EVOLUTION, ALTRUISM AND GENETIC SIMILARITY THEORY

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The author reviews his work on altruism, offering a time continuum for understanding levels of explanation in social behavior, showing that individual differences in both prosocial and antisocial behavior are about 50% heritable, and outlining how epigenetic rules guide development in one direction over alternatives. He also presents "genetic similarity theory," showing that humans are able to detect degrees of genetic simiarity in others and to prefer those most similar for friendship and marriage, a process which provides a basis for ethnic favoritism and group selection.

Numerous confusions have occurred in the behavioral sciences as a result of not separating distal from proximal levels of explanation (see Figure 1). When reasoning moves from distal to proximal, controversy does not ensue. Evolutionary biologists do not find the heritability of traits problematic; trait theorists accept that dispositions are modified by later learning, and learning theorists believe that the products of early experiences interact with subsequent situations to produce emotional arousal and cognition. Resistance is more likely, however, as explanations move from proximal to distal. Thus some phenomenologists mistrust the reduction that consciousness is partly the result of previous learning. Situationists and learning theorists do not always accept that people's choices and development may be guided by inherited traits. Often behavioral geneticists ignore evolutionary history.

Behavior can be analyzed usefully from each of the levels. It is well established that situations are important sources of behavioral variability, as when mood changes of happiness and anger alter people's altruism and aggression (Rushton, 1980). People can also be shown to differ, however, in average mood state. It is at this stage of the analysis that conceptual problems have occurred for some have found it difficult to see that if people alter their behavior with varying circumstances, they can be said to have enduring characteristics that reliably differentiate them from others. Indeed, there has been considerable debate in psychology about the degree to which "traits" reliably differentiate people. Social learning theorists, for example, have emphasized people's ability to modify their behavior across different situations. It is now known, however, that when people's behavioral responses are aggregated across numerous situations substantial average differences are found between people (Rushton, Brainerd & Pressley, 1983).

Social groups (age, sex, socio-economic, race) often differ in average traits scores, although it has become fashionable to deemphasize these. As with traits generally, group differences are best observed when several particulars are aggregated. This was recently shown in an analysis of questionnaire data gathered from 573 pairs of twins. Females have been found to be significantly more altruistic and empathic (and less aggressive) than males, and altruism had been found to increase with age from 20 to 60, while aggression decreased. These observations would have been missed if the analyses had relied on single items, for the variance accounted for by sex differences increased from 1 to 3 to 8 percent as the number of questionnaire items increased from 1 to 5 to 23 (Rushton & Erdle, 1987). Parallel results were found to occur when age and socio-economic status differences were examined. Combining age, sex and socio-economic status in a multiple regression equation, again differentiating a 1 to 23 item scale, led the multiple R to increase from an average of 0.18 for single items to 0.39 for the 23 items.

The origin of behavioral differences are consistently found to be about 50% heritable, even for traits such as altruism and aggression which parents are expected to socialize heavily. Too many assessment procedures and research designs have been involved for these findings not to be accepted (Holden, 1987). For example, according to American, Danish and Swedish adoption studies, children who were adopted in infancy were at greater risk for victimizing others if their biological parents had been convicted of a crime than if their adoptive parents had been (Cadoret, Cunningham, Loftus & Edwards, 1975; Cloninger, Sigvardsson, Bohman & von Knorring, 1982; Mednick, Gabrielli & Hutchings, 1984). In Mednick, Gabrielli and Hutchings' (1984) study of 14,427 children separated from parents at birth, it was found that siblings and half-siblings adopted separately into different homes were concordant for convictions. Converging with this adoption work, twin studies of adults have found that identical twins were roughly twice as

TABLE I

Estimates of Variance Components and Estimates Corrected for Unreliablity from a Biometrical Analysis of Aggressiveness, Assertiveness, Altruism, Empathy and Nurturance Questionnaires from 573 Adult Twin Pairs.
(After Rushton, Fulker, Neale, Nias and Eysenck, 1986.)

Trait	Additive genetic variance	Common environmental variance	Specific environmental variance
Aggressiveness	39% (54%)*	0% (0%)*	61% (46%)*
Assertiveness	53% (69%)*	0% (0%)*	47% (31%)*
Altruism	51% (60%)*	2% (2%)*	47% (38%)*
Empathy	51% (65%)*	0% (0%)*	49% (35%)*
Nurturance	43% (60%)*	1% (1%)*	56% (39%)*

*Estimate corrected for unreliability of questionnaire.

much alike in their aggressive and criminal behavior as fraternal twins (Christiansen, 1970; Cloninger, Christiansen, Reich & Gottesman, 1978; Rowe & Osgoode, 1984). As shown in Table 1, in Rushton et al.'s (1986) analysis of twins reared together, the heritability of both altruism and aggression was about 50%.

One of the less appreciated aspects of twin studies is the information they also provide about environmental effects. The important environmental variance turns out to be *within* a family, not *between* families (see Table 1). That is, the common family environment plays a very limited role in social development. Such factors as social class, family religion, parental values and child rearing styles, for example, are *not* found to have a common effect on siblings. This runs counter to prevailing "sociological" theories of social development that assume that the important environmental variance is between families, not within. Yet the observation that the environmental factors that influence development are those that are specific to each sibling, rather than common, is robust, having been replicated using samples of four different types: twins reared together, twins reared apart, adoptive parents and their offspring, and adoptive siblings (Plomin & Daniels, 1987). Regardless of whether one considers the transmission of socially undesirable traits such as crime, obesity, and schizophrenia, or more normative personality characteristics such as vocational interests and value systems, the evidence reveals that whereas genetic influences have an important role to play, the common family environment alone has little apparent effect.

These results are most readily grasped from the comparison of twins reared together and apart. They are also derived from the comparison of adoptive and biological siblings raised in the same family from infancy to adulthood, where the less related the siblings are, the increasingly divergent they grow with age. Table 2 presents a contrast of the world literature on adult identical twins reared apart in intelligence and personality, with that of other relationship categories (Bouchard, 1984; Rushton, in press). The results show substantial genetic effects on the traits in question and considerably weaker effects due to common environment. That siblings raised apart for many years in complex environments grow to be significantly similar to each other on a variety of traits, and that their degree of similarity is predicted by the number of genes they share, implies the presence of genetically based stabilizing systems that channel

TABLE II

World Literature on Similarity in Adult Twins Raised Apart Compared with Other Relationship Categories on Intelligence and Personality (After Bouchard, 1984 and Rushton, in press).

	Intelligence		Personality	
	Number of Pairs	Intraclass Correlation	Number of Pairs	Intraclass Correlation
Identical Twins Reared Together	4,672	.86	5,000	.52
Identical Twins Reared Apart	65	.72	106	.54
Fraternal Twins Reared Together	5,546	.60	>8,000	.23
Fraternal Twins Reared Apart	29	.47	20	.18
Biological Siblings Reared Together	26,473	.47	17	.20
Biological Siblings Reared Apart	203	.24	—	—
Adoptive Siblings Reared Together	369	.34	78	.07

development (Lumsden & Wilson, 1981; Rushton, Littlefield & Lumsden, 1986).

Epigenetic Rules in Social Development

Genes do not cause behavior directly. They code for enzymes which, under the influence of the environment, lay down tracts in the brains and nervous systems of individuals, thus differentially affecting people's minds and the choices they make about behavioral alternatives. In regard to altruism and aggression, for example, some people may inherit temperaments that dispose them to empathy or impulsivity, or a lack of conditionability. There are many plausible routes from genes to behavior and collectively these routes may be referred to as epigenetic rules.

Epigenetic rules, originating in the process of evolution, provide recipes by which individual development is guided in one direction over alternatives. Their operation is most apparent in embryology in which the construction of anatomical features occurs. To take a familiar example, the physical development from fertilized egg to neonate follows a preordained course starting in the head region and working its way down the body. By the end of the first month, a brain and spinal cord become evident, and a heart has formed and begun to beat. By the end of the eighth week, the developing fetus has a face, arms, legs, basic trunk and internal organs. By the sixth or seventy month, all major systems have been elaborated, and the fetus may survive if born prematurely.

The canalization of growth processes is also illustrated by findings from developmental behavioral genetics (Bouchard, 1984; Plomin & Daniels, 1987). Phenomena reflecting genetic timing mechanisms, for example, include the age of onset of puberty, first sexual experience, and menopause, in which identical twins are highly concordant. Another example is Huntington's chorea, a degenerative disorder of the central nervous system caused by a dominant gene. Age of onset varies from 5 to over 75, but family studies show that it is under genetic control. Chronogenetics also affects cognitive development as shown in a large sample of twins followed from 3 months to 15 years of age in which the synchronies between lags and spurts in mental development were found to average about 0.90 for identical twins, but only about 0.50 for fraternal twins.

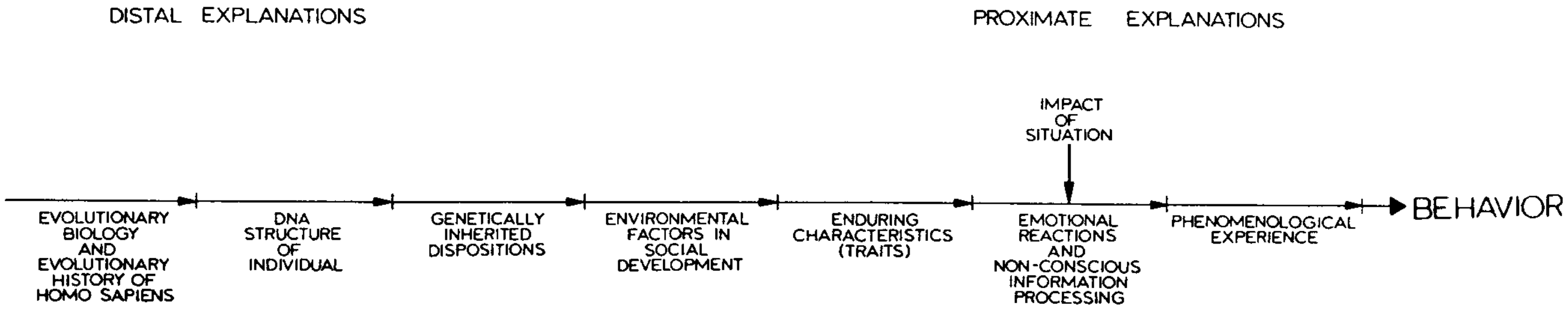

Figure 1: The distal-proximal dimension and levels of explanation in social behavior. When explanations move from distal to proximal controversy does not ensue whereas the converse is less true.
Source: Rushton, 1984.

Psychological development is also guided by epigenetic rules from sensory filtering through perception to feature evaluation to decision making (Lumsden & Wilson, 1981). For example, while the brain perceives variation in luminance along a continuum, it divides color into categories, using language to do so. Many social scientists used to believe that the divisions into red, green, and so forth are arbitrary, but linguistic and cross-cultural studies have shown that they are in fact closely tied to natural color perception. The application of epigenetic rules to more complex social behavior has also been made. For example, canalized end points appear to underlie the evolutionary function of smiling, attachment and separation responses in infants (Freedman, 1974). Similar interpretations can be made of the life-cycle stages documented to occur in ego-development, mortality, and psycho-social functioning (Loevinger, 1987). Epigenetically based physiological hypotheses can also be provided. Thus androgens may underlie Rushton, Fulker, et al.'s (1986) observations that altruism increases across the life-span while aggressiveness decreases, and that sex differences hold up consistently across time. Testosterone production is known to increase with age and to differentiate the sexes in the predicted direction.

The idea of genetic canalization provides an explanation for the important finding, shown in Tables 1 and 2, that common family environment has little impact on longer term personality development. Thus, within the same upbringing environment, the more belligerent sibling may observationally learn the items from the parents' aggressive repertoire, whereas his more nurturant sibling selects from the parents' altruism responses. For example, in an analysis of television effects, Rowe & Herstand (1986) found that although same-sex siblings resembled one another in their exposure to violent programs, it was the most aggressive sibling who a) identified most with aggressive characters, and b) viewed the consequences of the aggression as positive. Within-family studies of delinquents find that both IQ and temperament distinguishes delinquent siblings from those who are non-delinquent. It is not difficult to imagine how intellectually and temperamentally different siblings might acquire alternate patterns of social responsibility.

The potential of epigenetic rules to bias behavior and affect society may go well beyond ontogeny. Via cognitive phenotypes and group action, altruistic inclinations may be amplified into charities and hospitals, creative and educative dispositions into academies of learning, martial tempers into institutes of war, and delinquent tendencies into social disorder. The idea that genes have such extended effects beyond the body in which they reside, biasing individuals to the production of particular cultural systems, constitutes a central focus for current thinking in sociobiology (Dawkins, 1982; Lumsden & Wilson, 1981). Within the constraints allowed by the total spectrum of cultural alternatives, people create environments maximally compatible with their genotypes (Rushton, Littlefield, & Lumsden, 1986).

Genetic Similarity Theory

That genotypes seek out maximally conducive environments is particularly well illustrated by findings that people select similar others with whom to associate, both as friends and as marriage partners. Both friends and spouses assort on the basis of such characteristics as race, socio-economic status, physical attractiveness, religion, social attitudes, level of education, family size and structure, IQ, and longevity (Rushton, Russell & Wells, 1985; Thiessen & Gregg, 1980). Correlations tend to be higher for opinions, attitudes, and values (0.40 to 0.70) and lower for personality traits and personal habits (0.02 to 0.30). Advantages thought to accrue to optimizing similarity in personal relations include increased altruism, cooperation and trust.

That such assortment is genetically mediated is suggested by studies of animals where assortative mating occurs in species ranging from insects through birds to primates (Thiessen & Gregg, 1980), and where animals raised apart show a preference to interact with kin rather than non-kin (Holmes & Sherman, 1983). My colleagues and I have investigated the phenomena in humans. Using blood antigen analyses to estimate genetic distance across 10 blood loci using 7 polymorphic marker systems (ABO, Rhesus (Rh), P, MNSs, Duffy (Fy), Kidd (Jk), and HLA over 6 chromosomes, we found that both male friendship dyads and sexually interacting couples share more genetic markers than do randomly generated pairs from the same samples (Rushton, 1987; Rushton & Chan, 1987). We also found that the epigenetic rules inclining people to choose each on the basis of similarity appear to be fine tuned, biasing individuals to assort on the more genetically influenced of homogeneous attributes. Positive correlations between assortment and genetic influence have been observed on a variety of anthropometric, cognitive, personality and attitudinal characteristics in both friendships and marriages (Rushton & Nicholson, in press; Rushton & Russell, 1985; Russell, Wells & Rushton, 1985). Following the death of a child, for example, both mothers and fathers irrespective of sex of child are found to grieve more for children resembling their side of the family than they do for children resembling their spouse's side (Littlefield & Rushton, 1986). It would appear that people are able to detect genetic similarity in others and act accordingly.

The implications of these findings may be far-reaching. For example, they provide a biological basis for ethnic nepotism. Since two individuals from within an ethnic group will, on average, be genetically more similar to each other than two from different ethnic groups, an individual is expected to benefit his own group over others. Ethnic conflict and rivalry is of course, one of the great themes of historical and contemporary society (van den Berghe, 1981). Ethnic altruism is demonstrated by group members preferring to congregate in the same area and associate with each other in clubs and organizations. Charitable donations are typically made in greater quantities within ethnic groups than between them and social psychological studies have documented that people are more likely to help members of their own race or country than members of other races or foreigners.

The reason people give preferential treatment to genetically similar others is both simple and profound: they thereby replicate their genes more effectively. Altruism is a very interesting phenomenon, even recognized by Darwin as an anomaly for his theory. How could it evolve through his hypothesized "survival of the fittest" individual when such behavior would appear to diminish personal fitness? If the most altruistic members of a group sacrificed themselves for others, they ran the risk of leaving fewer offspring to carry forward their genes for altruistic behavior? Hence altruism would be selected out, and indeed, selfishness would be selected in. Altruistic behaviors, however, occur in many animal species, some to the point of self-sacrifice (Wilson, 1975). For example, honey bees die when they sting in the process of protecting their nests.

Darwin proposed the competition of "tribe with tribe" to explain altruism (1871, p. 179). Thus a tribe of people willing to cooperate and, if necessary, sacrifice themselves for the common good would be victorious over tribes made up of those less willing or able. Indeed, he actually titled his epoch-making 1859 publication: "On the Origin of Species by Means of Natural Selection, *or the Preservation of Favoured Races in the Struggle for Life*." Subsequently Herbert Spencer (1892/93) extended this, suggesting that the operation of a 'code of amity' towards the members of their own group, and a 'code of enmity' toward those of out-groups prevailed in successful groups. In non-elaborated forms, some version of "group-selection" was held by most evolutionists for several decades.

It wasn't until Wynne-Edwards (1962) however that the altruism issue finally began to dominate theoretical center-stage. Wynn-Edwards suggested that whole groups of animals collectively refrained from over-breeding when the density of the population became too great – even to the point of directly killing their own offspring if necessary. Such self-restraint, he argued, protected the animals' resource base and gave them an advantage over groups of individuals which did not practice restraint and which became extinct as a result of their profligacy. This extreme form of the group selection argument was immediately disputed by other biologists. A great deal of subsequent argument and data was marshalled against the idea (Williams, 1966).

A degree of polarization followed. As D. S. Wilson put it, "For the next decade, group selection rivaled Lamarkianism as the most thoroughly repudiated idea in evolutionary theory" (1983: 159). Mathematical models were presented apparently showing that group selection could override individual selection only under extreme conditions. Essentially, there did not seem to exist a mechanism by which altruistic individuals would leave more genes than individuals who cheated. The solution to this paradox is one of the triumphs that led to the new synthesis of sociobiology. Following Hamilton (1964) the answer proposed was that individuals behave so as to maximize their "inclusive fitness" rather than only their individual fitness by increasing the production of successful offspring by both themselves *and their relatives,* a process that has become known as kin selection. This formulation provided a conceptual breakthrough, redirecting the unit of analysis from the individual organism to his or her genes, for it is these which survive and are passed on.

Some of the same genes will be found in siblings, nephews and nieces, grandchildren, cousins, etc., as well as offspring. If an animal sacrifices its life for its siblings' offspring, it ensures the survival of shared genes for, by common descent, it shares 50% of its genes with each sibling and 25% with each siblings' offspring.

It is predicted, then, that the percentage of genes shared is an important determiner of the amount of altruism displayed, and this is borne out in a number of species. Social ants, for example, are one of the most altruistic species so far discovered and, because of a special feature of their reproductive system, also share 75% of their genes with their sisters. Thus by working for others, and sacrificing their lives if need be, they help to propagate their own genes. Extreme forms of altruism also may occur in clones (e.g., aphids), where individuals are 100% related.

Hamilton's (1964) theory of inclusive fitness was generally regarded as an extension of individual selection, not group selection (Dawkins, 1976). A compromise position was offered by E. O. Wilson (1975) who suggested that while the genes are the units of replication, their selection could take place through competition at both the individual and group levels which were viewed as opposite ends of a continuum of ever enlarging nested sets of socially interacting individuals. In this account, kin-selection is seen as intermediate between individuals and group selection. Under the rubric of "genetic similarity theory," Rushton Russell & Wells (1984) proposed an extension to the theory of kin-selection to the human case where altruism is provided to non-kin as well as to kin. Adopting the mechanistic perspective of the selfish gene, we argued that genes could maximize their replication by benefiting *any* organism in which copies of themselves were to be found. Thus kin-selection is but one form of genetic similarity selection. In order to pursue the strategy of benefiting similar genes, people must be able to discriminate degrees of genetic similarity in others. The results from our studies on marriage and friendship indicated they could do so.

Benefiting genetically similar others has been greatly enhanced through culture. Through the use of language, law, religious imagery, and patriotic nationalism replete with kin terminology, ideological commitment enormously extends altruistic behavior. Indeed recent analyses suggest that evolution under culturally driven group selection, including migration, war and genocide may account for the greatest amount of change in human gene frequencies (Ammerman & Cavalli-Sforza, 1984; Melotti, 1984; Vining, 1981; D. S. Wilson, 1983). The human propensity for deontological action may be guided by epigenetic rules which lead people to those cultural choices which maximally increase their genetic fitness (Lumsden & Wilson, 1981; Rushton, 1986; Rushton, Littlefield & Lumsden, 1986). In this analysis, the makeup of a gene pool causally affects the probability of any particular ideology being adopted, which subsequently affects relative gene frequencies. Religious, political, and other ideological battles may become as heated as they do because they have implications for genetic fitness; genotypes will thrive more in some cultures than others. From this perspective, Karl Marx did not take the argument far enough in the distal direction: ideology serves more than economic interest; it also serves genetic purpose.

For this account to be true, a) individual and group differences in ideological preferences must be partly heritable, and b) ideological practices must confer differential genetic fitness. Evidence exists to support both these propositions. With respect to a), while it has generally been assumed that political attitudes are for the most part environmentally determined, both twin and adoption studies demonstrate moderate to substantial heritabilities (e.g., 0.50) for both specific conservative social and political attitudes, as well as stylistic tendencies such as authoritarianism and degree of ideological commitment (Martin, Eaves, Heath, Jardine, Feingold, and Eysenck, 1986). With respect to b), whether the learning of ideologies can increase genetic fitness, obvious examples are to be found in those religious beliefs regulating sexual practices, marital custom, infant care, and child rearing (Reynolds and Tanner, 1983). Other evidence derives from cultural proscriptions on dietary habits. Amerindian tribes adopting the use of alkali cooking for maize, for example, had larger population densities and more complex social organizations than Amerindian tribes who did not, primarily because alkali cooking releases the most nutritious parts of cereal, enabling more tribal members to grow to reproductive maturity (Lumsden and Wilson, 1981). The native tribes were unable to explicate the biochemical reasons for the benefits of alkali cooking, but their cultural beliefs had evolved for good reasons.

The role of genetic similarity in politics is likely to become increasingly noticeable in both the U.S. and the USSR as the turn of the century approaches. Both of the superpowers have large ethnic minorities and, given the differential in birth rates between majority and minority populations, the current ruling groups are unlikely to maintain their positions much longer. One reason the USSR invaded Afghanistan was to suppress Moslem fundamentalism which, if spread to the southern socialist republics, could bring an end to the existing power structure. The genetic minorities have the highest birth rates in the USSR and can ultimately be expected to displace the currently dominant Russians. In the U.S. power shifts can be expected as the differential birth rates of Spanish-speaking Americans, black Americans, and the currently dominant North European Americans continues.

Genetic similarity can thus be expected to be one of the many influences operating on political alliances. Obviously causation is complex, and it is not intended to reduce relationships between ethnic groups to a single cause. Fellow ethnics will not always stick together, nor is conflict inevitable between groups anymore than it is between genetically distinct individuals. Behavioral outcomes are always mediated by multiple causes. The Western European world is currently aligned primarily against the Russians, their half-cousins, while the more genetically distant Japanese are allies. It is an empirical question though whether it would be easier to manipulate antipathy in white Americans toward the Japanese than toward the Russians, or whether class conflicts become more intense when there is a racial element to them. Thus while "politics make strange bedfellows" and human alliances are constantly shifting, behavior may become more predictable as genetic distance measures are added into the equation.

A note on a paradox is essential. If the replication of similar genes is as strong an evolutionary imperative as sociobiological theorizing suggests, why are descendants of European populations throughout the world currently experiencing negative growth while allowing extensive immigration from genetically less similar gene pools? Why also have ideologies been adopted which discourage nationalist and religious sentiments proportional to the degree to which they express concern about such issues? Clearly ideologies can arise which have the paradoxical effect of dramatically decreasing fitness. A classic example of such a lethal idea is to be found among the Shakers, a religious sect which considers sex to be so sinful that it imposes celibacy upon even its married members. This ideology has until recently been quite successful in replicating itself through several generations; new adherents being recruited, largely via adoptions. The member's genes, of course, fail to replicate.

The fertility paradox goes back centuries. Fisher (1958) raised the question of why civilizations decay, and documented evidence in favor of the hypothesis that the ruling group (often classes, sometimes races) failed to reproduce themselves, usually having much lower fertility than the ruled groups. Fisher (1958) hypothesized a trade-off between the capacity for economic success and fertility and there is increasing evidence that such a syndrome exists (Rushton, 1985; following Wilson, 1975). The fact that successful cultures arise whose members subsequently limit their own replication, giving less genetically similar others the opportunity to replace them, must be considered a major challenge for evolutionary biology (Vining, 1986). Its solution probably requires adding a stronger component of cultural transmission to the traditional concern with genetics. If successful, this explanatory breakthrough may herald a quantum jump in understanding the naure of gene-culture coevolution.

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