Sharing between Full and Half siblings: An Experimental Study of Altruistic Behavior Modulated by Asymmetric Relatedness

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Abstract:

Genomic imprinting implies a conflict on a genomic level in an individual. On a behavioral level the intra-genomic conflict is supposed to show in prosocial behavior, like altruistic sharing, directed towards asymmetric kin, such as half siblings. We thus expected closer kin to be treated in a more altruistic way, and the decision latency to increase as the difference between maternal and paternal inclusive fitness-effects increased. To test this, we conducted an experimental study, where 38 four-eight years old children made 918 decisions about who out of two children would receive candy. The alternative benefactors included the child self, a full sibling, a half sibling, and an unrelated child. The experiment was conducted as an image-based forced choice task on a touch screen. We did not find any statistically significant results in support our hypotheses. Unexpectedly, we found that unrelated, unknown children were favored over any other children. When unrelated children were excluded from the statistical analyses, the results were in line with our hypotheses, but not statistically significant. The results may have been influenced by the participating children knowing they were observed, or by the unrelated children causing a bias in their decision making. The sample size was also relatively small. The subject needs to be further investigated with larger sample sizes.

Keywords:
Genomic imprinting, asymmetric relatedness, altruism, children, experiment

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Abstrakt:

Teorin om genetisk prägling innebär att det hos varje individ finns en konflikt mellan gener nedärvda från mamman och från pappan. På beteendenivå antas denna konflikt synas i bland annat altruistiska handlingar riktade till personer en individ är asymmetriskt besläktad med, d.v.s. antingen släkt via sin mamma eller sin pappa, såsom halvsyskon. Vi antog att altruistiskt beteende skulle vara som störst när det riktade sig till nära släktingar, samt att det skulle ta längre tid att göra fatta ett beslt när skillnaden mellan släktskap via mamman respektive via pappan ökade. Vi studerade barns beslutskonflikt i förhållande till hel- och halvsyskon med hjälp av ett bildbaserat experiment på en pekplatta. Barnets uppgift var att välja vem av två möjliga barn som skulle få godis. De möjliga alternativen bestod av barnet själv, ett helsyskon, ett halvsyskon samt ett okänt, obesläktat barn. Trettioåtta barn i åldrarna 4-8 år deltog, och vi analyserade sammanlagt 912 beslutsfattningssituationer. De statistiska analyserna av datat gav inget statistiskt signifikant stöd för våra hypoteser. Däremot fann vi att okända, obesläktade barn favoriserades framom alla andra barn, vilket gick tvärt emot våra antaganden. Vi utförde ytterligare analyser utan de okända barnen, och fick då resultat i samma riktning som hypoteserna, men utan statistiskt signifikans. Deltagarna visste om att de observerades, vilket kan ha påverkat resultaten. Det är också möjligt, att deltagarnas uppfattning av de okända barnen förvrängde deras beslutsfattning i förhållande till dem. Sampelstorleken var också relativt liten. Forskningsfrågan behöver vidare studier med större sampel.

Nyckelord:
Genetisk prägling, asymmetriskt släktskap, altruism, barn, experiment

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Sharing with Full and Half siblings: An Experimental Study of Altruistic Behavior Modulated by Asymmetric Relatedness

Genetic expression determines the function of each cell, and consequently also the characteristics of the organism. According to Mendelian laws, humans and other diploid organisms inherit one allele, or gene copy, from each parent. However, Mendelian laws do not apply in all cases. Genomic imprinting is such an exception (Hall, 1990).

Genomic imprinting describes epigenetic processes that allow parent-specific expression of genes. On a molecular level, the process takes place in the gametes and involves, for example, methylation of certain genes (Barlow et al., 2014; Bartolomei & Ferguson-Smith, 2011; Delaval & Feil, 2004; Feil & Berger, 2007; Li & Sasaki, 2011; Morison & Reeve, 1998). Genomic imprinting occurs mostly in placental mammals (Ishida & Moore, 2013), even though the phenomenon was first discovered in maize (Kermicle, 1970). Ishida and Moore (2013) reports that more than 100 imprinted genes have been identified in mice, half of which are believed to be imprinted also in humans. Another study reports that approximately 1300 imprinted genes have been identified in mice, most of which are expressed in the brain (Gregg et al., 2010). To date, the exact number of imprinted genes in humans is unknown. As a consequence of this type of regulated gene expression, maternally or paternally inherited genes may be silenced. The silencing of a maternally or paternally inherited allele, and thus having only one copy of a gene, entails vulnerability to diseases, such as developmental and behavioral disorders, cancer, and diabetes (Falls, Pulford, Wylie, & Jirtle, 1999; Ishida & Moore, 2013; Isles & Wilkinson, 2000). That being said, genomic imprinting can be also associated with benefits for the organism. Ishida and Moore (2013) refer to Moore and Haig (1991) and their kinship theory as the most accepted theory for why genomic imprinting has evolved.

Relatedness and Asymmetric Relatedness

Relatedness is the measure of the probability that two individuals share genes due to common descent (Hamilton, 1964). A traditional view on relatedness gives that both parents are 50% related to their mutual child, as are full siblings and this child to its future offspring. Half siblings (as well as aunts and grandparents) are 25% related to the child, whereas the child is 100% related to him/herself. Because genomic imprinting shows that genes can be expressed differently depending on their parental origin, a distinction between maternal and paternal relatedness is needed. In fact, the relatedness of a maternally inherited gene to a mother is 100%, but 0% to a father. Conversely, the relatedness of a paternally inherited gene

to a mother is 0%, but 100% to a father. Full siblings are 50% related both maternally and paternally, while half siblings have 50% relatedness *either* maternally *or* paternally, and 0% relatedness via the other parent (see Figure 1). Relatives, to whom a person is related to both maternally and paternally, such as full-siblings and offspring, are considered symmetric kin, while parents, aunts, uncles and half siblings are considered asymmetric kin (Haig, 2000).

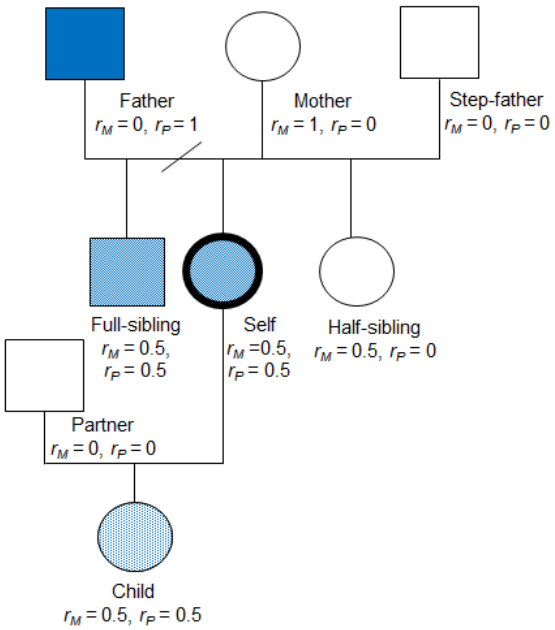

Figure 1. Relatedness according to genomic imprinting theory (r_M = maternal relatedness, r_P = paternal relatedness), blue indicating paternal relatedness, the darker shade the larger degree of relatedness. Circle indicates female and square male. Relatedness (*r)* is calculated from the perspectie of "Self", the middle blue circle with bold outline.

The Kinship Theory of Genomic Imprinting

The kinship theory is an extension of inclusive fitness theory. Inclusive fitness theory is based on the assumption that the closer an individual is to another, the more likely it is that the individual will behave in a way that benefits the other one (Hamilton, 1964). According to Hamilton's rule, prosocial, or altruistic behavior, can evolve if the benefit (*B*) to the recipient, weighted by the degree of relatedness (*r*), is larger than the cost (C) is to the actor: $rB > C$ (Trivers, 1974). In other words, when a person is sufficiently closely related to another, an act that benefits the fitness of one of them will also benefit the other, because of the genes they have in common (Schlomer, Del Giudice, & Ellis, 2011). If, as the phenomenon of genomic imprinting shows, maternally and paternally derived genes need to be considered separately, inclusive fitness theory leads to the kinship theory Haig (2000) proposes.

From an evolutionary point of view, both parents aim for their offspring to survive, but differences in parental certainty result in different, maternal and paternal interests (Isles, Davies, & Wilkinson, 2006). Human societies are hardly ever totally monogamous (Schlomer et al., 2011). A mother can have children with several different fathers, still knowing she is the mother of all the children she has given birth to, but a father can never be certain about a child being his (Schlomer et al., 2011). This means that the optimum for the mother and the maternally derived genes in her offspring would be to share maternal investment equally between all her offspring. In comparison, a father—and the paternally derived genes in offspring—are relatively less likely to be related to the mother's other offspring. Thus, the paternal optimum would be a child that requires and obtains a lot of maternal investment. The kinship theory suggests that paternally derived genes in a child thus aim to increase maternal investment (beyond what is beneficial to her fitness) in a given child of the father, whereas maternally derived genes aim to save maternal resources for her other, also future, children (Moore & Haig, 1991). Consequently, maternally inherited alleles also aim to decrease conflict between the mothers' offspring, who are all competing for the mothers' resources (Haig & Westoby, 1989; Schlomer, Del Giudice, & Ellis, 2011). This leads to intra-genomic evolutionary conflict between maternally and paternally derived genes (Haig, 2008). On a behavioral, interpersonal level, the conflict is predicted to appear in actions directed towards asymmetric kin, where the inclusive fitness of maternally derived genes will be increased at the expense of paternally derived genes, or *vice versa* (Haig, 2011; Haig, 2008).

Genomic Imprinting and Child Development

It has been shown that genomic imprinting affects fetal and embryonic development, more specifically by affecting the placenta and thus the nutrition and growth of the fetus (Hall, 1990; Hurst, 1997; Keverne, 2015; Reik & Walter, 2001). In line with the kinship theory, paternally expressed genes in the fetus increase the nutrition flow from the placenta and the mother to the fetus, whereas maternally expressed genes restrict the nutrition flow from placenta to fetus (Isles, Davies, & Wilkinson, 2006; Moore & Haig, 1991). Parallels can be drawn to the development of pre-eclampsia. Whereas pre-eclampsia pre-eclampsia is a serious disease for the mother, it can be also be an opportunity for a malnourished fetus to obtain more nutrition from the mother (Yuan, Haig, & Karumanchi, 2005).

Concerning behavior, genes associated with traits that enhance parental investment seem to be inherited paternally, and, *vice versa*, some traits that decrease parental investment appear to be inherited maternally (Úbeda, 2008). Often mentioned examples of this pattern are the Prader-Willi and the Angelman syndromes. Both syndromes are caused by anomalies on

chromosome 15q11-q13. In the Prader-Willi syndrome, paternally inherited genes are not fully expressed. In the Angelman syndrome, maternally inherited genes are not fully expressed (Bartolomei & Ferguson-Smith, 2011; Nicholls, Saitoh, & Horsthemke, 1998; Úbeda, 2008). Some central symptoms of the two syndromes are totally opposite. Infants with Prader-Willi syndrome tend to have low birthweight, sleep a lot and eat little until weaning—when mother-offspring conflict over nutrition ends—after which they overeat and often become obese (Úbeda, 2008). Infants and children with Angelman syndrome typically wake up repeatedly at night (Haig, 2014), smile a lot, and require lots of attention (Úbeda, 2008). In other words, the neonatal symptoms of Prader-Willi syndrome decrease maternal investment, while symptoms of Angelman syndrome increase maternal investment (Úbeda, 2008).

Genetically derived developmental disorders can tell us about how genomic imprinting works because of their special phenotype and patterns of inheritance. It is nevertheless probable that all individuals have imprinted genes that affect fetal development and developmental stages also later in life. Life history theory considers the ways an organism can maximize its fitness by allocating resources throughout life, with parental investment and social maturation playing important roles (Del Giudice, Angeleri, & Manera, 2009). Compared to other primates, human mothers give birth to their children with relatively short intervals (Haig, 2014; Kotler & Haig, 2018). As a consequence mothers often raise both infants who need nursing and pre-school aged children who both need a lot of parental care at the same time (Kotler & Haig, 2018). Adrenarche, or an increase in adrenal androgens associated with social maturation, occurs at approximately 5-8 years of age in humans, coinciding with the time that most children start school and peer relations become more important (Campbell, 2006; Del Giudice et al., 2009; Kotler & Haig, 2018). Kotler and Haig (2018) suggest that the timing of adrenarche is influenced by imprinted genes. From an evolutionary perspective adrenarche is also associated with increased independence of the child, which provides an opportunity for the mother to focus more on younger siblings. Conversely, later adrenarche and the associated prolonged dependency, is supposed to be associated with paternal interests and paternally expressed genes (Kotler & Haig, 2018), in line with paternally expressed genes increasing parental investment (Úbeda, 2008).

Kotler and Haig (2018) predict that adrenarche decreases conflict between siblings, because the older sibling is no longer as dependent of parental investment, and the siblings do not need to compete for parental resources to the same extent. At the same time, adrenarche is supposed to show also in terms of social skills, such as increased tendency to share with peers and siblings (Kotler & Haig, 2018).

Genomic Imprinting and Social Cognition

Imprinted genes in humans are suggested to be associated especially with the development of the nervous system (Hamed, Ismael, Paulsen, & Helms, 2012). Consequently genomic imprinting has also been suggested to affect different psychological functions (Isles & Wilkinson, 2000). The cerebral anomalies of individuals with genetic disorders caused by genomic imprinting have been studied in order to find connections between imprinted genes, brain, and behavior (Davies, Isles, & Wilkinshon, 2005). Brain-imaging studies have suggested that neural correlates of prosocial and sharing behavior involve activation in dorsal anterior cingulate cortex, anterior insula, dorsolateral prefrontal cortex, and occipital cortical areas (Güroğlu, Will, & Crone, 2014; Tashjian, Weissman, Guyer, & Galván, 2018; Will, Crone, van Lier, & Güroğlu, 2018). Pre-frontal cortex has been suggested to be an area with more maternally expressed genes (Badcock, 2009). Studies with mice have suggested, that paternally expressed genes on the other hand are associated with hypothalamic areas (Keverne, 2015).

In other words, cortical functions including social behavior and executive functions have been described as maternally influenced, and subcortical functions, regulating elemental aspects of emotions, sleep and hunger, as paternally influenced (Badcock, 2009; Davies et al., 2005). The imprinted brain theory by Crespi and Badcock (2008) suggests that autistic traits arise from paternally expressed genes that benefit the child and entail costs to the mother due to fast fetal growth and egocentric behavior as a child. On the other end of the spectrum, psychotic traits are suggested to have their origin in maternally expressed genes that benefit the mother, and as a consequence the fetus and child would be smaller and have an extreme tendency to mentalize (Crespi & Badcock, 2008; Ragsdale & Foley, 2012). Úbeda and Gardner (2010) also suggest that imprinted genes affect social behavior. They hypothesize that paternally imprinted genes increase maternal investment until weaning, after which paternal genes instead increase prosocial, altruistic behavior (Úbeda & Gardner, 2010).

To sum up, recent studies of genomic imprinting and social cognition seem to align with the theory that imprinted genes affect human social behavior.

Half siblings and Sibling Rivalry

Asymmetric kin include both parents and half siblings, so social behavior with asymmetric fitness-effects is very common. For example, half siblings are an especially interesting type of asymmetric kin. Around 10% of Finnish children live in reconstituted families (Suomen virallinen tilasto SVT, 2016), and at least 5,8% are estimated to have half siblings via their mother and 6,8 % have half siblings via their father (Antfolk, Lieberman, &

Santtila, 2012; here only half siblings of the opposite sex were considered, why the actual prevalence of half siblings is predicted to be higher).

As children are genetically less related to their siblings than to themselves, they are predicted to wish to direct more resources and parental attention to themselves than to their siblings. Sibling competition is predicted to increase between half siblings already because the inclusive fitness is smaller (Schlomer et al., 2011). Indeed, relations between half siblings are associated with more conflicts and arguments than relations between full-siblings (Haig, 2011; Schlomer et al., 2011), especially when age difference is small and the siblings live together, or in other words compete for the same parental resources (Salmon & Hehman, 2015). Children living with their half siblings also suffer from injuries more frequently than children living with full-siblings only (Tanskanen, Danielsbacka, & Rotkirch, 2015). Half siblings do not, however, cohabitate and interact as often as full-siblings, which on the other hand may decrease displays of conflict (Salmon & Hehman, 2015). In the case of half siblings inclusive fitness optima are unequal for maternally and paternally derived genes. Half siblings could be considered full-siblings from the perspective of their mutual parent, and at the same time be considered as unrelated from the perspective of the other parent. In the present study we predicted this ambiguity to show as a conflict over what kind of behavior would be beneficial when interacting with a half sibling. It is likely that behavioral differences between full-sibling and half sibling interactions have their origin in fundamental differences in social cognition, leading to conflict over decision-making in social situations.

The Present Study

The aim of the present study was to study decision conflict in children with maternal or paternal half siblings and full-siblings. Decision conflict was assumed to result from asymmetric relatedness. Children are of particular interest in studies of social cognition and social behavior as modulated by asymmetric relatedness, because children's most important relationships are with other family members, with whom they regularly interact. These family members also include siblings and half siblings, with whom children compete for resources.

The present study was conducted as an experimental study, with an image-based forced choice paradigm, in which participating children chose whom out of two siblings they wanted to give candy. The task was done using a touch screen tablet, and participating children were asked to manually drag a picture of candy to one out of two photographs presented on the same screen. In each trial the photographs represented either the participating child themselves, a full sibling, a half sibling, or a genetically unrelated child Decision conflict was measured as longer latency times in decision making (Fan, Flombaum,

McCandliss, Thomas, & Posner, 2003). In order to capture hesitancy in the decisions made, we also recorded the dragging pattern.

Reflecting the inclusive fitness theory, we expected that

1) More closely related kin would receive more candy than more distant kin.

As a test of decision conflict, we expected that

2) Decision latency would increase as the difference in fitness effects for maternally derived genes and paternally derived genes increases.

Method

Ethical Permission

As a part of a larger research project, the present study had received ethical permission from the Åbo Akademi University ethical review board. Because all participants were minors, they and their legal guardians were informed about confidentiality and participation being voluntary. All collected photographs were treated with confidentiality and the image files were erased directly after participation and all collected data was treated confidentially.

Participants

Thirty-eight children aged 4-8 years ($M = 6.26$, $SD = 1.41$) participated. Of these, 17 were female and 21 were male. Inclusion criteria were to have at least both a full-sibling and a half sibling, neither with an age difference larger than 7 years to the participating child. Participants were recruited via local schools in Turku and Helsinki areas, advertisement on public places and social media, via the Finnish national organization for reconstituted families, and by snowball sampling.

Measures

As a measure of altruistic behavior towards kin, the actual choices (self, full-sibling, maternal or paternal half sibling, or unrelated child) were recorded. The unrelated children were school photographs of boys and girls aged 4-8 collected from two voluntary families, a total of 10 photographs. Each participant was assigned an “unknown child” based on the participant’s age and gender. In order to measure decision-making conflict, latency time before first touching the candy and time until the candy was transferred were recorded. The transfer was made by dragging the candy with a finger from the middle of the screen to one of the children on each side of the screen. Two variables were coded: Think Times, that is, time (in ms) from trial start to start of the drag and Drop Times, that is, time (in ms) from trial start to the end of the drag. (See Figure 2).

Figure 2. Example of initial screen, before candy being dragged to one of the two children displayed. Because the used photographs are confidential, we use drawings in this figure.

We asked the legal guardians of the participants to report age and gender of the participating children and their full- and half siblings. The legal guardians also reported if the half siblings were maternal or paternal.

Procedure

The participating families could choose to participate in the lab at Åbo Akademi University or at home. Most of the participants chose to be tested at home, where the data collection was conducted in the kitchen or a separate room with at least a table and two chairs. School photographs or similar photographs of the children and their siblings of interest were collected before the test commenced. Every participating child was asked to name the persons on the photographs of themselves and their siblings before starting, in order to make sure they recognized them. The task was presented to the children as a game, and the rules were presented with a parent or sibling present, before the child was asked if he/she was ready to participate on his/her own. Photographs of the participating children, their full and half siblings and an unknown, unrelated child of the same age as the participants were shown pairwise in a program. The child was instructed to choose which of two shown children, e.g. self vs. maternal half sibling, should get the candy between them, and drag the candy to that child. This was repeated with all possible combinations occurring four times. The trials were structured into four, equally large blocks. Between each block there was a short break.

The families were given a gift voucher to an amusement park as an incentive for participating. The children who participated also got an immediate incentive, either candy or a sticker.

Statistical Analyses

To calculate significance tests for proportions of choices in choice categories, the exact Clopper-Pearson confidence intervals for observed proportions, and tested against a 50%-50% distribution. For hypothesis testing, multi-level regression models were built in the

lme4-package (Bates, Maechler, Bolker, & Walker, 2015) for *R* (R Core Team, 2008). For choice probabilities, we used a binary logistic regression model. For think times and drop times, we used linear regression models. In both cases, random intercepts were allowed for each participant.

Data exclusion and data trimming. Before analyses, we removed choice categories with four or less choices, indicating that only one participant had been presented with these choices. To exclude outliers, caps for think and drop times were put at 4000ms and 5000ms, respectively.

Results

Descriptive Results

Thirty-eight children aged from 4 to 8 years participated in the study. All of the participating children had full siblings, 12 participants had a maternal half sibling and 26 participants had a paternal half sibling. Full siblings were on average around the same age as the participating children, whereas maternal half siblings on average were slightly younger and paternal half siblings slightly older than the participating children (Table 1).

Table 1

Sex, Age, and Age Differences across Participants and Sibling Types

	N	Sex		Age			Age Difference[a]		
		Female	Male	*M*	*SD*	range	*M*	*SD*	range
Participants	38	17	21	6.26	1.41	4 - 8			
Full siblings	38	17	21	6.24	2.66	2 - 13	-0.13	2.43	-5 - 5
Maternal half siblings	12	1	11	5.17	4.73	1 - 12	-0.67	5.37	-6 - 7
Paternal half siblings	26	15	11	9.54	5.11	1 - 16	2.04	5.29	-7 - 7

Note: [a]Age difference defined in relation to participant.

Choice Probabilities and Average Relatedness

After removing trials with only four observations (i.e., the data included 912 observations in total. Of these 912 choices, the left stimulus had been chosen 468 times and the right stimulus chosen 444 times, suggesting that the random allocation of stimulus to either of the two sides was successful.

We first investigated the actual choices made by the participating children. Scrutinizing a descriptive table of the actual choices made for each of the possible actual

choice categories, three interesting patterns were observed. Firstly, unrelated children were more often chosen than any of its possible pair. Secondly, full siblings were more often chosen than the participant self. Thirdly, full siblings were also more often chosen than maternal or paternal half siblings (Table 2).

Table 2

Actual Choices and Fitness Difference by Choice Categories

Choice Categories (x vs. y)		x chosen	y chosen		*Fit differ.*
	n	*n* (%)	*n* (%)	*z*	
Self vs. Full sib	152	55 (36.1%)	97 (63.8%)	3.40***	0.50
Self vs. Maternal Half sib	48	24 (50.0%)	24 (50.0%)	0.00	0.25
Self vs. Paternal Half sib	104	59 (56.7%)	45 (43.3%)	1.37	0.25
Self vs. Unrelated child	152	40 (26.7%)	112 (74.7%)	5.23***	0.00
Full sib vs. Maternal Half sib	48	35 (72.9%)	13 (27.1%)	3.17**	0.50
Full sib vs. Paternal Half sib	104	64 (61.5%)	40 (38.5%)	2.37*	0.50
Full sib vs. Unrelated Child	152	61 (40.1%)	91 (59.9%)	2.44*	0.00
Maternal Half sib vs. Unrelated child	48	17 (35.4%)	31 (64.6%)	2.02*	0.00
Paternal Half sib vs. Unrelated child	104	21 (20.2%)	83 (79.8%)	6.08***	0.00

Note: * $p < .05$, ** $p < .01$, *** $p < .001$. Significance tests are calculated for the exact Clopper-Pearson confidence intervals for observed proportions, and tested against a 50%-50% distribution. *Fit. Differ* = Fitness difference calculated as the relative fitness value of choosing option *y* over *x*.

As a more formal test of our first hypothesis stating that more closely related kin would receive more candy than more distant kin, we conducted a multi-level binary logistic regression with random intercepts for each participant. To also weight choices probabilities against the relative fitness difference in each pair, the predictor was calculated as the relative fitness value of choosing one option (*y*) over (*x*), and the outcome was the option chosen. We found an association between the fitness difference and the choice probabilities (-1.82, $SE = 0.31$, $z = -5.85$, $p < .001$), showing that as the higher the value for the fitness difference, the more likely it was to choose the more fitness compromising choice. This association was in the opposite direction of what we expected. Because this negative association seemed to be driven by choices that included an unrelated peer, we also conducted a follow-up test after excluding all choice categories that included an unrelated peer. In this case the association between fitness difference and choice probabilities was in the predicted direction (0.64, $SE = 0.80$, $z = 0.80$, $p = .427$), but was not statistically significant.

Decision Times and Asymmetric Relatedness

After this, we investigated the think times and decision times for each choice category. The longest think and drop times occurred in choices between self and maternal half siblings. The shortest think and drop times occurred in choices between paternal half siblings and an unrelated child (Table 3).

Table 3

Means and Standard Deviations for Think Times and Drop Times for Decisions

Choice Categories	Think Times			Drop Times		
	n	*M*	*SD*	*n*	*M*	*SD*
Self vs. Full sib	142	1660.88	694.12	140	1688.48	792.97
Self vs. Maternal Half sib	44	1803.71	792.32	43	1818.84	795.25
Self vs. Paternal Half sib	97	1576.10	639.34	96	1660.00	792.65
Self vs. Unrelated child	134	1615.00	719.70	135	1654.28	796.04
Full sib vs. Maternal Half sib	42	1745.68	866.82	43	1814.09	946.81
Full sib vs. Paternal Half sib	97	1599.96	583.02	98	1659.89	691.20
Full sib vs. Unrelated Child	145	1728.36	733.65	146	1774.36	812.52
Maternal Half sib vs. Unrelated child	47	1582.65	678.94	47	1634.19	794.21
Paternal Half sib vs. Unrelated child	98	1571.61	721.30	96	1535.99	683.24

Note: Think Times = time (in ms) from trial start to start of the drag, Drop Times = time (in ms) from trial start to the end of the drag.

We then tested our second hypothesis that latency times for decisions would increase as the difference in fitness effects for maternally derived genes and paternally derived genes increases. We did this in two a linear mixed-model regression with random intercepts for each participant. In the first model, think time was the dependent variable. In the second model, drop time was the dependent variable. In both models the predictor was a binary measure, with one level for all choice categories that included either maternal or paternal half siblings and one level for all other choice categories, as this scenario allows most genetic conflict. The think time did not depend on whether choices categories included a half sibling or not, F (1, 830.82) = 1.33, p = 0.249. The drop time did not depend on whether choice categories included a half sibling or not, F (1, 872.02) = 0.35, p = 0.556). In both cases, the outcome did not support our second hypothesis.

Discussion

In the current study, we investigated how 4 - 8-year-old children, as a function of asymmetric relatedness, share fictional candy with their full and half siblings. The effects of

asymmetric relatedness on human prosocial behavior can be considered basic research in the field of evolutionary psychology. Knowledge about how asymmetrical relatedness affects human interaction gives us information about common psychological processes in all human beings, but can also be applied to more specific cases, such as the psychology of various processes in reconstituted families.

We expected that genetically more closely related kin would receive more candy than more distant kin, and that latency times for decisions would increase as a function of increased difference between inclusive fitness effects for maternal and paternal kin. The results of the present study did not support our hypotheses. Surprisingly, we found that children in the present study seem to behave in the most prosocial way towards unrelated, unknown children. It is possible that the results were influenced by the participants knowing that their choices were being observed by the test leader, or knowing that the results would be recorded. Studies in prosocial behavior show that humans tend to act in a more prosocial way when they are aware of being observed (Ernest-Jones, Nettle, & Bateson, 2011).

Another possible reason for why the unrelated, unknown children were given the most candy is that the participating children might have perceived them as being vulnerable. As all other photographs portrayed family members, the unrelated and unknown child may have been perceived as excluded and alone. It has been shown that empathy motivates children to behave altruistically towards distressed individuals and relieve their suffering (Davidov, Knafo-Noam, & Hastings, 2016). If the participants of the present study on some level perceived the unrelated children as being vulnerable, they theoretically could have helped them by giving them candy. The possible problems regarding the unrelated child could have been avoided by using photographs of genetically unrelated step-siblings or peers. Adding a sample criterion of also having a step-sibling would, however, have restricted our sample considerably, and using photographs of peers would have added another layer of permission and legal consent from legal guardians from different families.

Limitations

Due to specific inclusion criteria, the sample size in the present study was relatively small. Because we wanted the experimental study to be as systematic as possible to maintain internal validity, the ecological validity might have suffered. The comparability between dragging photographs of candy on a touch screen and the actual interaction between siblings is limited. No participant had both maternal and paternal half siblings and a full-sibling who met the criteria of maximum age difference of 7 years. Including both maternal and paternal half siblings would have maximized the asymmetry between paternal and maternal inclusive

fitness effects, allowing an even more interesting comparison between maternal and paternal relatedness within the same individuals. This was, unfortunately, not possible in the present study.

When conducting the statistical analyses, we did explore possible effects of age, gender, or cohabitation with siblings. These were not of principal interest regarding our hypotheses, but it is possible that including these variables explain the surprising results. Moreover, we did not ask the participants about why they made a particular decision. It is possible, that the children had their own criteria for why a certain sibling should or should not get candy. Some children spontaneously explained that they wanted to give all the candy to the cute baby of the family, or that they did not want to give any candy to a certain sibling because they had recently had a fight. These criteria may have obscured possible effects of relatedness.

It is important to consider the many other possible explanations for children interacting with their half siblings the way they do, and inclusive fitness and asymmetric relatedness is only one perspective. As an example societal norms regarding cohabitation might further obscure effects of genetic relatedness.

Conclusion

The results of the present study did not give support for a significant effect of asymmetric relatedness on children's sharing with their full and half siblings. The topic needs to be investigated further, with a larger sample size and possibly an exclusion of the category of unknown children, or the unrelated children being actual peers in order to avoid them being perceived as vulnerable. Perhaps the tendency of unknown and unrelated children being favored could also be subject for further investigation.

Swedish summary

Hur barn delar med sig med halvsyskon: En experimentell studie av hur altruistiskt beteende påverkas av asymmetriskt släktskap

Genetisk prägling är en epigenetisk process som antas förekomma främst hos däggdjur, och som innebär att en gen uttrycks på olika sätt beroende på vilken förälder genen nedärvts från (Ishida & Moore, 2013). Präglingen sker i föräldrarnas könsceller, där vissa gener i och med en metyleringsprocess blir tystade (Barlow et al., 2014; Bartolomei & Ferguson-Smith, 2011; Delaval & Feil, 2004; Feil & Berger, 2007; Li & Sasaki, 2011; Morison & Reeve, 1998). När en gen nedärvd från mamman eller pappan blivit tystad leder detta till att individen endast har en kopia av en gen, vilket kan medföra häslorisker (Falls et

al., 1999). Det finns trots det vissa betydande fördelar med genetisk prägling. Ishida och Moore (2013) anger Moore och Haig's (1991) teori om släktskapsselektion (*the kinship theory*) som den mest vedertagna förklaringen till varför genetisk prägling har uppstått.

Släktskap och asymmetriskt släktskap

Släktskap är ett mått på hur sannolikt det är att identiska gener på grund av gemensamt påbrå finns hos två individer. Enligt traditionell syn på släktskap är två biologiska föräldrar båda 50% besläktade med sitt gemensamma barn. Också helsyskon är 50% besläktade med varandra, medan halvsyskons släktskap är 25%. En person är 100% besläktad med sig själv. Eftersom teorin om genetisk prägling visat på att gener kan komma till uttryck på olika sätt beroende på om de nedärvts från mamman eller pappan, behöver en skillnad göras mellan släktskap via mamman och släktskap via pappan. Då är en gen nedärvd från mamman besläktad med mamman till 100%, men 0% besläktad med pappan. Detsamma gäller, men tvärtom, för gener nedärvda från pappan. Helsyskon är då 50% besläktade både via sin mamma och sin pappa, medan halvsyskon är 50% besläktade via antingen sin mamma eller sin pappa, och 0% via den andra föräldern. De personer en individ är besläktad med i lika hög grad både via sin mamma och sin pappa kallas symmetriska släktingar, medan t.ex. föräldrar och halvsyskon räknas som asymmetriska släktingar (Haig, 2000).

Släktskapsselektion och genetisk prägling

Teorin om släktskapsselektion bygger på Hamiltons regel om inkluderande lämplighet (*inclusive fitness;* Hamilton, 1964). Teorin om inkluderande lämplighet bygger på antagandet att altrustiskt beteende kan vara till fördel för en individ, förutsatt att mottagaren är en tillräckligt nära släkting. Om graden av släktskap överstiger graden av reproduktiv kostnad, lönar sig altruistiskt beteende (Trivers, 1974). Detta eftersom handlingen då ökar den reproduktiva lämpligheten (*reproductive fitness*) hos de gener som sannolikt både finns hos individen som utför en altruistisk handling och hos mottagaren av handlingen (Schlomer et al., 2011).

Haigs (2000) teori om släktskapsselektion och genetisk prägling bygger på Trivers (1974) teori om släktskapsselektion, men tar också i beaktande geners olika prägling beroende på nedärvning via endera föräldern.

En mamma vet så gott som alltid att hon är mamma till sitt barn, medan en pappa inte kan vara säker på det (Schlomer et al., 2011). Denna skillnad i föräldraskapssäkerhet leder till att mammans och pappans evolutionära intressen blir olika, trots att båda två i grunden strävar efter att det gemensamma barnet ska överleva (Isles et al., 2006). Mamman och hennes gener strävar efter att resurser delas rättvist mellan alla hennes barn, medan pappan inte kan veta om

hans gener finns hos barnets eventuella syskon, varför det är mera fördelaktigt för pappan och hans gener att hans barn kräver och får så mycket resurser som möjligt, på bekostnad av syskonen (Moore & Haig, 1991). Mammans gener strävar med andra ord också efter att mildra konflikten mellan hennes barn, som alla tävlar om samma uppmärksamhet och resurser (Haig & Westoby, 1989; Schlomer et al., 2011). Genernas olika evolutionära drivkrafter leder till en intragenetisk konflikt hos barnet, mellan gener nedärvda från mamman respektive från pappan (Haig, 2008). På beteendenivå antas denna konflikt synas i handlingar riktade mot asymmetriskt besläktade personer, där den inkluderande lämpligheten för mammans gener gagnas på bekostnad av pappans geners inkluderande lämplighet, eller vice versa (Haig, 2008; Haig, 2011).

Genetisk prägling och barnets utveckling

Genetisk prägling spelar en stor roll i fosterskedets utveckling i och med att genetisk prägling antas reglera tillförseln av näring från mamman genom moderkakan till fostret (Hall, 1990; Hurst, 1997; Keverne, 2015; Reik & Walter, 2001). Pappans gener i fostret antas öka näringstillförseln, och således öka fostrets chanser att överleva samtidigt som mammans egen hälsa sätts på spel, medan mammans gener antas begränsa näringen som tillförs till fostret och således skona mamman (Isles, Davies, & Wilkinson, 2006; Moore & Haig, 1991). I linje med detta antas pappans gener vara associerade med drag som hos det födda barnet ökar föräldrars investering i just det barnet, medan mammans gener associerats med drag som minskar föräldrars behov av att investera i ett barn (Úbeda, 2008). Detta antagande stöds av att Angelmans syndrom och Prader Willis syndrom orsakas av tystade gener nedärvda från pappan respektive mamman på exakt samma kromosomställe, men med diametralt olika symptom (Bartolomei & Ferguson-Smith, 2011; Nicholls et al., 1998; Úbeda, 2008). Flera av de centrala symptomen i respektive sjukdom passar påfallande bra in på endera förälderns teoretiska evolutionsmässiga intresse. Barn med Prader Willis syndrom, där endast mammans gener uttrycks, sover mycket och äter lite under spädbarnstiden, vilket kan liknas vid mammans intresse av att spara sina egna resurser och dela dem jämnt mellan barnen (Úbeda, 2008). Barn med Angelmans syndrom å andra sidan sover dåligt (Haig, 2014), ler mycket och kräver mycket uppmärksamhet, vilket passar ihop med pappans genetiska arvs intresse (Úbeda, 2008).

Eftersom människor föder barn med relativt korta intervall, är det inte ovanligt att mammor har både spädbarn och barn i lekåldern som samtidigt är beroende av henne och tävlar om hennes resurser (Haig, 2014; Kotler & Haig, 2018). Vid ungefär 5-8 års ålder infaller en endokrinologisk process som associeras med social mognad och mindre beroende

av föräldrars omvårdnad (Campbell, 2006; Del Giudice et al., 2009; Kotler & Haig, 2018). Ur ett evolutionspsykologiskt perspektiv är ett tidigt mognande fördelaktigt för mamman, eftersom mera självständiga äldre syskon mildrar konflikten om mammans resurser mellan syskon, och ger mamman bättre förutsättningar att ta hand om yngre syskon (Kotler & Haig, 2018). Samtidigt sammanfaller den mognaden med att sociala färdigheter hos barn utvecklas, till exempel ökar benägenheten att rättvist dela med sig med syskon och kamrater (Kotler & Haig, 2018).

Genetisk prägling och social kognition

Studier har visat på samband mellan hjärnområden och prosocialt, altruistiskt beteende (Güroğlu et al., 2014; Tashjian et al., 2018; Will et al., 2018). Prefrontala cortex, som har förknippats med socialt beteende, har också associerats med genetisk prägling där gener nedärvda från mamman uttrycks (Badcock, 2009), medan gener nedärvda från pappan har förknippats med subkortikala områden (Keverne, 2015). I linje med detta har antagits att prefrontala, sociala funktioner har samband med gener nedärvda från mamman, medan subkortikala funktioner som har med grundläggande emotionella aspekter och fysiologiska behov att göra, förknippas med gener nedärvda från pappan (Badcock, 2009; Davies et al., 2005).

Halvsyskon och syskonrivalitet

Ur evolutionsperspektiv tävlar syskon med varandra om föräldrarnas uppmärksamhet och resurser, och denna konflikt trappas upp i och med att graden av släktskap och inkluderande lämplighet minskar (Schlomer et al., 2011).

Asymmetriska släktingar innefattar såväl föräldrar som halvsyskon. Halvsyskon är speciellt intressanta, eftersom de från den ena förälderns genetiska perspektiv betraktas som helsyskon, samtidigt som de från den andra förälderns synvinkel inte är besläktade alls. Vi antar att den kognitiva dissonansen kan synas som en konflikt om vilket slags beteende som är fördelaktigt i förhållande till ett halvsyskon.

Den föreliggande studien

Syftet med den föreliggande studien var att undersöka beslutskonflikt som funktion av asymmetriskt släktskap hos barn med både halvsyskon och helsyskon.

Studien utfördes som en experimentell studie där barn fattade beslut om vem av två barn som skulle få godis. I praktiken utfördes studien på en pekplatta, i ett program där två fotografier som representerade barnets olika syskon, barnet själv eller ett obesläktat jämnårigt barn presenterades samtidigt, och barnets uppgift var att med fingret dra en bild av godis till ett av fotografierna och bildligt ge det barnet godis. Beslutskonflikt mättes som längre tid för

beslutsfattningen (Fan et al., 2003). För att kunna observera tvekan i beslutsfattningen registrerades också det mönster barnet drog med sitt finger på pekplattan.

I enlighet med teorin om inkluderande lämplighet antog vi att

1) Närmare besläktade personer skulle få mera godis än personer med lägre grad av släktskap.

I fråga om beslutskonflikt antog vi att

2) Tid för beslutsfattningen skulle öka när skillnaden mellan effekter av inkluderande lämplighet för gener nedärvda från pappan respektive mamman ökade.

Metod

Den föreliggande studien hade beviljats etiskt tillstånd av etiska nämnden vid Åbo Akademi, eftersom den är en del av ett större forskningsprojekt vid Åbo Akademi. Deltagarna och deras vårdnadshavare informerades om deltagandets frivillighet och konfidentialitet. Alla insamlade uppgifter och fotografier behandlades konfidentiellt, och fotografierna raderades genast efter användning.

Trettioåtta barn i åldrarna 4-8 år deltog (M = 6.26, SD = 1.41), varav 17 var flickor och 21 pojkar. Inklusionskriterier var att det deltagande barnet skulle ha minst ett helsyskon (med två gemensamma biologiska föräldrar) och ett halvsyskon (en gemensam biologisk förälder), ingendera med större åldersskillnad än sju år i förhållande till det deltagande barnet. Deltagare rekryterades via skolor i Åboland och Nyland, sociala medier och med hjälp av Finlands förbund för nyfamiljer Supli ry. En del deltagare rekryterades också med hjälp av familjer som redan deltagit och kände någon som passade in på inklusionskriterierna.

Som mått på altruistiskt beteende riktat till familjemedlemmar registrerades de egentliga besluten om vem som fick godis (själv, helsyskon, halvsyskon via mamman eller pappan, eller obesläktat jämnårigt barn). Som mått på beslutskonflikt registrerades hur lång tid det tog för barnet att först röra bilden av godis, samt hur lång tid det tog innan bilden av godis dragits till ett av fotografierna föreställande barn. Vi bad också deltagarnas vårdnadshavare att rapportera ålder samt kön på barnets hel- och halvsyskon, samt om halvsyskon var släkt via mamman eller pappan.

Deltagarna fick delta i studien antingen i Åbo Akademis utrymmen eller hemma. De flesta deltagarna valde att delta hemma, där studien sedan utfördes i köket eller i ett annat rum där det fanns åtminstone ett bord och två stolar. Skolfotografier eller dylika bilder av det deltagande barnet samt ett helsyskon och ett halvsyskon samlades in på förhand eller vid tidpunkten för deltagandet. För att säkerställa att deltagarna kände igen barnen på bilderna, ombads de före det egentliga experimentent namnge barnen. Studien presenterades sedan som

ett spel, där uppgiften var att välja vem av två barn som skulle få godis, ta tag i godiset med ett finger och föra det till det barnet. Denna procedur upprepades sedan tills alla möjliga kombinationer hade förekommit fyra gånger.

Familjerna som deltog fick ett presentkort till en nöjespark som incentiv för deltagandet. För att motivera barnen att delta, fick de också antingen lite godis eller ett klistermärke som belöning genast efter deltagandet.

Det insamlade datat analyserades statistiskt i programmet R, med hjälp av hierarkiska binära och linieära regressionsmodeller.

Resultat

Det analyserade materialet bestod av sammanlagt 912 observationer av beslutsfattning i förhållande till barn med olika grad av släktskap.

Vi förväntade oss att närmare besläktade barn skulle tilldelas mera godis än de med lägre grad av släktskap, samt att det skulle ta längre tid att besluta vem som skulle få godis när skillnaden mellan inkluderande lämplighetseffekt för mamman respektive pappan ökade. Vi fann inget stöd för någondera av hypoteserna. Däremot fann vi att okända barn, som inte alls var besläktade med de deltagande barnen, tilldelades överlägset mest godis. De okända barnen favoriserades framom alla andra möjliga kategorier. Eftersom denna effekt gick i motsatt riktning till vad vi förväntat oss, att högre släktskap skulle ge större tendens att tilldelas godis, gjorde vi en analys utan de obesläktade barnen. Då var resultatet enligt förväntad riktning, med inte statistiskt signifikant.

Diskussion

Det insamlade datat i den föreliggande studien torde vara unikt. Effekterna av genetisk prägling och asymmetriskt släktskap utgör basforskning inom evolutionspsykologi, och tillför kunskap om både allmänpsykologiska funktioner och mänskligt beteende i specifika sammanhang. Ett specifikt sammanhang där denna kunskap är relevant, är den växande uppmärksamhet som riktas till psykologiska processer i nyfamiljer.

En metodologisk begränsing att ta i beaktande var att samplet till följd av strikta inklusionskriterier förblev litet, samt att den ekologiska validiteten på grund av experimentets digitaliserade karaktär blev lidande.

Det är möjligt att resultaten påverkades av deltagarnas vetskap om att testledaren observerade deras beslut. Tidigare studier har visat att människor i testsituationer som mäter prosocialt beteende tenderar att bete sig mera prosocialt än vanligt om det finns åskådare (Ernest-Jones et al., 2011).

De okända, obesläktade barnen tilldelades oväntat mycket godis. En möjlig orsak till detta kan har varit att alla andra bilder som förekom i experimentsituationen var familjemedlemmar och således bekanta för barnet som deltog, och att barnet i ljuset av detta på något sätt upplevde det okända barnet som exkluderat och nödställt. Davidov et al. (2016) beskriver att altruistiskt hjälpbeteende motiveras av att en person upplever sin nästa som nödställd, vilket väcker empati. Detta sker både hos barn och vuxna (Davidov et al., 2016). För att undvika eventuella problem som uppstod på grund av att de obesläktade barnen var totalt okända för deltagarna, kunde vi ha använt fotografier av styvsyskon eller lekkamrater. Tyvärr skulle ett ytterligare krav på att utöver hel- och halvsyskon också ha styvsyskon i rätt åldersspann ha begränsat deltagarunderlaget märkbart. Att använda fotografier på lekkamrater från andra familjer skulle å sin sida ha medfört förhållandevis omständliga förberedelser med tillstånd från vårdnadshavare i olika familjer.

Barnen som deltog ombads inte kommentera sina val. Det är möjligt att deltagana valde hur godiset skulle delas enligt andra, egna kriterier och inte enligt släktskap. Ett barn berättade spontant att storebror inte skulle få något godis alls eftersom de hade grälat dagen innan, medan ett annat barn sade att familjens baby var så söt att han skulle få allt godis. Sådana här kriterier kan ha dolt eventuella underliggande effekter av genetik och asymmetriskt släktskap.

Det är viktigt att ta i beaktande att flera sociala faktorer kan antas spela in på hur barn interagerar med sina syskon. Samhälleliga normer och lagstiftning som berör vilken förälder barn bor tillsammans med spelar sannolikt en stor roll för samspelet mellan syskon, vilket inte nödvändigtvis tas i beaktande i ett evolutionspsykologiskt, genetiskt perspektiv.

När vi tog utförde statistka analyser av det insamlade datat, analyserade vi inte effekter av ålder, kön och hur stor del av tiden barnet bor tillsammans med varje syskon. Dessa frågor var inte av central betydelse för våra hypoteser, men kunde eventuellt ha bidragit till att förklara varför ingen hypotes fick något stöd, samt möjligen varför de okända barnen i så hög grad favoriserades.

Sammantaget kan sägas att den föreliggande studien inte kan ge stöd för hypotesen om att asymmetriskt släktskap och inkluderande lämplighet påverkar barns beslutsfattande. Det är ändå möjligt att i framtida studier med större sampel och åtgärdade metodologiska brister kunde leda till andra resultat.

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GABRIELLE LINDHOLM

Press release – Pressmeddelande

Resultaten från en avhandling pro-gradu vid Åbo Akademi gav inget stöd för teorin om att 4-8-åriga barns sociala beslutsfattning påverkas av genetisk konflikt. Teorin om genetisk konflikt innebär att det i en person finns en konflikt mellan de gener som nedärvts från mamman respektive från pappan, vilket antas synas i handlingar riktade mot personer vi är besläktade med endast via en förälder. Forskarna fann däremot överraskande att barn tenderade att favorisera okända barn som de inte är besläktade med. I analyser av beslutsfattningssituationer som gällde enbart familjemedlemmar fanns inte heller några stöd för att barn helst riktar altruistiska handlingar mot så nära genetiskt besläktade personer som möjligt. Den experimentella studien, där barn på en pekplatta fick dela ut godis till olika personer, utfördes under hösten 2017 och våren 2018 vid Åbo Akademi och var den första i sitt slag.

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