Human Ethology Bulletin **28** No 4 (2013): Special Issue on Tinbergen 31-38
Theoretical Review

On aims and methods of facial attractiveness research: The lasting influence of Tinbergen (1963)

Ian D. Stephen

School of Psychology, University of Nottingham Malaysia Campus Jalan Broga, Malaysia

Abstract
Tinbergen's influential paper, On Aims and Methods of Ethology, has had a lasting impact on facial attractiveness research. While researchers rarely explicitly acknowledge the influence of Tinbergen's ideas, the field has embraced evolutionary thinking in recent years. This focus on functional and phylogenetic explanations has led to the generation of hypotheses that, when tested, produce knowledge at all four explanatory levels – hypotheses about the survival value, in Tinbergenen`s terms, of facial preferences have led to knowledge about the facial cues that are perceived as healthy and attractive. The focus on phylogeny as an important way of confirming predictions at the functional level has also led to the adoption of traditional ethological techniques of observation, as comparative and cross-cultural anthropological studies are brought into what is, at heart, an experimental science. The influence of Tinbergen's ideas on facial attractiveness research is discussed with examples from the literature.

Key words: *Faces, Attractiveness, Tinbergen*

Introduction
If I am asked into what field my research falls, I will usually answer that I study face perception. Other times I may say "perceptual psychology" or "evolutionary psychology". Of course, by the definition of Tinbergen (1963), I could define the whole of the field of face perception as a branch of ethology.

Much of recent facial attractiveness research has been based on evolutionary foundations, representing an extension of animal behavior and behavioral ecology methodology to human mate choice behavior. That is, facial cues to attractiveness are usually posited to relate to some aspect of underlying, physiological health (Coetzee et al., 2009), since individuals who show preferences for mating with healthy individuals will have increased reproductive success (see Kokko et al., 2003 for a discussion). This follows from the fact that individuals who mate with healthy, disease-free individuals are expected to gain a range of direct and indirect benefits from doing so: First, they expose themselves to fewer pathogens. Second, attractive facial cues may cue fertility, increasing the probability of conception. Third, it is likely that the healthy mate will survive in order to provide direct provisioning to the individual, and parental investment to his/her offspring. Fourth, they may gain 'good genes' benefits for their offspring (Kokko et al., 2003).

The focus on evolutionary explanations generates hypotheses that, when tested, produce knowledge of the cues and mechanisms that underlie this evolutionary explanation; predictions derived from animal behavior literature about the importance of developmental stability in cueing quality led to the identification of fluctuating asymmetry (FA) as an important cue to health. In this way, evolutionary psychological explanations of attractiveness, whether consciously or not, do as Tinbergen suggests and focus both on the *how* and on the *why* questions concerning behavior.

Tinbergen's (1963) Four Questions have had widespread influence, including in facial attractiveness research. In the remainder of this paper, I will outline the Four Questions, and explain how research in the area of facial attractiveness is guided by these principles.

The four Questions

Tinbergen identified four levels of explanation that can be used to explain the existence of a particular behavior. First, and perhaps most obvious is the *causal* level. This is a mechanistic explanation that asks what the immediate cause of the behavior was. For example, if we ask a why a woman is breastfeeding her child, a *causal* explanation might be 'because he was crying'. *Causal* explanations also extend to the cognitive and even neuroscientific realms. An explanation such as 'the baby's cry activated specific pathways in the mother's brain that caused her to initiate feeding' is also a *causal* explanation.

Second, Tinbergen specified developmental or *ontogenetic* explanations. Our breastfeeding mother might be explained in terms of her development and learning, such that 'the mother was breastfed as a child; she also observed other mothers breastfeeding their own children and read articles and had discussions about breastfeeding; now that she has her own children, she puts this experience into practice and breastfeeds her own baby'.

Both of these first two explanatory levels are commonly used in psychology. Cognitive psychologists and neuroscientists are largely *causal* in their analysis, interested as they are in mechanistic explanations of *how* the mind and brain process information. Developmental psychology is largely ontogenetic, concerned as it is with changes over time and learning. Social psychology draws on both *ontogenetic* and *causal* explanatory levels. Tinbergen's insight was, therefore, most impactful in calling for two further, evolutionary explanatory levels to be used to gain a fuller understanding of human behavior.

The third level of explanation is *phylogenetic*. This asks about the evolutionary history of a behavior, and modern interpretations of this often draw either on comparative studies with non-human animals (e.g. Waitt & Little, 2006), cross-cultural studies (Buss, 1986), particularly with 'traditional' and hunter-gatherer societies (Little et al., 2007), or by invoking the much contested concept of the Environment of Evolutionary Adaptedness (EEA; Tooby & Cosmides, 1990). Thus, our breastfeeding mother may be explained by an argument such as 'she is a mammal; mammals produce milk to feed their young, and so she does the same'.

Finally, with his fourth level of explanation, the *functional* level, Tinbergen draws upon evolutionarily *functional* explanations to ask what is the survival value of specific behaviors (Tinbergen, 1963; today we might add consideration of the behavior's value in influencing reproductive success). Our breastfeeding mother, thereby, might be described such that 'she is breastfeeding her child to give him nutrients and immune benefits that will help him to be healthy as he grows, so that he can himself reproduce and pass on my genes to the next generation'.

Face research and Tinbergen's legacy

While face researchers often do not think in terms of Tinbergen's four levels of explanation, focusing instead on individual levels of explanation to explain data, the body of literature in this field is building into a more comprehensive narrative. Particularly when researchers approach the problem from a *functional* or *phylogenetic* perspective, the hypotheses generated often lead to knowledge at the causal and *ontogenetic* levels that are unlikely to have been discovered without this perspective. Tinbergen's suggestion that observational data be considered is also being integrated into what is, at heart, an experimental science, and is being greatly enriched by consideration of comparative and anthropological literature. Contrary to Rose & Rose's (2000) suggestion that *causal* explanations are more explanatory, the application of evolutionary explanations to the problem of facial attractiveness has allowed us to understand the problem at all of Tinbergen's (1963) four levels.

Averageness

In the case of facial attractiveness, substantial research effort has been spent in identifying the *causal* (mechanistic) cues that people perceive as attractive. Early work identified that more average Caucasian faces – that is, faces close to the population mean - were rated as more attractive (Langlois & Roggman, 1990). This result was later replicated in an Asian population (Rhodes et al., 2001a). Both *ontogenetic* (developmental) and *functional* (evolutionary) explanations were proposed to explain the attractiveness of averageness. Valentine (1991) proposed the *causal* level explanation that people hold prototype faces in their minds. These prototypes are based on averaging the faces that we encounter in our lives. Valentine (1991) suggested that faces are recognized by identifying deviations from the prototype. Langlois & Roggman (1990) proposed that this explains the attractiveness of average faces. More average faces are more similar to the prototype face, therefore looking more 'face-like' and being easier to process.

Thornhill & Gangestad (1993), on the other hand, proposed an *functional* explanation for the attractiveness of averageness. They proposed that averageness is attractive because it is the opposite of distinctiveness. By avoiding potential mates with very distinctive appearance, individuals are avoiding people with high loads of deleterious recessive alleles. This evolutionary approach has since become dominant in studies of attractiveness.

Symmetry

This focus on *phylogenetic* and *functional* levels of explanation has led to hypothesis generation that often produces new knowledge at all four levels. Fluctuating asymmetry (FA) has been identified as an important contributor to mate choice in bird species, with female barn swallows preferring males with more symmetrical tales (Møller, 1993) and female zebra finches preferring more symmetrical males (Swaddle & Cuthill, 1994). This observation in birds is explained using the *functional* level idea of developmental stability. This hypothesis proposes that individuals' faces and bodies will develop symmetrically if development is not interrupted. However, most individuals experience some developmental disruption, which is manifested as fluctuating asymmetry – small deviations from perfect bilateral symmetry in the face and body. These disruptions may take the form of parasites, malnourishment or other illnesses. Researchers working on the question of human facial attractiveness used the insights offered by *phylogenetic* approaches to make hypotheses about cues to attractiveness in human faces. Symmetry has since been identified as a facial cue that enhances the attractiveness of faces in Caucasian (Perrett et al., 1999), Asian (Rhodes et al., 2001a) and Hadza (Tanzanian hunter-gatherers; Little et al., 2007) populations. Thus, this hypothesis, derived from a phylogenetic interpretation of an *functional* level explanation, led to knowledge of part of the mechanism - or causal explanation – of human facial attractiveness. Further phylogenetic thinking has since confirmed a preference for symmetrical opposite-sex faces in Rhesus macaques (Waitt & Little, 2006). It is thought that confirmation of phenomena in cross-cultural and even cross-species samples is evidence for the evolved nature of face preferences and stands opposed to the view of attractiveness as culturally defined and socially imposed.

However, the original *functional* level explanation has not found much empirical support. Rhodes et al. (2001b) measured fluctuating asymmetry from photographs, had raters rate asymmetry from the same photographs, and examined the childhood, adolescent and current medical records of the individuals in the photographs. No relationship was found between measured symmetry and any of the current or developmental health measures. A more recent and much larger study, using the ALSPAC longitudinal database, and measuring fluctuating asymmetry using a 3D laser scanner, also found no relationship between childhood illness and FA (Lawson et al., 2011).

Sexual Dimorphism

Sexual dimorphism is a facial cue that has been studied extensively in the attractiveness literature. A *functional* hypothesis posited that, since sexually dimorphic features develop under the influence of testosterone and estrogen (Penton-Voak & Chen, 2004; Law Smith et al., 2006), and since testosterone is thought to underlie honest handicapping signals of quality (Zahavi, 1975; Folstad & Karter, 1992) and estrogen is thought to be associated with female fertility (Baird et al, 1999), sexually dimorphic features should be considered attractive in both male and female faces as a cue to health and fertility (Thornhill & Gangestad, 1999). This hypothesis was further bolstered by examination of the animal literature. However, when the *causal* mechanism of this hypothesis was tested, femininity of female faces was shown to be considered attractive (Perrett et al., 1994, 1998), while women's preferences for male masculinity were found to be more complicated. Initial studies found that women preferred more feminine male faces (Perrett et al., 1998). Further thinking at the *functional* level led to predictions about masculinity preferences at the ontogenetic level – perhaps women's masculinity preferences develop differentially depending on ecological or social environment. Women who grew up in geographical regions of high pathogen load (DeBruine et al., 2010) and income inequality (Brooks et al., 2010) were found to prefer more masculine faces than those who grew up in regions of lower pathogen prevalence and income inequality. This has been explained by suggesting that, in regions of high pathogen prevalence, women should show preferences for cues to better immunocompetence (DeBruine et al., 2010), and in regions of high income inequality, women should have a preference for men who display cues of competitiveness and ambition, in order to compete in areas of more intense competition for resources (Brooks et al., 2010). In this way, *functional* level thinking led to hypothesis generation at the causal and ontogenetic levels, and to knowledge that would not otherwise have been discovered.

Color

In my own research, my investigation of skin color's impact on attractiveness was spurred by a consideration of *functional* and *phylogenetic* explanations of the variation of skin color across the world. Previous researchers had proposed *functional* level explanations. For example, while dark skin is necessary to protect against ultraviolet (UV) damage (Jablonski & Chaplin, 2000) near the equator, Frost (1986) proposed that sexual selection had driven the evolution of light skin at Northern latitudes. This led me to examine the *causal* claim that skin color affects the perceived health of human faces. I found a preference for increased lightness (CIELab L*), redness (a*) and yellowness (b*; Stephen et al., 2009a). The comparative literature showed that health is reflected in carotenoid-colored feather ornaments in bird species (Saks et al., 2003) and scales in fish (Pike et al., 2007), and that blood-based red skin color signals health and dominance and affects mate choice in primate species (Setchell, 2005, Waitt, 2006). Using this *phylogenetic* level examination of the literature, and the *functional* level hypothesis that healthy and attractive looking facial cues indicate health, I formulated and tested *causal* level hypotheses. Thus, it was found that skin carotenoid color and oxygenated blood color drive healthy appearance to a greater extent than melanin and deoxygenated blood color (Stephen et al., 2009b, 2011).

Conclusion

Here, I have argued that consideration of *functional* and *phylogenetic* level explanations for face preferences can drive hypothesis generation at the *causal* and *ontogenetic* explanatory levels. These hypotheses are often unlikely to have been formulated without consideration of the *functional* and *phylogenetic* levels. In this way, an evolutionary approach to understanding human facial attractiveness supports Tinbergen's (1963) argument that a consideration of all four explanatory levels is necessary for a full understanding of human behavior and cognition. Investigations in other areas of psychology could benefit from a similar integration of theory and examination of behavior across all four of Tinbergen's (1963) levels of explanation.

References

Baird, D., Weinberg, C. R., Zhou, H., Kamel, F., McConnaughey, D. R., Kesner, J. S. & Wilcox, A. J. (1999). Preimplantation urinary hormone profiles and the probability of conception in healthy women. Fertility and Sterility, 71, 40–49.

Brooks, R., Scott, I.M., Maklakov, A.A., Kasumovic, M.M., Clark, A.P., Penton-Voak, I.S. (2010) .National income inequality predicts women's preferences for masculinized faces better than health does. Proceedings of the Royal Society B, 278, 810-812. doi: 10.1098/rspb.2010.0964

Buss, D. (1986). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behavioural and Brain Sciences, 12, 1-49. doi: http://dx.doi.org/10.1017/S0140525X00023992

Coetzee, V., Perrett, D.I., Stephen, I.D. (2009). Facial adiposity: A cue to health? Perception, 38, 1700-1711. doi:10.1068/p6423

DeBruine, L.M., Jones, B.C., Crawford, J.R., Welling, L.L.M., Little, A.C. (2010). The health of a nation predicts their mate preferences: Cross-cultural variation in women's preferences for masculinized male faces. Proceedings of the Royal Society of London B, 277, 2405-2410. doi: 10.1098/rspb.2009.2184

Folstad, I. & Karter, A.J. (1992). Parasites, bright males and the immunocompetence handicap. The American Naturalist, 139, 603-622. doi: 10.1086/285346

Frost, P. (1994) Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. Perceptual and Motor Skills, 79, 507-514.

Jablonski, N.G., & Chaplin, G. (2000). The evolution of human skin coloration. Journal of Human Evolution, 39, 57-106.

Kokko, H., Brooks, R., Jennions, M.D., Morley, J. (2003). The evolution of mate choice and mating biases. Proceedings of the Royal Society B, 270, 653-664. doi: 10.1098/rspb.2002.2235

Langlois, J.H. & Roggman, L.A. (1990). Attractive faces are only average. Psychological Science, 1, 115-121. doi: 10.1111/j.1467-9280.1990.tb00079.x

Lawson, D. Pound, N., Penton-Voak, I.S., Toma, A. & Richmond, S. (2011). Childhood health and facial symmetry in contemporary British teenagers. Human Behaviour and Evolution Society Conference Proceedings, 23, 60-61.

Law Smith, M.J., Perrett, D.I., Jones, B.C., Cornwell, R.E., Moore, F.R., Feinberg, D.R., Boothroyd, L.G., Durrani, S.J., Stirrat, M.R., Whiten, S., Pitman, R.M., Hillier, S.G. (2006). Facial appearance is a cue to oestrogen levels in women. Proceedings of the Royal Society B, 273, 135-140. doi: 10.1098/rspb.2005.3296

Little, A.C., Apicella, C.L., Marlowe, F.W. (2007). Preferences for symmetry in human faces in two cultures: data from the UK and the Hadza, an isolated group of hunter-gatherers. Proceedings of the Royal Society B, 274, 3113-3117. http://dx.doi.org/10.1098/rspb.2007.0895

Møller, A.P. (1993). Female preference for apparently symmetrical male sexual ornaments in the barn swallow Hirundo rustica. Behavioural Ecology and Sociobiology, 32, 371-376. doi: 10.1007/BF00168820

Penton-Voak, I.S. & Chen, J.Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. Evolution and Human Behavior, 25, 229-241. http://dx.doi.org/10.1016/j.evolhumbehav.2004.04.003

Perrett, D.I., May, K.A., Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. Nature, 368, 239-242. doi:10.1038/368239a0

Perrett, D.I., Lee, K.J., Penton-Voak, I.S., Rowland, D., Yoshikawa, S., Burt, D.M., Henzi, S.P., Castles, D.L., Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. Nature, 394, 884-887. doi:10.1038/29772

Perrett, D.I., Burt, D.M., Penton-Voak, I.S., Lee, K.J., Rowland, D.A., Edwards, R. (1999). Symmetry and human facial attractiveness. Evolution and Human Behavior, 20, 295-307. http://dx.doi.org/10.1016/S1090-5138(99)00014-8

Pike, T.W., Blount, J.D., Lindstrom, J., Metcalfe, N.B. (2007). Availability of noncarotenoid antioxidants affects the expression of a carotenoid-based sexual ornament. Biology Letters, 3, 353-356. doi: 10.1098/rsbl.2007.0072

Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R., Akamatsu, S. (2001). Attractiveness of facial averageness and symmetry in non-Western cultures: In search of biologically based standards of beauty. Perception, 30, 611-625. doi: 10.1068/p3123

Rhodes, G., Zebrowitz, L.A., Clark, A., Kalick, S.M., Hightower, A., McKay, R. (2001b). Do facial averageness and symmetry signal health? Evolution and Human Behavior, 22, 31-46.

Rose, H., & Rose, S. (2000). Introduction. In H. Rose & S. Rose (Eds.) Alas Poor Darwin: Arguments Against Evolutionary Psychology (pp. 1-15). New York: Harmony Books.

Saks, L., Ots, I., Horak, P. (2003). Carotenoid-based plumage coloration of male greenfinches reflects health and immunocompetence. Oecologia, 134, 301-307.

Stephen, I.D., Law Smith, M.J., Stirrat, M.R., Perrett, D.I., (2009). Facial skin coloration affects perceived health of human faces. International Journal of Primatology, 30, 845-857. doi: 10.1007/s10764-009-9380-z

Stephen, I.D., Coetzee, V., Law Smith, M.J., Perrett, D.I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. PLOS ONE, 4, e5083. doi: 10.1371/journal.pone.0005083

Stephen, I.D., Coetzee, V., Perrett, D.I. (2011). Carotenoid and melanin pigment coloration affect perceived human health. Evolution and Human Behavior, 32, 216-227. doi: 10.1016/j.evolhumbehav.2010.09.003

Swaddle, J.P., Cuthill, I.C. (1994). Preference for symmetric males by female zebra finches. Nature, 367, 165-166.

Thornhill, R. & Gangestad, S.W. (1993). Human facial beauty. Human Nature, 4, 237-269. doi: 10.1007/BF02692201

Thornhill, R. & Gangestad, S.W. (1999). Facial attractiveness. Trends in Cognitive Sciences, 3, 452-460.

Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift fur Tierpsychologie, 20, 410-433. doi: 10.1111/j.1439-0310.1963.tb01161.x

Tooby J. and Cosmides L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. Ethology and Sociobiology, 11, 375-424.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion and race in face recognition. The Quarterly Journal of Experimental Psychology Section A, 43, 161-204. doi: 10.1080/14640749108400966

Waitt, C. & Little, A.C. (2006). Preferences for symmetry in conspecific facial shape among Macaca mulatta, 27, 133-145. doi: 10.1007/ s10764-005-9015-y

Waitt, C. (2006). Selective attention toward female secondary sexual color in male rhesus macaques. American Journal of Primatology, 68, 738-744. doi: 10.1002/ajp.20264

Zahavi, A. (1975). Mate selection – a selection for a handicap. Journal of Theoretical Biology, 53, 205-214.