscuity (Anderson et al., 2007). Sperm competition helps explain the variability found in primate genitals. There is an association between relative testis size and primate mating systems (Dixson and Mundy, 1994a,b; Harcourt and Gardiner, 1994; Harcourt et al., 1981; Hosken and Stockley, 2004; Shamloul et al., 2010; Verrell, 1992). Sperm competition is low in one male mating systems and here the testes are generally smaller. Sperm competition should be highest in multimale–multifemale systems due to promiscuous mating and indeed testes size is much larger. Relative testes size is now taken as a good indicator of the strength of sperm competition. Sperm vigor follows the same correlation. Faster sperm are found in groups of multiple adults of both sexes while the slowest sperm are found in one male mating systems (Nascimento et al., 2008).

The morphology of the penis (head, length and width) may evolve to both safely deposit sperm and to facilitate the removal of competitors' sperm. It has been hypothesized that one function of larger penises would be both to remove rivals' sperm