Advancement Pathways in Social Hierarchy and Their Evolution: Insights from Comparative Research

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Abstract

Social hierarchy is a dynamically evolving multidimensional system, whose acquisition can be categorized into three major pathways. The dominance pathway emphasizes resource acquisition through aggression and threat, having evolved under intense sexual selection pressure. The competence pathway highlights the role of knowledge/skills in status acquisition, originating from the cultural learning demands generated by technical foraging. Unlike the first two pathways, the virtue pathway, characterized by psychological altruism, is unique to human societies. It is a product of cultural evolution, existing to solve problems of large-scale collective action. The three pathways differ in scope of existence, behavioral patterns and outcomes, evolutionary drivers, and emotional mediators. Future research could further clarify the relationship between sexual selection patterns in different animal taxa and dominance hierarchies, examine the special environmental conditions for the evolution of the human competence pathway through interdisciplinary approaches, and explore the biological foundations of the virtue pathway.

Full Text

Routes to Ascend the Social Hierarchy and Their Evolution: Insights from Comparative Studies

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Abstract

Social hierarchies are dynamic, multidimensional systems. Status acquisition can be categorized into three primary routes. The dominance route emphasizes resource acquisition through aggression and threat, evolving under intense sexual selection pressure. The competence route highlights the role of knowledge and skills in attaining status, originating from the need for cultural learning driven by increasingly sophisticated foraging techniques. Unlike the first two routes, the virtue route—characterized by psychological altruism—is unique to human societies. It is a product of cultural evolution that exists to solve problems of large-scale collective action. These three routes differ in their scope of existence, behavioral patterns and outcomes, evolutionary causes, and emotional mediators. Future research could further clarify the relationship between sexual selection patterns and dominance hierarchies across different animal species, employ multidisciplinary approaches to examine the unique environments in which the human competence route evolved, and explore the biological basis of the virtue route.

Keywords: social hierarchies, dominance route, competence route, virtue route, evolutionary cause

1 Introduction

In studies of animal social structures, the concept of "social hierarchy" refers to the relative position an individual obtains within a group based on their influence, sometimes also called status hierarchy or social status [?, ?]. It originated from Norwegian scientist Schjelderup-Ebbe' s (1922) concept of "pecking order" in his research on domestic fowl social behavior, which later evolved into "dominance hierarchy." However, this single dimension of dominance is insufficient to capture the complexity of human social hierarchy systems. Consequently, the academic community has ultimately formulated the concept of "social hierarchy" to encompass various hierarchical systems including dominance hierarchies [?]. From a macro perspective, these different systems constitute the dimensions (or criteria) of social hierarchy; from a micro perspective, they represent pathways for individuals to elevate their social status. Previous research has explored the static characteristics of social hierarchies within populations, yet how human multidimensional hierarchy systems evolved and how they differ from animal hierarchy systems remains poorly understood. Building upon this gap, this paper attempts to systematically review theories and research on social hierarchies from an evolutionary perspective, comparing similarities and differences between animal and human social hierarchy systems to reveal the iterative process from single-dimensional to multidimensional hierarchies and to explore the underlying evolutionary causes and conditions.

2 The Dominance Route

What determines rank in animal groups? In Schjelderup-Ebbe' s (1922) research, domestic hens initially engaged in frequent attacks over food. Over time, aggressive behavior decreased while feeding became orderly. Researchers speculated that each hen remembered its competitive wins and losses against others, establishing a hierarchical order within the group. Thus, the primary means for animals to elevate their social status involves using aggression and threat in conflicts to instill fear in other group members, thereby winning resource competitions—this is the dominance route [?]. However, dominance is not equivalent to aggression; rather, aggression is merely one tool for acquiring dominant status. Individuals who obstruct others from achieving their goals are also perceived as dominant [?, ?], because these individuals control important resources and can evoke fear in subordinates through threats of resource deprivation, thereby gaining competitive advantages [?].

In essence, groups establish hierarchical order through aggression and threat. By accurately assessing the dominance ranks of conspecifics, individuals can make optimal behavioral decisions during conflicts without resorting to force in every competition. Paradoxically, the very purpose of hierarchies established through aggression is to reduce aggressive behavior [?].

2.1 Scope of the Dominance Route

The dominance route can effectively reduce intragroup conflict and allocate resources at relatively low cost, which explains why dominance hierarchies exist in the vast majority of social animals, including primates [?, ?, ?]. Researchers have developed multiple methods to detect dominance relationships among animals. Field studies typically record naturalistic aggression-submission behavioral indicators such as grooming, courtship, chasing, and mounting. Experimental studies generally employ approach-retreat resource competition paradigms, including food contests, territory marking, and right-of-way games [?, ?, ?]. Although humans have evolved high levels of prosociality and social norms that can suppress dominance behaviors to some extent, bullying, aggression, denigration, and other antisocial behaviors continue to help individuals gain status in both experimental settings and real life [?, ?].

In recent years, with the development and application of neural manipulation techniques such as optogenetics, an increasing number of researchers have explored the neural mechanisms underlying dominance behavior. While the neural circuits of social hierarchy involve multiple brain regions, evidence suggests that the medial prefrontal cortex (mPFC) may serve as the core region for this regulatory mechanism. The mPFC can encode competitive behavior, represent dominance ranks, and predict future competitive outcomes [?, ?, ?]. When dominance hierarchies become unstable, upward comparisons activate not only the mPFC to track rank changes but also the amygdala [?, ?], which induces fear conditioning through observational learning [?]. Fear thus serves as the emotional medium of the dominance route. Animals represent dominance hierarchies through two primary mechanisms: first, through trial-and-error in direct dyadic confrontations—that is, via reinforcement learning; and second, through observing interactions among other group members, or observational conditioning [?]. Both behavioral and neural level research demonstrate that dominance hierarchies are ubiquitous among social animals.

2.2 Evolutionary Causes of the Dominance Route

Although dominance hierarchies confer numerous group benefits, such as strengthening social bonds and stability [?] and punishing free-riding behavior [?], male-male competition likely represents the primary selective pressure driving the dominance route. According to Trivers' (1972) parental investment and sexual selection theory, females cannot increase their offspring number by mating with more males and thus invest more time in parental care. In contrast, males can enhance reproductive success by increasing their number of mates, leading them to invest more time in same-sex competition and intensifying mate competition among males. The "challenge hypothesis" further posits that when females are in estrus, male testosterone levels rise sharply, resulting in higher aggression levels that confer advantages in the "mating market" [?].

Consequently, the vast majority of dominance research has focused on male animals. Studies ranging from rodents [?, ?] to non-human primates [?, ?] demonstrate that dominance status effectively explains variation in reproductive success among males.

Leimar and Bshary (2022) employed evolutionary game theory to investigate dominance hierarchy formation mechanisms, finding that dominance status positively correlates with fighting ability. Because such hierarchical competition among males is often violent and lethal, the benefits of pre-fight assessment create selective pressure for the evolution of external signals of fighting ability [?]. Although weapons, skills, hormones, and fat reserves all affect fighting capacity [?], body size is generally considered the most direct and accurate external indicator of fighting ability [?, ?]. Numerous studies have found that body size reliably predicts male dominance status and reproductive success [?, ?, ?].

Males competing for dominance through body size creates differences between male and female body size, a phenomenon known as sexual size dimorphism (SSD). While SSD is also influenced by other factors such as resource competition and female choice, extremely strong male-biased SSD typically indicates a polygynous mating system with intense male-male competition [?]. Among extant primates, gorillas exhibit the greatest sexual size dimorphism; they practice polygyny, and male body size positively correlates with the number of female mates [?]. Australopithecus, the earliest hominin appearing over four million years ago, displayed sexual size dimorphism approaching or even exceeding that of gorillas, suggesting they also practiced polygyny with intense male physical competition [?, ?].

In summary, the dominance route represents the most extensively studied area in hierarchy research. Current evidence suggests that intense male-male competition for mates constitutes the primary evolutionary driver of the dominance route, manifested as males continuously strengthening their size advantages to compete for dominance, ultimately resulting in sexual size dimorphism. Dominance hierarchies established through sexual selection may subsequently be extended to other resource allocation contexts. Neurobiological research further reveals the neural substrate underlying dominance route evolution: the medial prefrontal cortex is considered the decision-making center for dominance behavior, with activation or inhibition of this region altering animals' attack/retreat choices during hierarchical conflicts; the amygdala may serve as the emotional center for dominance behavior, involved in fear conditioning through observational learning.

3 The Competence Route

However, some researchers have challenged dominance route theory. Human societies engage in extensive cooperation to accomplish complex tasks. In task-oriented groups, dominance-based social hierarchies may hinder group continuity and development because dominants possess priority in resource allocation yet may lack the knowledge and skills required for the task. Groups typically punish members who attempt to attain high status through violence and aggression [**?**]. Consequently, human social status is primarily acquired through the competence route [**?**, **?**, **?**].

Competence is defined as skills, expertise, ideas, or information that hold explicit value for achieving specific task goals [**?**]. Cross-cultural research across 14 major economies (including China, the United States, Germany, etc.) demonstrates that possessing extensive knowledge represents an important means for individuals to elevate their social status [**?**]. Garfield et al. (2019) employed ethnographic methods, identifying over 1,000 relevant archival records from 60 randomly sampled cultures in the Human Relations Area Files (HRAF), confirming that knowledge and skills similarly enhance status in extant hunter-gatherer societies. Thus, the competence route is widespread in human groups.

3.1 Scope of the Competence Route

Research findings are inconsistent regarding whether competence hierarchy systems exist in non-human animals. Some researchers argue that in many mammals, group leaders are typically older individuals, and age can serve as an external indicator of knowledge and experience, suggesting that animals also possess competence hierarchies [**?**, **?**, **?**]. However, these studies suffer from two problems. First, they conflate the concepts of social status and leadership. J. E. Smith and van Vugt (2020) note that although leadership correlates highly with status, they are fundamentally distinct: leadership refers to an individual' s disproportionate influence on group decisions during collective action, whereas status represents priority access to resources. In animals, leadership and status do not always align perfectly. For instance, low-status spotted hyenas often lead group movements during hunts [?], while older elephants possess leadership rights without gaining additional food or mating opportunities [?]. Second, age is not necessarily a reliable indicator of competence. Age is a composite variable encompassing knowledge, skills, fighting ability, and other information. Although an individual's knowledge and experience may increase with age, physical decline can reduce fighting capacity and skill levels, and empirical studies have not found a direct relationship between age and status [?, ?].

Other researchers propose using social centrality to measure competence hierarchies in non-human primates, constructed from the frequency of being approached by others and receiving grooming services. In competence hierarchies, low-status individuals actively approach high-status ones, seeking proximity and maintaining attention toward them, whereas in dominance hierarchies, low-status individuals avoid contact and maintain distance [?, ?]. For example, Kulahci et al. (2018) found that lemurs capable of solving novel foraging problems were not only more frequently imitated but also increased their social centrality. However, social centrality is influenced by multiple factors including kinship, age, and sex [?, ?], and can also be positively predicted by dominance rank because individuals may affiliate with high-dominance individuals to secure support during conflicts [?]. Therefore, social centrality cannot effectively distinguish between the two hierarchy systems.

3.2 Evolutionary Causes and Diagnostic Criteria of the Competence Route

Because identifying the competence route in animal groups is fraught with difficulty, Henrich and Gil-White (2001) argued that this route is unique to humans because it depends on cultural learning—a form of social learning peculiar to our species. Social learning is learning achieved through observing or interacting with other animals or people; it can effectively reduce the cost of acquiring adaptive information and help organisms rapidly adapt to their environment, with its basic forms being widespread in animal groups [?]. Cultural learning, by contrast, is a "high-fidelity" form of social learning that enables "lossless" information transmission within groups, allowing members sufficient time to make incremental improvements to knowledge and skills, thereby generating cultural phenomena [?]. This high-fidelity information transmission is built upon true imitation. Imitation refers to copying an agent' s actions, including complete action sequences, behavioral intentions, and outcomes. Animal learning, however, is more often emulation—copying behavioral results or goals. For example, chimpanzees observing a human model fill a bottle with water to obtain peanuts will spit into a container to make peanuts float within reach [?]. Compared to imitation, emulation ignores substantial potentially useful information and represents an inefficient learning method; acquired knowledge is repeatedly lost during transmission and must be continually relearned.

Henrich and Gil-White (2001) proposed "information goods theory" to explain the emergence of the competence route. As foraging methods became increasingly sophisticated, humans had to master more survival skills. Learning from competent group members represents a low-cost way to acquire adaptive knowledge. Individuals use respect as a "currency" to exchange for opportunities to closely observe and imitate models, thereby more accurately mastering relevant skills—failure to do so results in elimination. This selective pressure requires individuals to learn to rank group members by competence and select appropriate models for imitation. Consequently, highly competent individuals gain high prestige [?, ?, ?]. Prestigious individuals receive more attention [?, ?] and are more frequently imitated than their low-prestige counterparts [?, ?]. Cultural learning thus serves both as the cause of the competence route' s emergence and as a diagnostic indicator of its existence.

However, experiments show that chimpanzees, like humans, also select competent individuals as models for imitation [?]. Further research reveals that non-human primates can copy not only behavioral outcomes but also the behaviors themselves. In "artificial fruit" feeding experiments with vervet monkeys, monkeys in different action groups tended to imitate their own group' s actions to obtain food, demonstrating that they could copy behaviors themselves—exhibiting true imitation [?, ?]. Field surveys have also found that across ten different wild chimpanzee communities, each group developed unique combinations of termite-feeding techniques. Researchers argue that ecological factors cannot explain differences in foraging methods across groups because these techniques involve specific body postures indicative of high-fidelity action imitation [?]. Neuroimaging research indicates that this action imitation ability is built upon mirror neurons, which help identify actions rather than intentions [?]. Such neurons have been found in non-human primates including macaques [?]. Both neural and behavioral evidence thus demonstrate that non-human primates possess true imitation capabilities.

3.3 Comparison of Competence Routes Between Humans and Non-Human Primates

Even if non-human primates possess cultural learning and competence hierarchy systems, their breadth and depth cannot compare to those of humans. For example, chimpanzee imitation is limited to situations where the means-ends relationship is transparent and visible. When causal relationships operate as a "black box," their imitation becomes selective and cannot replicate complete action sequences. In such cases, human children can still faithfully copy action sequences due to their overimitation tendency. Overimitation ensures that children can master complex skills with high fidelity even without understanding the causal relationships [?]. Additionally, Vale et al.' s (2021) experimental research shows that in chimpanzee groups, when task difficulty increases, complex problem-solving solutions become difficult for other members to acquire and transmit. Neuroimaging research offers a potential neural mechanism explanation: interspecies differences exist in action processing circuits, with the dorsal stream to the ventrolateral prefrontal cortex (vlPFC) gradually strengthening from macaques to chimpanzees to humans, reflecting increasingly refined motor skills and bodily imitation abilities during evolution [**?**].

Teaching is considered another form of cultural learning, where instructors deliberately modify their behavior in the presence of novices to facilitate others' learning [**?**]. Previous researchers believed teaching might be a uniquely human form of cultural learning, but recent studies indicate that teaching behavior is more common in the animal kingdom than anticipated. For instance, adult meerkats remove scorpion stingers in advance, allowing pups to learn how to hunt scorpions under safe conditions, thereby improving their hunting skills. Besides meerkats, 27 other species (such as ants and bees) also exhibit potential teaching behavior [**?**]. However, these teaching interactions typically occur between parents and offspring, with information transmitted vertically. This learning mode lacks model selection issues, and vertical transmission is extremely limited in scope, making it difficult to facilitate information exchange across broader groups and thereby form culture. Human teaching, by contrast, involves more oblique transmission, where individuals select knowledgeable and skilled elders who are not their parents as models for imitation, promoting rapid spread of adaptive information within groups [**?**]. Thus, only human teaching behavior is based on the competence route.

In conclusion, research on the competence route in animal groups is far more challenging than that on the dominance route. Neither age nor social centrality serves as a precise measurement indicator. While cultural learning certainly does not equate to competence hierarchy, it can serve as a key characteristic of competence hierarchies. Imitation and its neural basis—mirror neurons—have been observed in multiple non-human primate species, indicating that the competence route is not unique to humans. Future research could quantify tool use among different individuals in a group as a measure of competence level, establish hierarchical gradients based on resource allocation order and quantity, and control for body size to exclude interference from dominance hierarchies, thereby investigating the relationship between competence level and social rank in animals. Building upon this, researchers could further examine whether animal groups with competence hierarchies also exhibit cultural learning phenomena, to determine the role of cultural learning in competence route formation.

4 The Virtue Route

Although the dominance and competence routes may represent primary means for humans to elevate social status, they are insufficient to explain all ways through which humans acquire status. For instance, Kyl-Heku and Buss (1996) noted that among the 26 status acquisition tactics they surveyed, half could not be classified as either dominance or competence routes. Therefore, some researchers believe that other important pathways must exist.

4.1 Independence of the Virtue Route

Bai (2017) proposed a third pathway: the virtue route. Virtue refers to morally praiseworthy characteristics of an individual. Virtue differs from morality, which involves adherence to everyday behavioral norms, whereas virtue includes voluntary self-sacrifice for others' benefit. Moral individuals are "matchers" who follow principles of reciprocal altruism, seeking equivalence between contributions and returns. Virtuous individuals, by contrast, are "givers"who consistently give more than they receive.

Bai further argued that the virtue route exists independently, rather than being a component of the competence route that cannot function separately as Henrich and Gil-White (2001) suggested. He contended that the emotional foundation of the virtue route is admiration, whereas that of the competence route is respect. Moreover, the two routes differ in their antecedent variables, behavioral consequences, and neural correlates. In Henrich and Gil-White' s theory, competence and virtue are integrated into the prestige concept, where virtues such as altruism and generosity help competent individuals gain more attention, thereby increasing the imitation of their knowledge and skills and elevating their status [?, ?, ?].

Empirical research, however, has found that the interaction between virtue and competence is not significant, with both independently contributing to status enhancement [?]. Anthropological and cross-cultural psychological studies also demonstrate that willingness to share resources is crucial for both men and women to gain status in peer groups, whether in modern industrial societies [?] or hunter-gatherer tribes [?, ?]. Therefore, the virtue route is independent rather than a component or moderating factor of the competence route.

4.2 Scope of the Virtue Route

Virtue standards are diverse, but according to Bai' s (2017) definition, the essential characteristic of virtue is altruism. Whether animals, especially non-human primates, possess a virtue route first requires addressing whether they have altruistic attributes. In practice, this question typically leads to research on prosociality. Food-sharing paradigms are most commonly used in prosocial experiments with non-human primates. Most studies indicate that active food sharing is extremely rare in these species [?, ?], though some researchers consider bonobos a potential exception. Bonobos exhibit higher prosociality and social tolerance than chimpanzees and show food-sharing behavior [?, ?]. However, previous experiments may have suffered from practice effects and excessive cognitive demands. Recent studies using multiple paradigms to examine bonobo prosociality have found that they will not provide food rewards to other group members even when the cost is minimal [?, ?]. In previously observed food-sharing events, bonobos did not actively offer food but merely tolerated other individuals taking or stealing it [?]. Therefore, bonobos may possess passive prosocial behavior but lack active prosocial behavior.

Furthermore, according to Bai' s (2017) theory, only the ultimate form of prosociality—altruism—is considered virtue. Prosocial behavior refers to any positive social action that benefits others, whether selfless or selfish, costly or cost-free [?, ?]. Altruistic behavior, by contrast, refers to any action that benefits others while imposing direct costs on the actor. It includes two types: biological altruism and psychological altruism [?]. Biological altruism focuses on behavior and involves increasing others' reproductive success at the expense of one' s own—that is, kin altruism (helping relatives who share some of one' s genes) and reciprocal altruism (current altruistic acts that receive future returns) found in animals. Ultimately, both increase the overall fitness of one' s genes and thus represent "enlightened self-interest." Psychological altruism focuses on motivation and refers to the desire to benefit others. Only humans exhibit non-kin, non-reciprocal psychological altruism, such as donating money to strangers during disasters—actions that often reduce one' s overall genetic fitness and thus represent genuine altruism.

4.3.1 Costly Signaling Theory and Collective Action Problems

How does psychological altruism help individuals gain status? Costly signaling theory posits that altruism is an expensive yet effective means of transmitting an individual' s qualities as a potential cooperative partner or mate, thereby earning higher social evaluation; because it is costly, it is difficult to fake [?]. Researchers have used various experimental methods to test costly signaling theory. Results show that in virtue inference, people value motivations behind behaviors more than the behaviors themselves, and behavioral costs (which must reach a certain threshold) better reflect individuals' altruistic motivations than benefits do [?]. Therefore, even when some altruistic behaviors have greater actual utility, people consider higher-cost behaviors more praiseworthy [?]. Once people suspect that altruistic acts contain selfish motives, altruists fail to gain corresponding status due to authenticity concerns [?, ?].

Furthermore, Willer (2009) argued that altruistic behavior signals that individuals prioritize group interests over personal interests. As compensation, group members grant them high status to encourage further contributions to the collective, thereby helping solve collective action problems. Lang et al. (2022) employed a 2 (high/low cost) × 2 (public/hidden) public goods game experiment to investigate how costly altruistic signals promote collective action. They found that participants in the high-cost public condition were more willing to invest more money in subsequent experiments and attracted cooperation-prone individuals when forming teams later. Conversely, selfish-prone individuals refused to team up due to the high investment required. These results indicate that costly altruistic signals promote collective action in two ways: first, by facilitating the screening of team members with altruistic tendencies; and second, by motivating altruists to contribute more in subsequent collective actions.

4.3.2 Unique Conditions for the Emergence of the Human Virtue Route

Why does psychological altruism exist only in human groups? Richerson et al. (2016) proposed that as early human productivity increased, population size expanded rapidly, creating novel pressures: intensified intergroup competition and strengthened intragroup cooperation. When intergroup competition intensified, groups with high levels of intragroup cooperation could form larger group sizes and greater fighting capacity, thereby defeating other groups. Only psychological altruism can promote large-scale intragroup cooperation (biological altruism functions only in small-scale groups). This behavior cannot emerge through natural selection because free-riders would have higher fitness than altruists and would be more likely to pass on their genes. Groups must therefore employ cultural selection to assign social value (high status) to altruistic behavior, enabling its spread and persistence within groups. This process is termed cultural group selection. Research shows that intergroup competition promotes rewards for intragroup cooperative behavior and punishment of free-riding, thereby enhancing group competitiveness [?]. Moreover, cultural similarity positively predicts group cooperation tendencies, indicating that cooperation norms within different groups evolved through group selection on cultural variation [?].

In addition to group size, cognitive constraints represent another reason why other animals cannot generate a virtue route. As costly signaling theory indicates, motivations better reflect altruistic qualities than behaviors do, requiring people to first infer motivations behind actions. This necessitates a sophisticated theory of mind [?]. Although non-human primates including chimpanzees possess foundational theory of mind functions, they cannot infer other individuals' beliefs about the external world and are more adept at using theory of mind in competitive contexts. They therefore may be unable to understand companions' benevolent intentions or cooperative motives [?]. Furthermore, the self-domestication hypothesis posits that during evolution, humans enhanced self-control abilities and weakened emotional responses, substantially increasing social tolerance in human groups and providing conditions for the evolution of psychological altruism [?]. In summary, external environmental selective pressures (group size) and internal cognitive constraints (theory of mind, self-control, and emotional responses) determine that only human societies can produce the virtue route.

4.4 Uniqueness of the Virtue Route

The purpose of hierarchy is to establish an order for resource distribution; individuals pursue high rank to acquire more resources and thereby increase biological fitness. However, the virtue route is built upon psychological altruism, where individuals reduce their biological fitness through self-sacrifice, creating an essential contradiction. To resolve this contradiction, it is necessary to distinguish between broad and narrow senses of social hierarchy. Narrow social hierarchy refers to the "pecking order" established by animals including humans for resource allocation—a product of biological evolution. In the broad sense, humans pursue social status not purely to acquire more resources but also to obtain high evaluation from others and satisfy psychological needs for self-esteem [?]—a product of cultural evolution. Since this study focuses on humans, we adopt the broad concept of social hierarchy, encompassing the virtue route to more accurately and completely describe the evolution of human hierarchy systems.

In summary, the virtue route exists independently and only in human groups. While animals possess biological altruism, only humans have psychological altruism. Costly altruistic behavior signals genuine altruistic motivation and potential as a cooperative partner, thereby generating prosocial norms within groups and facilitating solutions to large-scale cooperation problems. This judgment of altruistic motivation is built upon sophisticated theory of mind, which nonhuman primates lack the ability to infer other group members' benevolent intentions. However, it remains unclear what group size threshold exceeds the effective range of biological altruism, thereby generating psychological altruism and the virtue route.

5 Comparative Analysis of the Three Hierarchy Routes

As a form of group organization, human hierarchy systems have evolved from simple to complex and from single-dimensional to multidimensional. The dominance, competence, and virtue routes all represent effective means of attaining status. Some previous researchers (e.g., [?, ?]) failed to recognize the complexity and multidimensionality of human hierarchies, conflating different pathways. An evolutionary perspective clearly reveals that the three routes differ markedly across multiple dimensions (see Table 1).

Among these differences, behavioral patterns and outcomes constitute the essential distinctions among the three routes. The dominance route employs aggression and threat, with hierarchical competition essentially being a zero-sum game where an individual' s status elevation necessarily comes at the expense of others' interests [?]. The competence route resembles "free trade," where knowledge and skills constitute "information goods" in social transmission. Group members exchange voluntary deference for opportunities to learn at close proximity, creating win-win situations and positive-sum resource distribution among members. Unlike the first two routes, the virtue route is built upon psychological altruism, where individuals sacrifice their own interests for the benefit of others or the collective.

Additionally, controversy persists regarding the emotional mediators of the competence and virtue routes. Bai (2017) argued that admiration serves as the emotional mediator of the virtue route. However, other researchers view admiration as a positive emotion elicited during upward comparisons when feeling less competent than others, thereby promoting social learning in the competence domain [?, ?]. Under this interpretation, admiration is the emotional mediator of the competence route. In previous theories, respect was considered the emotional mediator of the competence route [?, ?, ?]. This confusion arises because both admiration and respect belong to the "other-praising" emotion family [?]. Initially, admiration simultaneously referred to appreciation for excellence in both competence and moral domains, but deepening research created a need for conceptual differentiation across these domains.

Algoe and Haidt (2009) first proposed restricting the concept of "admiration" to the competence domain and using "elevation" to refer to the emotion elicited by virtue that exceeds standards. Elevation produces a sensation of chest expansion or opening, feelings of warmth and pleasure, and a sense of uplift, thereby motivating individuals to imitate and practice virtuous behaviors. In contrast, admiration for excellent competence motivates self-improvement. This classification has been recognized and adopted by most researchers [?, ?, ?, ?] and has received support from empirical studies. Onu, Kessler, and Andonovska-Trajkovska et al. (2016) found that outgroup competence evaluation significantly predicted admiration, whereas virtue evaluation only marginally predicted admiration. Pizarro et al. (2021) discovered that elevation promotes personal collective identity and enhances helping intentions. Nakatani et al. (2019) argued that admiration targets excellent behaviors, whereas respect concerns the person as a whole. Using neuroimaging to investigate neural basis differences, they found that although admiration and respect activate largely overlapping brain regions, a portion of the left anterior temporal lobe (ATL) was more strongly affected by respect. This region is associated with semantic information processing, and respect requires not only processing behavior itself but also integrating current and past information to evaluate the whole person. Based on this difference in information quantity, they speculate that admiration may be a subset of respect. Therefore, this study adopts Algoe and Haidt' s (2009) perspective: admiration is the emotional mediator of the competence route, elevation is the emotional mediator of the virtue route, and respect may be an emotional reflection of comprehensive social status judgments.

Table 1. Comparative Analysis of the Three Hierarchy Routes

Dimension	Dominance Route	Competence Route	Virtue Route
Scope of Existence	Vast majority of social animals	Humans and some primates	Humans only
Behavioral Means	Aggression and threat	Mastery of knowledge and skills	High-cost altruistic behavior
Outcome Pattern	Zero-sum game: status elevation at others' expense	Positive-sum game: voluntary deference exchanged for learning opportunities, creating mutual benefit	Individual sacrifices self-interest for others' or collective benefit

Dimension	Dominance Route	Competence Route	Virtue Route
Evolutionary Cause	Intense sexual selection from male mate competition	Need for technical foraging	Need to solve large-scale collective action problems
Selection Level	Individual selection	Cultural group selection	Cultural group selection
Learning Mechanism	Reinforcement learning and observational conditioning	Cultural learning via imitation and teaching	Inferring benevolent intentions and cooperative motives
Neural Basis	Neural circuits centered on medial prefrontal cortex and amygdala	Ventrolateral prefrontal cortex and mirror neurons	(To be studied)

6 Summary and Outlook

Social hierarchies are products of group living. They can effectively reduce intragroup conflict, save group members' time and energy, and decrease injury risk [?, ?], while also significantly impacting individuals' physical and mental health and longevity [?, ?]. Since the discovery of the "pecking order," the multidimensionality and complexity of social hierarchies have been gradually revealed. From the dominance route to the competence route and then to the virtue route, the evolution of hierarchy systems has propelled human society toward greater civilization. Extensive researcher attention has yielded fruitful results in this field, yet we remain distant from obtaining a complete evolutionary picture, and existing conclusions contain some contradictions and deficiencies. Future research can proceed in the following directions:

6.1 Relationship Between Sexual Selection Patterns and Dominance Hierarchies in Different Animal Species

Although multiple lines of evidence suggest that same-sex competition may be the primary evolutionary driver of the dominance route, we cannot exclude the potential role of natural selection. Theoretically, various resources could trigger intragroup competition and facilitate dominance hierarchy formation. However, current research indicates that dominance hierarchies primarily exist in male groups, with males being larger, stronger, and more aggressive than females, and exhibiting greater reproductive variance. Sexual dimorphism is typically a result of sexual selection, though some studies show that natural selection often establishes different phenotypes in males and females, such as women increasing body fat for reproductive needs [?].

To further confirm the role of same-sex competition in dominance hierarchy formation, future research could compare dominance hierarchy differences across mating systems. Polygynous social animals likely have steeper dominance hierarchies than monogamous ones. Even among polygynous animals, the intensity of mate competition within groups varies, typically measured by reproductive skew (the variance in number of surviving offspring) [**?**]. Higher reproductive skew indicates more intense mate competition and potentially steeper dominance hierarchies. Additionally, animal mating patterns are not static. Humans, for example, formed low-dominance, small-scale egalitarian hunter-gatherer societies during the Pleistocene and evolved motivations for relatively monogamous pair bonds. As male mate competition intensity decreased, human sexual size dimorphism also diminished [**?**, **?**]. In other words, reduced sexual selection intensity and moderated dominance hierarchy gradients occurred simultaneously. However, humans represent just one case. Future research could systematically examine longitudinal changes in male mate competition intensity and dominance hierarchy gradients over time in different animals, especially primates, to better explore underlying causal mechanisms.

6.2 Special Environments for the Evolution of the Human Competence Route

The formation of specific routes must consider recurrent selective pressures in human ancestral environments. Van Boekholt et al. (2021) found that among all primate species, only human social structures exhibit various favorable characteristics that promote social learning. Additionally, around 3.4 million years ago, human dietary structure underwent dramatic shifts from scattered plant resources to nutrient-dense, predictable animal resources. Important evolutionary events such as flake stone tool production, large animal butchery, and cranial capacity expansion emerged successively. This transition enabled humans to develop more complex technologies than other primates [**?**]. Moreover, Pleistocene hominins primarily engaged in cooperative hunting of large animals, making the ability to coordinate group activities particularly crucial for human ancestors [**?**].

In summary, technical foraging, cooperative hunting, and unique social structures together may have created pressures that differentiated human societies from other animal communities, facilitating the transformation from dominance-based to competence-based hierarchy systems. This transition was not accomplished overnight but likely occurred over extremely long periods. How these environmental factors interact with cultural learning remains unknown. Future research should conduct comparative studies on social morphology, cultural learning, and competence hierarchy differences across more social animal species to determine the importance of various environmental factors in creating hierarchy form differences. This will likely require multidisciplinary collaboration among archaeology, anthropology, and primatology, particularly investigations into the social morphology of extinct human ancestors, which will provide critical information for better understanding the evolution of competence hierarchies.

6.3 Exploring the Biological Basis of Virtue Route Evolution

Cultural group selection explains the emergence of the virtue route from an ultimate mechanism perspective, but the biological basis of this pathway—its proximate mechanisms—remains inadequately explored. Neuroimaging research reveals that altruistic behavior activates brain regions associated with empathy and reward processing, stimulating the release of hormones such as dopamine, oxytocin, and serotonin [**?**]. In other words, altruism can provide psychological satisfaction through self-reinforcement. This may be built upon the neuroplasticity and dopaminergic reward systems of the human brain, which play important roles in forming and remodeling neural circuits [**?**]. Does the human capacity to transcend biological evolution and make status pursuit an end in itself rather than a means to acquire resources also rest upon similar neural mechanisms? Is this "self-purposiveness" of hierarchical psychology unique to the virtue route, or does it apply to all routes? Animal brains in the dominance route also exhibit similar reward mechanisms—why have they not developed motivations beyond survival and reproduction?

Future research should employ empirical methods combining cross-species comparisons at neural, cognitive, and behavioral levels to further explore relevant neural mechanisms and their universality.

Additionally, genetic-level research has found that 972 genes explain heritable variation in human modernity features including prosociality, with 267 of these genes being absent in chimpanzees or Neanderthals [**?**]. Such genotypic differences may determine phenotypic differences in prosociality among the three species. Consequently, chimpanzees struggle to cooperate beyond familiar social partnerships because they show strong self-interest tendencies in cooperative tasks [**?**]. Neanderthals, our close relatives, despite possessing strong visuospatial abilities and tool-making skills, were less adept at social interaction and group cooperation compared to humans and eventually went extinct 40,000 years ago [**?**, **?**]. Perhaps these differences in prosociality prevented chimpanzees and Neanderthals from developing a virtue route like humans to solve large-scale collective action problems. Future research should address this possibility, seeking definitive evidence through interdisciplinary collaboration among archaeology, neuroscience, and genetics to reveal underlying genetic mechanisms.

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Note: Figure translations are in progress. See original paper for figures.

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