



## CURRENT ISSUES – PERSPECTIVES AND REVIEWS

**Perspectives: Hamilton's Legacy: Mechanisms of Kin Recognition in Humans**

Jill M. Mateo

Department of Comparative Human Development, Institute for Mind and Biology, The University of Chicago, Chicago, IL, USA

(Invited Review)

**Correspondence**

Jill M. Mateo, Department of Comparative Human Development & Institute for Mind and Biology, The University of Chicago, 940 East 57th Street, Chicago, IL 60637, USA.  
E-mail: [jmateo@uchicago.edu](mailto:jmateo@uchicago.edu)

Received: October 18, 2014

Initial acceptance: November 18, 2014

Final acceptance: December 26, 2014

(M. Hauber)

doi: 10.1111/eth.12358

**Keywords:** kin recognition, humans, Hamilton, inclusive fitness, discrimination

**Abstract**

The behavior literature is replete with examples of individuals exhibiting costly acts that benefit someone else. These examples troubled Darwin so much so that he thought they would be fatal to his theory of natural selection. A century later, W. D. Hamilton refined that theory by showing, quantitatively, that such acts could be favored if the individuals involved were relatives. His theory of inclusive fitness is generally considered one of the greatest theoretical advances in evolution since Darwin's time. Less appreciated from Hamilton's 1964 paper is the hypothesis that mechanisms favoring accurate kin recognition will also be selected. Here, I review those recognition mechanisms and survey the literature on human kin recognition. Although not often considered, humans both produce cues to kinship that vary with genetic relatedness and have perceptual abilities to detect these cues in others and assess that relatedness. The potential functions of these abilities are discussed. Importantly, gaps in our understanding of the development and use of recognition mechanisms are noted.

**Introduction**

Fifty years ago, W. D. Hamilton not only made the most significant refinement to Darwin's theory of natural selection with his concept of inclusive fitness (Hamilton 1964a), but also predicted the evolution of mechanisms to facilitate the accurate recognition of kin (Hamilton 1964b). He posited that if one 'could learn to recognize those of his neighbors who were really close relatives and could devote his beneficial actions to them alone an advantage to inclusive fitness would at once appear' (Hamilton 1964b, p. 21). Kin recognition is an unobservable internal process of assessing genetic relatedness that is inferred by kin discrimination, the observable differential treatment of conspecifics based on cues that vary with relatedness. Hamilton posited that if relationships persist, weak selection could favor the evolution of discrimination, even among distant kin. He added that although it may seem improbable that genes could cause the

perception of like genes in other individuals, at the minimum, genes should affect '(1) some perceptible feature of the organism, (2) the perception of that feature, and (3) the social response consequent upon what was perceived' (Hamilton 1964b; p. 25). Today, an understanding of kin recognition involves three components: the production of unique phenotypic cues, or 'labels', the perception of these labels and their degree of correspondence with a 'recognition template' (these components are the mechanism of recognition), and the action taken by an animal as a function of the similarity between its template and an encountered phenotype (Beecher 1982; Sherman & Holmes 1985; Reeve 1989; Gamboa et al. 1991; Mateo 2003, 2004). In this essay, honoring the 50th anniversary of Hamilton's theory of inclusive fitness and mechanisms of kin recognition, I discuss these processes in humans, briefly summarize behaviors that influence inclusive fitness and then survey the literature on mechanisms leading to kin-differentiated behaviors.

Recognition can be based on prior association, as organisms learn the labels of related individuals during early development (e.g., siblings) and later discriminate these familiar individuals from unfamiliar ones, or, organisms can learn their own phenotypes and/or those of their familiar kin and later compare or match the phenotypes of unknown individuals to this learned template (phenotype matching). Both mechanisms involve comparisons between phenotypes and templates, but prior association leads to recognition of familiar individuals only, whereas phenotype matching, through generalization from templates, permits 'recognition' of unfamiliar kin (Holmes & Sherman 1982; Sherman et al. 1997; Tang-Martinez 2001; Mateo 2004). This distinction is important when considering kin-directed behaviors such as nepotism or inbreeding avoidance, because phenotype matching allows more refined discrimination among kin classes than does prior association. Note that some species can utilize both recognition mechanisms (and others) depending on the age of kin and the context (Mateo 2008). Finally, phenotype matching would be difficult if production cues do not vary predictably with kinship, but such cues could be used reliably for recognition when prior association correlates with relatedness, such as for parent–offspring recognition.

Kin-recognition abilities have been studied most broadly in rodents (reviewed in Mateo 2003), although several species in other taxa have been elegantly studied (birds: Beecher 1988; insects: Getz 1991; Gamboa 1996; Waldman 1991; anurans: Blaustein & Waldman 1992; Pfennig et al. 1999; primates: Kazem & Widdig 2013; Pfefferle et al. 2014). Most empirical studies of kin-recognition mechanisms have focused on visual and olfactory discrimination of conspecifics (see below), but relatedness potentially could be assessed through other modalities, such as vibrational signaling (e.g., Randall 1993; O'Connell-Rodwell et al. 2007), behavioral cues (e.g., Michener 1973; Boncoraglio et al. 2009), or vocalizations (e.g., Rendall et al. 1996; Insley 2001; Briefer et al. 2012; Akcay et al. 2013). It is important to note that there may be multiple, overlapping modalities indicating kinship (e.g., Coleman 2009).

According to Hamilton's theory of inclusive fitness, costly behaviors can evolve when the benefit ( $b$ ) to the recipient, devalued by the coefficient of relationship ( $r$ ), is greater than the cost ( $c$ ) to the actor ( $rb > c$ ). Here, benefits and costs are measured in terms of fitness effects (Hamilton 1964a). Among humans, there are many examples of kin-biased behaviors, although not all involve costly behaviors. For example, spouses and step children are more likely to be killed in

households than are genetic kin (Daly & Wilson 1980, 1982a), demonstrating clear fitness differentials as a function of relatedness. Adoption occurs more frequently among close kin ( $r = 0.125\text{--}0.25$ ) than more distant kin ( $r \leq 0.0625$ ); such acts may constrain future reproduction by the adopting parent (Silk 1980). People leave a larger proportion of their estate to their close kin than to distant kin or non-kin (Smith et al. 1987; Judge & Hrdy 1992; see also Kalbarczyk-Steclik & Nicinska 2012 for data on financial transfers to parents as a function of relatedness). Genetic fathers also invest more in their children than do stepfathers (e.g., Anderson et al. 1999). Differential financial investments may not be costly to the parents, certainly not after death, but can have long-lasting effects on the offspring, particularly when young. Although helping behaviors (e.g., with housing, finances, health) are more likely to be reciprocated among friends, close kin help each other more often than distant kin, and larger acts of helping are more likely to come from kin (e.g., Essock-Vitale & McGuire 1985; see also Korchmaros 2006). These helping behaviors are not costly in fitness terms and may only have short-term benefits, but demonstrate that even when the stakes are low, individuals pay attention to kinship and behave differentially.

How do humans assess genetic relatedness? Conventionally, we know who our kin are because we grow up with them or our parents inform us (e.g., Lieberman et al. 2007), and the established kinship terminology of each culture can provide additional indicators of relatedness (e.g., Fox 1967). Barring errors or intentional withholding of information (e.g., in cases of adoption), this is a reliable mechanism. Indeed, sharing a parent and growing up together are excellent cues to relatedness, at least for close kin (Lieberman et al. 2007). However, humans are capable of using several perceptual modalities and physiological cues to discriminate among familiar kin and to discriminate among unfamiliar kin and non-kin.

### Visual Modality of Kin Recognition

Given the reliance of humans on visual cues (indeed, there are neural areas that specifically respond to faces; see below), facial resemblance might be expected to serve as indicators of kinship. Recognition of offspring would be especially important for appropriate allocation of parental investment. Mothers can recognize photographs of their infants within 33 h of birth, and strangers can match photographs of mothers to their infants, suggesting a physical resemblance among kin (Porter et al. 1984). Because the mothers

had direct contact with their infants ( $\bar{X} = 4.7$  h), their recognition could be at the level of individual (via familiarity) or kin (via familiarity or phenotype matching), but the strangers did not have contact with the infants, so their ability to match photographs is based on kin recognition through phenotype matching. Notably, however, in social situations, mothers and their families and friends are more likely to say a newborn resembles its father more than its mother, perhaps to reassure the father of paternity (Daly & Wilson 1982b; Regalski & Gaulin 1993; McLain et al. 2000; Alvergne et al. 2007). Using photographs of children at one, ten, and twenty years of age and their parents, Christenfeld & Hill (1995) reported that people can match fathers to 1-yr-olds, consistent with the idea that babies resemble their fathers. However, subsequent efforts to replicate this study have found that subjects can better match children to mothers (Nesse et al. 1990; McLain et al. 2000), to both parents equally well (Bredart & French 1999; Bressan & Grassi 2004), or to mothers as newborns and then to same-sex parent starting at 2–3 yr of age (Alvergne et al. 2007). People can also match faces of siblings to whom they are not related (Maloney & Dal Martello 2006) and assess the relatedness of pairs of close and distant kin (e.g., grandparents and grandchildren, aunts and nephews/nieces; Kaminski et al. 2009). Thus, there appear to be cues to genetic relatedness in facial features, but it does not appear that selection has favored newborns to look like (or not look like) their fathers specifically.

Because of the risk of cuckoldry and misdirected investment, and known preferential investment in self-resembling offspring (see above), many studies have investigated the role of resemblance in hypothetical social contexts, with mixed results. This work typically involves morphing an image of the subject with infant photographs, below the threshold of conscious detection, and asking the subject a series of questions about investment in or attraction to that infant versus others. Platak and colleagues found that males would be more likely to invest in a child whose face had been morphed with their own, and would be more likely to adopt it and less likely to punish it, whereas women are less affected by self-resemblance (Platak et al. 2002, 2003, 2004; Volk 2007). However, other studies have found no sex difference or that women prefer self-resembling faces (DeBruine 2004b; Bressan et al. 2009; Welling et al. 2011). And there is no evidence that males are better than females at assessing resemblance. The equivocal findings may be due in part to the ages of the target children or the morphing algorithm,

among other methodological differences. For example, female preferences for self-resembling faces change across the menstrual cycle, perhaps reflecting shifting benefits of affiliating with kin (DeBruine et al. 2005). Finally, prosocial attitudes toward self-resembling faces are higher than for twin-resembling faces and do not differ between mono- and dizygotic twins (Bressan & Zucchi 2009). American siblings report more closeness and prosocial behavior toward siblings who more closely resemble them (Lewis 2011). Thus, facial similarity can affect the nature of social dynamics within families.

Facial morphing techniques have been used to test predictions of inbreeding-avoidance theories; specifically, people should perceive faces closely resembling their family as unattractive (see DeBruine et al. 2008 for a review; see also Rushton & Bons 2005 for genetic similarity and mate choice as a function of environmental factors). Same-sex faces morphed with a person's own face are judged as more attractive than other faces (DeBruine 2004a), whereas opposite-sex morphed faces are judged as more trustworthy but less attractive for a short-term relationship (DeBruine 2005). Faces that are manipulated to be dissimilar to an individual (negative resemblance) are rated as less trustworthy and attractive (Krupp et al. 2012), which the authors suggest could be a mechanism for the allocation of spite. Individuals rate photographs of their romantic partners morphed with their own photograph (beneath the level of detection) as more attractive than partners' photographs morphed with other individuals' photographs, consistent with an optimal level of outbreeding and inbreeding (Laeng et al. 2013).

In many taxonomic groups, young learn the features of parents during critical periods of development and prefer those features in others when reproductively mature, a process called sexual imprinting (ten Cate & Vos 1999; Kendrick et al. 2001). In turn, in humans, many studies also have found significant facial resemblance among married couples, and one study on adopted adult women suggests that such similarities come about through sexual imprinting on opposite-sex parents rather than phenotype matching (Berezkei et al. 2004; but see Rantala & Marcinkowska 2011). This preference for self-resemblance in opposite-sex, but not same-sex, individuals by women may be modulated by self-reports of emotional closeness to fathers but not mothers (Watkins et al. 2011).

Which facial cues provide information about genetic relatedness? Although the eye region is more important than the mouth region, the upper half of

the face provides even more information than the eyes alone (Dal Martello & Maloney 2006; see also Alvergne et al. 2014; Ghahramani et al. 2014). The lower face changes across development, especially in males, and thus provides fewer stable cues to genetic relatedness (e.g., Dal Martello & Maloney 2006; Alvergne et al. 2014).

In humans, facial processing occurs largely in the fusiform gyrus (also called the fusiform facial area; Platek & Kemp 2009; sheep and monkeys also have areas in the temporal cortex that respond preferentially to faces; Kendrick & Baldwin 1987; Perrett et al. 1988). Functional magnetic resonance imaging (fMRI) reveals that faces activate the fusiform gyrus similarly in both male and female humans, as expected for facial processing, but females show greater activation when viewing children's faces, as predicted by sex differences in parental investment (Platek et al. 2005). Detection of resemblance in children's faces activates the left frontal cortex in men, but not women, suggesting possible decision-making processes involved in assessment of paternity and possible investment (Platek et al. 2004). Kin faces (versus unknown faces) activate regions involved in self-face recognition (e.g., anterior cingulate gyrus and medial frontal gyrus), whereas kin versus friend faces activate posterior cingulate and cuneus, again suggesting a need to process for identification (Platek & Kemp 2009). Multiple mechanisms for discriminating kin faces may have been favored by selection due to the need for fast and accurate recognition.

### Olfactory Modality of Kin Recognition

Olfactory cues may be the most reliable kin labels for assessing kinship, as they are known to covary with genetic relatedness in a variety of taxa (insects: Jaisson 1991; Gamboa 1996; Dani et al. 2004; amphibians: Waldman 1991; mammals: Brown & MacDonald 1985; Halpin 1986; Swaisgood et al. 1999; Beauchamp & Yamazaki 2003; Johnston 2003; fish: Olsén et al. 1998; Neff & Sherman 2003; birds: Coffin et al. 2011). Kin recognition in some vertebrates is facilitated by the major histocompatibility complex (MHC), which influences the production of distinct odors (Lenington & Coopersmith 1992; Brown & Eklund 1994; Olsén et al. 1998; Eggert et al. 1999). Odors, or other recognition cues, can have multiple functions, particularly in mammals where odors are often complex mixtures of several to hundreds of compounds (Albone 1984). In addition to indicating an organism's individual identity, age, sex, or relatedness, an odor may also reveal its location, diet, health,

reproductive status, or even genetic quality (Brown & MacDonald 1985; Penn & Potts 1998; Johnston 2003; Mateo 2006).

Studies of odor-based human discrimination began in earnest in the early 1980s by Richard Porter and colleagues. For example, siblings and mothers can identify clothing worn by individual children in a family, and parents can correctly distinguish between the odors of shirts worn by identical twins, demonstrating the robustness of odors for recognition (Porter & Moore 1981; see also Weisfeld et al. 2003). Mothers, but not fathers, can identify their infant's odor with as little as 2 h of direct contact (Porter & Cernoch 1983; Russell et al. 1983; and at all ages, women are better than men at identifying odors; Doty et al. 1985). Fathers, grandmothers, and aunts can also identify their related infant with little prior contact (Porter et al. 1986; but see Russell et al. 1983 for contrasting data on fathers), suggesting a shared genetic component in the odors of family members. Infants are preferentially attracted to the breast or axillary odor of their mother as versus unfamiliar females within days of birth (Schaal 1988; Porter et al. 1992). Note that the prior examples could be considered instances of odor-based individual recognition, rather than examples of kin recognition *per se*, but at the ultimate level both yield the same fitness benefits. Also note that odor-based recognition is not limited to kin. For example, high school students can pick the odor of their friend from an array of odors, using the prior association mechanism (Olsson et al. 2006; see also Weisfeld et al. 2003).

Odor-based recognition of kin can go beyond simple familiarity with individual's cues, however. People can match the odors of mothers and their children, despite being unrelated to the odor donors, indicating discrimination based on phenotype matching. That husbands and wives cannot be reliably matched by odor indicates that odor recognition is mediated through shared genes rather than a shared environment (Porter et al. 1985). Accordingly, extended periods of separation do not diminish the ability to recognize kin (Porter et al. 1986). Finally, an habituation–discrimination study using rats shows that human odors covary directly with genetic relatedness, with close kin (e.g., mother, sister) having more similar odors than distant kin (e.g., aunt, niece, grandmother), which in turn have more similar odors than non-kin (Ables et al. 2007).

Odors can also influence social interactions. For example, mothers who are better able to recognize their infant's odor also report better nursing experiences and positive mothering attitudes (Fleming et al.



1995). Fathers have greater attachment and show more affection toward offspring they can identify by odor. In contrast, mothers use more punishment with offspring whose odors they cannot identify and use less punishment with children with odors they rate as pleasant (Dubas et al. 2009). When presented with odors of 2-d-old infants while in an fMRI scanner, mothers have increased processing in the thalamus and dorsal caudate nucleus compared with nulliparous women, which suggests that infant odors might prepare mothers for reinforcement learning, and both groups have increased processing in dopaminergic neostriatal areas, which might facilitate the bonding process (Lundstrom et al. 2013). Higher levels of cortisol can facilitate recognition of and attraction to an infant's odor by first-time mothers (Fleming et al. 1997). In a population in Senegal, the amount of investment by fathers is positively correlated with the degree of odor (and facial) similarity between fathers and children, suggesting that men attend to possible cues to paternity, and such discrimination influences child growth and health (Alvergne et al. 2009). Finally, the MHC of humans, human leukocyte antigen (HLA), influences mate choice in at least one population, leading to moderate disassortative mating (Ober et al. 1997), and the HLA influences odor preferences (Jacob et al. 2002), suggesting that odors may mediate mate choice. This has functional consequences, because couples with dissimilar HLAs have fewer miscarriages than those with similar HLAs (Ober 1999; cf. Hedrick & Black 1997). The MHC/HLA may play a role in mate choice to increase heterogeneity, especially in immune functioning, and to minimize inbreeding (e.g., Penn & Potts 1998), and thus genetic diversity regarding the immune function of offspring would be increased by disassortative mating.

#### Acoustic Modality of Kin Recognition

Because kin labels best serve as cues for relatedness when they are heritable, acoustic cues are seldom good candidates. However, through prior association they can be used to recognize familiar kin. For example, both mothers and fathers reliably recognize their infant's cries with experience (Gustafsson et al. 2013). Fetuses respond with tachycardia to their mother's and father's voices, but prefer their mother's voice after birth (Kisilevsky et al. 2003; Lee & Kisilevsky 2014). This is likely due to differential exposure to the voices, as fetuses are capable of learning speech sounds during the third trimester (Decasper et al. 1994). It is possible that adults use vocal cues for kin

recognition as well (see Rendall et al. 1996 for an example in non-human primates).

#### Development of Kin-Recognition Abilities

Hamilton (1964b) suggested that recognition of young will improve or become more accurate as the likelihood of young mixing with non-kin increases. For example, female Belding's ground squirrels (*Urocitellus beldingi*) switch from spatially based recognition of their young to prior association-based recognition when young emerge above-ground from their natal burrows and potentially encounter other juveniles, and those juveniles may enter that female's own burrow (Holmes & Sherman 1982). Although many studies have focused on the mechanisms of kin recognition in humans and other species, few have addressed the development of such abilities. In humans, adults can match photographs of children and parent's faces, and vice versa (Kaminski et al. 2010; references above), but children do not perform as well (Kaminski et al. 2012). Children aged 5–11 yr can match photographs of infants to parents at levels above chance, but not parents to infants. The authors suggest this difference in ability may be due to greater experience with young faces, despite the presumed functional benefit of recognizing adult kin. However, as noted above, odor-based recognition abilities are well developed in infants, perhaps because of prenatal exposure to kin odors or because odors are more developmentally stable than faces.

#### Conclusion

Hamilton's seminal contribution to our understanding of inclusive fitness in 1964 revolutionized how we think about social behavior across all taxa. Less appreciated but no less important was his attention to the proximate mechanisms that direct helping behaviors to the appropriate targets. In humans, given our long periods of development, social memories, and verbal communication styles, physiological cues to kinship may seem unnecessary. But as I show here, there are many modalities producing such kin labels that covary with genetic relatedness, particularly visual and olfactory cues. How and when we use these cues can inform the ways that natural and sexual selection have favored them. Future work is needed to explore the development of kin-recognition abilities, the use of other modalities (e.g., acoustic) in kin discrimination, our ability to recognize unfamiliar kin, and the full extent to which these recognition mechanisms

influence our social relationships. Lastly, as with most species, we have some understanding of the production, perception, and action components of kin recognition, but an integration of the three still remains necessary.

### Acknowledgements

I thank Mark Hauber, Glenn Weisman, and an anonymous reviewer for helpful comments on the manuscript. I declare no conflict of interests.

### Literature Cited

- Ables, E. A., Kay, L. M. & Mateo, J. M. 2007: Rats assess degree of relatedness from human odors. *Physiol. Behav.* **90**, 726–732.
- Akçay, C., Swift, R. J., Reed, V. A. & Dickinson, J. L. 2013: Vocal kin recognition in kin neighborhoods of western bluebirds. *Behav. Ecol.* **24**, 898–905.
- Albone, E. S. 1984: *Mammalian Semiochemistry*. John Wiley & Sons Inc, New York.
- Alvergne, A., Faurie, C. & Raymond, M. 2007: Differential facial resemblance of young children to their parents: who do children look like more? *Evol. Hum. Behav.* **28**, 135–144.
- Alvergne, A., Faurie, C. & Raymond, M. 2009: Father–offspring resemblance predicts paternal investment in humans. *Anim. Behav.* **78**, 61–69.
- Alvergne, A., Perreau, F., Mazur, A., Mueller, U. & Raymond, M. 2014: Identification of visual paternity cues in humans. *Biol. Lett.* **10**, 20140063.
- Anderson, K. G., Kaplan, H., Lam, D. & Lancaster, J. 1999: Paternal care by genetic fathers and stepfathers II: reports by Xhosa high school students. *Evol. Hum. Behav.* **20**, 433–451.
- Beauchamp, G. K. & Yamazaki, K. 2003: Chemical signalling in mice. *Biochem. Soc. Trans.* **31**, 147–151.
- Beecher, M. D. 1982: Signature systems and kin recognition. *Am. Zool.* **22**, 477–490.
- Beecher, M. D. 1988: Kin recognition in birds. *Behav. Genet.* **18**, 465–482.
- Bereczkei, T., Gyuris, P. & Weisfeld, G. E. 2004: Sexual imprinting in human mate choice. *Proc. R. Soc. B-Biol. Sci.* **271**, 1129–1134.
- Blaustein, A. R. & Waldman, B. 1992: Kin recognition in anuran amphibians. *Anim. Behav.* **44**, 207–221.
- Boncoraglio, G., Caprioli, M. & Saino, N. 2009: Fine-tuned modulation of competitive behaviour according to kinship in barn swallow nestlings. *Proc. R. Soc. B-Biol. Sci.* **276**, 2117–2123.
- Bredart, S. & French, R. M. 1999: Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld and Hill (1995). *Evol. Hum. Behav.* **20**, 129–135.
- Bressan, P. & Grassi, M. 2004: Parental resemblance in 1-yr-olds and the Gaussian curve. *Evol. Hum. Behav.* **25**, 133–141.
- Bressan, P. & Zucchi, G. 2009: Human kin recognition is self-rather than family-referential. *Biol. Lett.* **5**, 336–338.
- Bressan, P., Bertamini, M., Nalli, A. & Zanutto, A. 2009: Men do not have a stronger preference than women for self-resemblant child faces. *Arch. Sex. Behav.* **38**, 657–664.
- Briefer, E. F., de la Torre, M. P. & McElligott, A. G. 2012: Mother goats do not forget their kids' calls. *Proc. R. Soc. B-Biol. Sci.* **279**, 3749–3755.
- Brown, J. L. & Eklund, A. 1994: Kin recognition and the major histocompatibility complex: an integrative review. *Am. Nat.* **143**, 435–461.
- Brown, R. E. & MacDonald, D. W. 1985: *Social Odours in Mammals*, Vol. 1. Oxford Univ. Press, New York.
- ten Cate, C. & Vos, D. R. 1999: Sexual imprinting and evolutionary processes in birds: a reassessment. *Adv. Study Behav.* **28**, 1–31.
- Christenfeld, N. J. S. & Hill, E. A. 1995: Whose baby are you? *Nature* **378**, 669.
- Coffin, H. R., Watters, J. V. & Mateo, J. M. 2011: Odor-based recognition of familiar and related conspecifics: a first test conducted on captive Humboldt penguins (*Spheniscus humboldti*). *PLoS ONE* **6**, e25002.
- Coleman, S. W. 2009: Taxonomic and sensory biases in the mate-choice literature: there are far too few studies of chemical and multimodal communication. *Acta Ethol.* **12**, 45–48.
- Dal Martello, M. F. & Maloney, L. T. 2006: Where are kin recognition signals in the human face? *J. Vis.* **6**, 1356–1366.
- Daly, M. & Wilson, M. 1980: Discriminative parental solicitude: a biological perspective. *J. Marriage Fam.* **42**, 277–288.
- Daly, M. & Wilson, M. 1982a: Homicide and kinship. *Am. Anthropol.* **84**, 372–378.
- Daly, M. & Wilson, M. 1982b: Whom are newborn babies said to resemble? *Ethol. Sociobiol.* **3**, 69–78.
- Dani, F. R., Foster, K. R., Zacchi, F., Seppä, P., Massolo, A., Carelli, A., Arevalo, E., Queller, D. C., Strassmann, J. E. & Turillazzi, S. 2004: Can cuticular lipids provide sufficient information for within-colony nepotism in wasps? *Proc. R. Soc. B-Biol. Sci.* **271**, 745–753.
- DeBruine, L. M. 2004a: Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proc. R. Soc. B-Biol. Sci.* **271**, 2085–2090.
- DeBruine, L. M. 2004b: Resemblance to self increases the appeal of child faces to both men and women. *Evol. Hum. Behav.* **25**, 142–154.

- DeBruine, L. M. 2005: Trustworthy but not lust-worthy: context-specific effects of facial resemblance. *Proc. R. Soc. B-Biol. Sci.* **272**, 919–922.
- DeBruine, L. M., Jones, B. C. & Perrett, D. I. 2005: Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Horm. Behav.* **47**, 379–383.
- DeBruine, L. M., Jones, B. C., Little, A. C. & Perrett, D. I. 2008: Social perception of facial resemblance in humans. *Arch. Sex. Behav.* **37**, 64–77.
- Decasper, A. J., Lecanuet, J. P., Busnel, M. C., Granier-deferre, C. & Maugeais, R. 1994: Fetal reactions to recurrent maternal speech. *Infant Behav. Dev.* **17**, 159–164.
- Doty, R. L., Applebaum, S., Zusho, H. & Settle, R. G. 1985: Sex differences in odor identification ability: a cross-cultural analysis. *Neurophysiologia* **23**, 667–672.
- Dubas, J. S., Heijkoop, M. & van Aken, M. A. G. 2009: A preliminary investigation of parent-progeny olfactory recognition and parental investment. *Hum. Nat.* **20**, 80–92.
- Eggert, F., Ferstl, R. & Muller-Ruchholtz, W. 1999: MHC and olfactory communication in humans. In: *Advances in Chemical Signals in Vertebrates* (Johnston, R. E., Muller-Schwarze, D. & Sorensen, P. W., eds). Plenum, New York, pp. 181–188.
- Essock-Vitale, S. M. & McGuire, M. T. 1985: Women's lives viewed from an evolutionary perspective. II. Patterns of helping. *Ethol. Sociobiol.* **6**, 155–173.
- Fleming, A. S., Corter, C., Surbey, M., Franks, P. & Steiner, M. 1995: Postpartum factors related to mother's recognition of newborn infant odours. *J. Reprod. Infant Psychol.* **13**, 197–210.
- Fleming, A. S., Steiner, M. & Corter, C. 1997: Cortisol, hedonics, and maternal responsiveness in human mothers. *Horm. Behav.* **32**, 85–98.
- Fox, R. 1967: *Kinship and Marriage: An Anthropological Perspective*. Penguin, Baltimore.
- Gamboa, G. J. 1996: Kin recognition in social wasps. In: *Natural History and Evolution of Paper Wasps* (Turillazzi, S. & West-Eberhard, M. J., eds). Oxford Univ. Press, Oxford, pp. 161–177.
- Gamboa, G. J., Reeve, H. K. & Holmes, W. G. 1991: Conceptual issues and methodology in kin-recognition research: a critical discussion. *Ethology* **88**, 109–127.
- Getz, W. M. 1991: The honey bee as a model kin recognition system. In: *Kin Recognition* (Hepper, P. G., ed.). Cambridge Univ. Press, Cambridge, UK, pp. 358–412.
- Ghahramani, M., Yau, W. Y. & Teoh, E. K. 2014: Family verification based on similarity of individual family member's facial segments. *Mach. Vis. Appl.* **25**, 919–930.
- Gustafsson, E., Levrero, F., Reby, D. & Mathevon, N. 2013: Fathers are just as good as mothers at recognizing the cries of their baby. *Nat. Comm.* **4**, 1698.
- Halpin, Z. T. 1986: Individual odors among mammals: origins and functions. *Adv. Study Behav.* **16**, 39–70.
- Hamilton, W. D. 1964a: The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16.
- Hamilton, W. D. 1964b: The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52.
- Hedrick, P. W. & Black, F. L. 1997: HLA and mate selection: no evidence in South Amerindians. *Am. J. Hum. Genet.* **61**, 505–511.
- Holmes, W. G. & Sherman, P. W. 1982: The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.* **22**, 491–517.
- Insley, S. J. 2001: Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* **61**, 129–137.
- Jacob, S., McClintock, M. K., Zelano, B. & Ober, C. 2002: Paternally inherited HLA alleles are associated with women's choice of male odor. *Nat. Genet.* **30**, 175–179.
- Jaisson, P. 1991: Kinship and fellowship in ants and social wasps. In: *Kin Recognition* (Hepper, P. G., ed.). Cambridge Univ. Press, Cambridge, UK, pp. 60–93.
- Johnston, R. E. 2003: Chemical communication in rodents: from pheromones to individual recognition. *J. Mammal.* **84**, 1141–1162.
- Judge, D. S. & Hrdy, S. B. 1992: Allocation of accumulated resources among close kin: inheritance in Sacramento, California, 1890–1984. *Ethol. Sociobiol.* **13**, 495–522.
- Kalbarczyk-Steclik, M. & Nicinska, A. 2012: Private transfers to parents from their genetically related and non-genetically related children. *J. Fam. Stud.* **18**, 36–46.
- Kaminski, G., Dridi, S., Graff, C. & Gentaz, E. 2009: Human ability to detect kinship in strangers' faces: effects of the degree of relatedness. *Proc. R. Soc. B-Biol. Sci.* **276**, 3193–3200.
- Kaminski, G., Meary, D., Mermillod, M. & Gentaz, E. 2010: Perceptual factors affecting the ability to assess facial resemblance between parents and newborns in humans. *Perception* **39**, 807–818.
- Kaminski, G., Gentaz, E. & Mazens, K. 2012: Development of children's ability to detect kinship through facial resemblance. *Anim. Cogn.* **15**, 421–427.
- Kazem, A. J. N. & Widdig, A. 2013: Visual phenotype matching: cues to paternity are present in rhesus macaque faces. *PLoS ONE* **8**, e55846.
- Kendrick, K. M. & Baldwin, B. A. 1987: Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. *Science* **236**, 448–450.
- Kendrick, K. A., Haupt, M. A., Hinton, M. R., Broad, K. D. & Skinner, J. D. 2001: Sex differences in the influence of mothers on the sociosexual preferences of their offspring. *Horm. Behav.* **40**, 322–338.
- Kisilevsky, B. S., Hains, S. M. J., Lee, K., Xie, X., Huang, H. F., Ye, H. H., Zhang, K. & Wang, Z. P. 2003: Effects of

- experience on fetal voice recognition. *Psychol. Sci.* **14**, 220—224.
- Korchmaros, J. D. 2006: An evolutionary and close-relationship model of helping. *J. Soc. Pers. Relat.* **23**, 21—43.
- Krupp, D. B., DeBruine, L. M., Jones, B. C. & Lalumiere, M. L. 2012: Kin recognition: evidence that humans can perceive both positive and negative relatedness. *J. Evol. Biol.* **25**, 1472—1478.
- Laeng, B., Vermeer, O. & Sulutvedt, U. 2013: Is beauty in the face of the beholder? *PLoS ONE* **8**, e68395.
- Lee, G. Y. & Kisilevsky, B. S. 2014: Fetuses respond to father's voice but prefer mother's voice after birth. *Dev. Psychobiol.* **56**, 1—11.
- Lenington, S. & Coopersmith, C. 1992: Genetic basis of mating preferences in wild house mice. *Am. Zool.* **32**, 40—47.
- Lewis, D. M. G. 2011: The sibling uncertainty hypothesis: facial resemblance as a sibling recognition cue. *Pers. Individ. Dif.* **58**, 969—974.
- Lieberman, D., Tooby, J. & Cosmides, L. 2007: The architecture of human kin detection. *Nature* **445**, 727—731.
- Lundstrom, J. N., Mathe, A., Schaal, B., Frasnelli, J., Nitzsche, K., Gerber, J. & Hummel, T. 2013: Maternal status regulates cortical responses to the body odor of newborns. *Front. Psychol.* **4**, 597.
- Maloney, L. T. & Dal Martello, M. F. 2006: Kin recognition and the perceived facial similarity of children. *J. Vis.* **6**, 1047—1056.
- Mateo, J. M. 2003: Kin recognition in ground squirrels and other rodents. *J. Mammal.* **84**, 1163—1181.
- Mateo, J. M. 2004: Recognition systems and biological organization: the perception component of recognition. *Ann. Zool. Fenn.* **41**, 729—745.
- Mateo, J. M. 2006: Development of individually distinct recognition cues. *Dev. Psychobiol.* **48**, 508—519.
- Mateo, J. M. 2008: Kinship signals in animals. In: *Encyclopedia of Neuroscience* (Squire, L. R., ed.). Academic Press, Oxford, 281—290.
- McLain, D. K., Setters, D., Moulton, M. P. & Pratt, A. E. 2000: Ascription of resemblance of newborns by parents and nonrelatives. *Evol. Hum. Behav.* **21**, 11—23.
- Michener, G. R. 1973: Field observations on the social relationships between adult female and juvenile Richardson's ground squirrels. *Can. J. Zool.* **51**, 33—38.
- Neff, B. D. & Sherman, P. W. 2003: Nestling recognition via direct cues by parental male bluegill sunfish (*Lepomis macrochirus*). *Anim. Cogn.* **6**, 87—92.
- Nesse, R. M., Silverman, A. & Bortz, A. 1990: Sex-differences in ability to recognize family resemblance. *Ethol. Sociobiol.* **11**, 11—21.
- Ober, C. 1999: Studies of HLA, fertility and mate choice in a human isolate. *Hum. Reprod. Update* **5**, 103—107.
- Ober, C., Weitkamp, L. R., Cox, N., Dytch, H., Kostyu, D. & Elias, S. 1997: HLA and mate choice in humans. *Am. J. Hum. Genet.* **61**, 497—504.
- O'Connell-Rodwell, C. E., Wood, J. D., Kinzley, C., Rodwell, T. C., Poole, J. H. & Puria, S. 2007: Wild African elephants (*Loxodonta africana*) discriminate between familiar and unfamiliar conspecific seismic alarm calls. *J. Acoust. Soc. Am.* **122**, 823—830.
- Olsén, K. H., Grahn, M., Lohm, J. & Langefors, Å. 1998: MHC and kin discrimination in juvenile Arctic charr, *Salvelinus alpinus* (L.). *Anim. Behav.* **56**, 319—327.
- Olsson, S. B., Barnard, J. & Turri, L. 2006: Olfaction and identification of unrelated individuals: examination of the mysteries of human odor recognition. *J. Chem. Ecol.* **32**, 1635—1645.
- Penn, D. & Potts, W. K. 1998: Chemical signals and parasite-mediated sexual selection. *Trends Ecol. Evol.* **13**, 391—396.
- Perrett, D. I., Mistlin, A. J., Chitty, A. J., Smith, P. A. J., Potter, D. D., Brönnimann, R. & Harries, M. H. 1988: Specialised face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behav. Brain Res.* **29**, 245—258.
- Pfefferle, D., Ruiz-Lambides, A. V. & Widdig, A. 2014: Female rhesus macaques discriminate unfamiliar paternal sisters in playback experiments: support for acoustic phenotype matching. *Proc. R. Soc. B-Biol. Sci.* **281**, 2013.1628.
- Pfennig, D. W., Collins, J. P. & Ziemba, R. E. 1999: A test of alternative hypotheses for kin recognition in cannibalistic tiger salamanders. *Behav. Ecol.* **10**, 436—443.
- Platek, S. M. & Kemp, S. M. 2009: Is family special to the brain? An event-related fMRI study of familiar, familial, and self-face recognition. *Neuropsychologia* **47**, 849—858.
- Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H. & Gallup, G. G. 2002: Reactions to children's faces - Resemblance affects males more than females. *Evol. Hum. Behav.* **23**, 159—166.
- Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E. & Gallup, G. G. 2003: How much paternal resemblance is enough? Sex differences in hypothetical investment decisions but not in the detection of resemblance. *Evol. Hum. Behav.* **24**, 81—87.
- Platek, S. M., Raines, D. M., Gallup, G. G., Mohamed, F. B., Thomson, J. W., Myers, T. E., Panyavin, I. S., Levin, S. L., Davis, J. A., Fonteyn, L. C. M. & Arigo, D. R. 2004: Reactions to children's faces: males are more affected by resemblance than females are, and so are their brains. *Evol. Hum. Behav.* **25**, 394—405.
- Platek, S. M., Keenan, J. P. & Mohamed, F. B. 2005: Sex differences in the neural correlates of child facial resemblance: an event-related fMRI study. *NeuroImage* **25**, 1336—1344.
- Porter, R. H. & Cernoch, J. M. 1983: Maternal recognition of neonates through olfactory cues. *Physiol. Behav.* **30**, 151—154.



- Porter, R. H. & Moore, J. D. 1981: Human kin recognition by olfactory cues. *Physiol. Behav.* **27**, 493—495.
- Porter, R. H., Cernoch, J. M. & Balogh, R. D. 1984: Recognition of neonates by facial-visual characteristics. *Pediatrics* **74**, 501—504.
- Porter, R. H., Cernoch, J. M. & Balogh, R. D. 1985: Odor signatures and kin recognition. *Physiol. Behav.* **34**, 445—448.
- Porter, R. H., Balogh, R. D., Cernoch, J. M. & Franchi, C. 1986: Recognition of kin through characteristic body odors. *Chem. Senses* **11**, 389—395.
- Porter, R. H., Makin, J. W., Davis, L. B. & Christensen, K. M. 1992: Breast-fed infants respond to olfactory cues from their own mother and unfamiliar lactating females. *Infant Behav. Dev.* **15**, 85—93.
- Randall, J. A. 1993: Behavioural adaptations of desert rodents (Heteromyidae). *Anim. Behav.* **45**, 263—287.
- Rantala, M. J. & Marcinkowska, U. M. 2011: The role of sexual imprinting and the Westermarck effect in mate choice in humans. *Behav. Ecol. Sociobiol.* **65**, 859—873.
- Reeve, H. K. 1989: The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407—435.
- Regalski, J. M. & Gaulin, S. J. C. 1993: Whom are Mexican infant said to resemble? Monitoring and fostering paternal confidence in the Yucatan. *Ethol. Sociobiol.* **14**, 97—113.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1996: Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Anim. Behav.* **51**, 1007—1015.
- Rushton, J. P. & Bons, T. A. 2005: Mate choice and friendship in twins - Evidence for genetic similarity. *Psychol. Sci.* **16**, 555—559.
- Russell, M. J., Mendelson, T. & Peeke, H. V. 1983: Mothers' identification of their infant's odors. *Ethol. Sociobiol.* **4**, 29—31.
- Schaal, B. 1988: Olfaction in infants and children: developmental and functional perspectives. *Chem. Senses* **13**, 145—190.
- Sherman, P. W. & Holmes, W. G. 1985: Kin recognition: issues and evidence. In: *Experimental Behavioral Ecology and Sociobiology* (Hölldobler, B. & Lindauer, M., eds). G. Fischer Verlag, Stuttgart, pp. 437—460.
- Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997: Recognition systems. In: *Behavioural Ecology: An Evolutionary Approach*, 4th edn (Krebs, J. R. & Davies, N. B., eds). Blackwell Scientific Publications, Oxford, UK, pp. 69—96.
- Silk, J. B. 1980: Adoption and kinship in Oceania. *Am. Anthropol.* **82**, 799—820.
- Smith, M. S., Kish, B. J. & Crawford, C. B. 1987: Inheritance of wealth as human kin investment. *Ethol. Sociobiol.* **8**, 171—182.
- Swaigood, R. R., Lindburg, D. G. & Zhou, X. 1999: Giant pandas discriminate individual differences in conspecific scent. *Anim. Behav.* **57**, 1045—1053.
- Tang-Martinez, Z. 2001: The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behav. Processes* **53**, 21—40.
- Volk, A. A. 2007: Parental investment and resemblance: replications, revisions, and refinements. *Evol. Psychol.* **5**, 1—14.
- Waldman, B. 1991: Kin recognition in amphibians. In: *Kin Recognition* (Hepper, P. G., ed.). Cambridge Univ. Press, Cambridge, UK, pp. 162—219.
- Watkins, C. D., DeBruine, L. M., Smith, F. G., Jones, B. C., Vukovic, J. & Fraccaro, P. 2011: Like father, like self: emotional closeness to father predicts women's preferences for self-resemblance in opposite-sex faces. *Evol. Hum. Behav.* **32**, 70—75.
- Weisfeld, G. E., Czilli, T., Phillips, K. A., Gall, J. A. & Lichtman, C. M. 2003: Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *J. Exp. Child Psychol.* **85**, 279—295.
- Welling, L. L. M., Burriss, R. P. & Puts, D. A. 2011: Mate retention behavior modulates men's preferences for self-resemblance in infant faces. *Evol. Hum. Behav.* **32**, 118—126.