On Faces, Gazes, Votes, and Followers: Evolutionary Psychological and Social Neuroscience Approaches to Leadership

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Abstract Leadership is arguably one of the most important themes in the social sciences, permeating all aspects of human social affairs, from the Euro zone crisis to the re-election of the first black president in the US. Parallel findings across the biological and social sciences suggest that there are both commonalities and differences between humans and non-humans in leadership and followership. Here I propose a new theory of leadership inspired by an evolutionary perspective and informed by recent findings in evolutionary biology, social and cognitive psychology, and social cognitive neuroscience. I will identify some of the evolved functions, developmental origins, and proximate mechanisms underlying leadership and followership in humans. In addition, I will suggest which aspects of leadership are unique and which are shared with other animals and offer new ways of studying leadership and followership employing psychological and neuroscience methods.

Introduction

When a honeybee returns to its hive after foraging for nectar, it performs a dance for the other bees. The bee skips around making a figure-of-eight movement, waggling its abdomen as it does so. Recent findings suggest that the dancer is indicating through its moves the location and quality of a foraging site (Riley et al. 2005), which confirms an earlier discovery by the biologist Karl von Frisch. The direction the bee is facing points to the direction of the food source relative to the sun; the

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duration of the waggle dance represents how far the source lies and its quality. The dancer bee is, in fact, acting as a leader by scouting out food resources for the hive. The best dancers recruit the most followers and this interaction produces a very efficient group performance. The waggle dance of the honeybee is one of many forms of leadership and followership that have been observed in non-human animals, from the migration patterns of birds to foraging activities of fish and peacekeeping and warfare among chimpanzees (King et al. 2009; Van Vugt and Ahuja 2010).

In humans leadership is common, too, and it helps group members to coordinate their actions. When four individuals play a coordination game (the weak-link game) in which they each have to pick a number between 1 and 10, and they get a higher pay-off if they coordinate on higher numbers; their individual pay-offs are suboptimal if they make their individual choices simultaneously. Yet by having one individual move first – leadership by example – and announcing his choice to the others in the group, the team members coordinate on a higher number, and as a consequence, their pay-offs increase (Cartwright et al. 2013). This result is intriguing because the actions almost exactly correspond to the outcomes of models and simulations designed to explore coordination in animal groups (Couzin et al. 2005). It suggests that similar coordination mechanisms are found across species and highlights the importance of leadership and followership, where one or a few individuals initiate an action by moving first and the rest follow.

In his influential, award-winning book, "Leadership," the political scientist James McGregor Burns wrote: "Leadership is one of the most observed and least understood phenomena on earth" (Burns 1978, p. 2). There is little argument about the first part of the statement. Human history is littered with examples of individuals who take charge of a group and lead it – often against the odds – to safety, victory, and prosperity. Military leaders like Alexander the Great, Nelson, and Patton, political leaders like Roosevelt, Nasser, and Mandela, revolutionaries like Mao, Ghandi, and Rosa Luxembourg, business leaders like Ford, Gates, and Branson, and religious leaders like Jesus, Mohammed and Buddha all fit this description. Anthropologists have found evidence of leadership everywhere they looked. Their conclusion is that there are no known human societies without some form of leadership, whereby individuals coordinate the activities of a group although they are not usually institutionalized leaders (Brown 1991). Social psychological research reveals that a leader-follower structure emerges spontaneously when individuals come together to perform a particular task, even when groups set out to be leaderless (Van Vugt 2006). Whenever a group of people comes together, a leader-follower relationship naturally develops. In our laboratory, we have found that leadership develops in around 25 s when individuals are put together in a group to solve a particular task (Gillet et al. 2010).

The psychological literature on leadership is overwhelming. There are more than 1,500,000 hits in Google Scholar on the combined search terms "leadership" and "psychology." Yet most studies in psychology tend to focus on finding proximate explanations for leadership (e.g., "Who emerges as leader when group members are in conflict"). This literature tends to ignore questions about the evolutionary roots

and functions of leadership or about the consistencies and inconsistencies between leadership in humans and nonhumans. Biological scientists have had an enduring interest in leadership as well, but there is a dearth of empirical data on the subject in this field. Only recently was the first review article on leadership in animals published in Current Biology (King et al. 2009). The evolutionary biologist E. O. Wilson (1975) summarized his discipline's perspective on leadership some decades ago: "When zoologists speak of leadership, they usually mean the simple act of leading other group members during movement from one place to another" (p. 311). Although group movement is indeed a classic coordination problem for which leadership could have evolved (King et al. 2009), there may be additional evolved functions of leadership.

The biological and psychological literatures on leadership have much in common, and an integrated evolutionary perspective offers a much needed scientific basis for advancing leadership theory and research across the behavioral sciences. Evolutionary leadership theory (Van Vugt and Ahuja 2010) offers such an integrative framework. Utilizing Tinbergen's four questions framework, I first argue why leadership emerged in various species – the ultimate evolutionary function – noting similarities and differences between leadership in humans and nonhumans. Then I address the comparative aspects of leadership, examining who emerges as leaders in animal groups and how they lead. Third, I address the developmental origins of leadership, where I will present new data on gaze following and mimicry as manifestations of leadership and followership. Fourth, I present a time line for the phylogenetic development of leadership, from simple coordination movements between brainless organisms to the complex leadership structures that characterize modern human societies. This review concludes with a list of recent empirical findings from biology, anthropology, psychology and social neuroscience that shows the generativity of adopting an integrative evolutionary approach to leadership.

Leadership and the Need to Coordinate

According to evolutionary leadership theory (Van Vugt and Ahuja 2010), the critical adaptive problem that gave rise to the emergence of leadership and followership across various species is the need for coordination. In species where individuals are better off acting and moving together, leader-follower patterns are likely to emerge (Girardeau and Beauchamp 1999; Van Vugt et al. 2008). A concise review of leadership in nonhumans shows instances of leadership across diverse taxa such as insects, fish, birds, and mammals. Leadership is not only restricted to challenges involving group movement but also to coordinated hunting, group defense against predators, teaching and learning, and peacekeeping (King et al. 2009).

That leadership is the inevitable outcome of strategic interactions between actors can be demonstrated with a simple coordination game with the following constraints (Van Vugt 2006; Van Vugt and Kurzban 2007): (1) organisms must do things to stay alive, and (2) they must do these things with one or more conspecifics. Imagine Jamie and Pat – two humans but they could be members of any social species – who must coordinate on the same waterhole to relieve their thirst (Fig. 1). Suppose they could go to waterhole A or B and will get the same pay-off if they coordinate on the same hole yet they are indifferent as to which hole they coordinate on. If one individual moves first, this leaves the other no option but to follow. Further, if one assumes that for some reason Jamie is always thirstier first, then he will automatically emerge as the leader. More generally, any trait – physical, psychological or behavioral – that increases the likelihood of one of them moving first will make them emerge as the leader more often. This two-player game can be easily generalized to a multiple player game where one or a few knowledgeable or motivated individuals can coordinate a much larger group (Dyer et al. 2009). Turning a simultaneous game into a sequential game paves the way for the emergence of leadership (Van Vugt 2006).

What happens if we introduce conflict among the players? Conflict is rife among members of many group-living species. Jamie prefers Waterhole A over B but the reverse is true for Pat. This is now a "Leader" or "Battle of the Sexes" game (Van Vugt 2006; King et al. 2009), and coordination is more difficult to achieve because whatever hole they coordinate on they will end up with unequal pay-offs. Here there is suddenly an incentive to be the leader (Van Vugt and Kurzban 2007). Greater payoff differences will make it harder for individuals to achieve coordination (Fig. 2).

The sequential version of the game is akin to an ultimatum game. In an ultimatum game, one individual is the proposer and the other is the receiver. The proposer has, say, 10 Euro that he can divide between himself and another player. If the other player accepts the offer, both get what was proposed; yet, if the other player refuses the offer, nobody gets anything. Thus, depending upon whether his offer is accepted, the proposer either emerges as leader or else his attempt to lead fails. Experiments with humans suggest that offers below 40 % are often rejected (Solnick and Schweitzer 1999).

In comparing leadership in humans and nonhumans, one striking difference is that leadership in humans fulfills a number of additional functions beyond organizing group movement. One of these is maintaining group cohesion. In human evolutionary history, as groups get larger and more socially complex, it would have been important to find mechanisms to keep groups together, and leadership (supported by language) might have played a role in this (Dunbar 1993). Anthropologists find that the social lives of hunter-gatherers involve constant conflict, so there is a niche for individuals to step up as peacebrokers or peacekeepers (Boehm 1999). To demonstrate the power of "coercive" leadership, we had groups of four players each play a public-good game over several rounds in different group compositions (O'Gorman et al. 2009; cf. Van Vugt and De Cremer 1999). In each round, one individual was designated as the solitary punisher and he or she could spend his/her earnings to punish others in the group (each unit of punishment subtracted the earnings of others by three units).

Fig. 1 The coordination game. Payoffs are for Pat and Jamie, respectively. Hole A and B constitute alternative game strategies (underpinned by genes); game equilibria are indicated with *asterisks*

		Pat	
		Hole A	Hole B
Jamie	Hole A	1, 1*	0, 0
	Hole B	0, 0	1, 1*

Fig. 2 The leader (battle of sexes) game. Payoffs are for Pat and Jamie, respectively. Hole A and B constitute alternative game strategies (underpinned by genes); game equilibria are indicated with *asterisks*

		Pat	
		Hole A	Hole B
Jamie	Hole A	9, 1*	0, 0
	Hole B	0, 0	1, 9*

The main finding was that this one-punisher condition stabilized cooperation in groups whereas, in groups without punishment, cooperation declined over time. Furthermore, the single-punisher condition was as effective as the all-punisher conditions in the frequently cited Fehr and Gächter experiment (2002). Finally, we compared conditions in which the solitary punisher emerged from the group (endogenous condition) or was randomly picked by the experiment (exogenous condition), but there was no difference between the endogenous or exogenous leaders in terms of punishment or their impact on group cooperation. Across all conditions, the leaders did worse in terms of their earnings than the non-leaders. There are some parallels in the execution of this leadership role between humans and other great apes. For instance, chimpanzees, bonobos, and gorillas all practice peacekeeping and, therefore, I believe that it was almost surely a feature of early human societies as well (Boehm 1999; De Waal 1989).

Another particular niche for human leadership is maintaining relationships with other groups. At various stages of human evolution, there would have been intense competition among groups for scarce reproductive resources such as food, waterholes, and mates (Boehm 1999). Sometimes this competition might have resulted in the formation of alliances with other groups; at other times it may have produced severe intergroup conflict (Chagnon 1997; Van Vugt et al. 2007). Leadership may play a role in warfare and peace-brokering (Van Vugt and Spisak 2008). In traditional societies such as some Native American tribes, different chiefs emerge in war or peacetime and these are different individuals. War leaders tend to be physically stronger, younger, and of a lower class, whereas peace leaders are less formidable, older and of a higher class (Johnson and Earle 2000). This finding is supported by research showing that, when voters elect political leaders during wartime, they prefer a more masculine-looking leader over a more feminine-looking leader whereas the reverse is found during peacetime (Spisak et al. 2012).

In addition, there may be planning and allocation problems in human groups that may require some form of coordination through leadership. For instance, among hunter-gatherers, when a large animal is being killed, how is the meat being shared among the band members? Again, some form of leadership may be useful here where one individual has been assigned to divide the meat.

A final niche for the emergence of leadership in humans is in situations where some individuals in the group are informed and others are uninformed. There is a coordination challenge here, whereby informed individuals take the lead and teach uninformed individuals relevant knowledge and skills. Teaching as a form of leadership has been observed in various other species, such as the social insects. We have already discussed the scout leaders among the honeybees. Teaching has also been observed in ants, where an informed individual teaches an uninformed individual the location of a food resource (Franks and Richardson 2006).

In sum, different coordination challenges may have opened up opportunities for some individuals to emerge as leaders and for others to follow in animal groups. A basic coordination challenge, with deep evolutionary roots, involves movement of individuals in flocks, shoals, swarms or crowds. In humans and perhaps other species, there are additional functions of leaders as peacekeepers, war leaders, diplomats, managers, and teachers.

Leadership Emergence

The coordination game shows that individuals are more likely to emerge as leaders if they have a particular physiology, personality or position in the group that increases their propensity to be a first mover and attract followers. A previously published review of the animal literature (King et al. 2009) suggests that there are at least four behavioral traits that are consistently associated with leadership emergence across species: (1) motivation, (2) personality, (3) experience, and (4) dominance.

First, more motivated individuals are more likely to become leaders. A mathematical model shows that, when two individual coordinate their actions, the one with the lower energy resources will spontaneously emerge as the leader (Rands et al. 2003). Real-world data support this. To the extent that fish are more food-deprived, they are more likely to take the front position in a shoal where they have greater influence on group movement. In addition, among several species such as zebra, lemur and gibbon, the females are found to assume coordinate-group actions when they are in their reproductive phase and hence require more food. Interestingly, more autonomous individuals are also more likely to be leaders, as they have

a higher tolerance for allowing distance between themselves and their conspecifics and thus have a lower motivation to coordinate their actions with others. This finding could explain why, in humans, leadership is correlated with autonomy, independence, and internal locus of control (Judge and Bono 2000; Van Vugt 2006).

Differences in personality also underlie leadership and followership across species. Correlations between leadership and specific personality attributes are well documented in humans (Judge and Bono 2000) and to a lesser extent in nonhumans (King et al. 2009). Biologists have traditionally conceived of personality differences as noisy variations in traits that are "adaptive on average." Yet it is now generally agreed that personality differences may be the result of frequency-dependent selection forces, where alternative strategies are viable because they may exploit some ecological or social niche (Nettle 2006). Recent studies had pairs of stickleback fish coordinating their actions to get food. The researchers showed that personality differences between the fish were crucial to achieve coordination. Bold fish emerged as leaders and shy fish emerged as followers, and this difference was enhanced by social feedback (Harcourt et al. 2009). A meta-analysis of the personality literature in humans also reveals that extraversion, which equates to boldness, is most consistently related to leadership emergence (Judge and Bono 2000). Such a correlation across species raises the intriguing question of whether personality differences are maintained through frequency-dependent selection or even group selection to improve social coordination (Wilson et al. 2008).

A third trait that is consistently linked to leadership emergence across species is knowledge or experience. Older females guide herd movement presumably because they possess knowledge of far away waterholes during drought (Foley et al. 2008). In bottle-nose dolphins, more experienced individuals emerge as leaders in foraging expeditions, and having consistent, knowledgeable leaders improves foraging efficiency in groups (Lewis et al. 2013). In humans, individuals with unique, task-relevant expertise also assume leadership roles more often. Research has shown that, after just a few minutes, they can identify the individuals with expertise in a group and these experts achieve greater status and influence (Van Vugt 2006). A final unpublished study from our research group shows that individuals are more likely to vote for older-looking leaders when groups rely on traditional knowledge to solve problems and younger leaders when groups need to find new solutions (Spisak et al. 2012).

Finally, individuals can emerge as leaders because they occupy a dominant position in their group and can sometimes afford to do things by themselves without having to follow anyone. This "byproduct dominance" hypothesis (Van Vugt 2006) is supported by research on wolves and gorill, where the dominant individual sometimes takes on particular leadership roles. One should realize that dominant individuals lead not because they are dominant per se but because they can operate more autonomously given their superior body size, alliances, or access to resources. Specifically, high-ranked individuals are in a better position to elicit followership since they hold a particularly strong influence over the behaviors of group members. Research on baboons confirms that alpha males consistently lead groups to specific food sources despite the followers doing a lot worse than the leader in getting a meal (King and Cowlishaw 2009). Correlations between leadership and dominance are also present in humans, although in humans dominance tends to manifest itself socially (Van Vugt 2006).

Leadership emergence across the animal kingdom has been found to be associated with at least four different traits: motivation, personality, experience, and dominance. Similar patterns have been obtained in humans. Yet the main differences are that in humans leadership is more flexible and, depending upon conditions, anyone can take the lead if he can bring some benefit to the group. In humans, leaders emerge because they possess traits that signal their ability to help the group further their goals (prestige; Henrich and Gil-White 2001).

Styles of Leadership

A further question is how do leaders lead in animal groups. Leadership can be weak, situational, and accidental, such as when dominant individuals emerge as leaders because they simply can afford to be on their own. Leader-follower patterns can also emerge through relatively spontaneous self-organizing processes, where individuals follow a simple coordination rule such as staying close to one's neighbor (Couzin et al. 2005). These coordination mechanisms are likely to be found in relatively homogeneous groups like insect swarms, fish shoals, and bird flocks, where there is little conflict of interest between individual actors (King et al. 2009; Van Vugt et al. 2008).

Conversely, leadership can be strong, active and sometimes even coercive. Potential leaders can explicitly signal their intentions to the rest of the group. For instance, in ants, individuals who have learned the route to feeding sites use 'tandem running' to lead another ant from the nest to food, with signals between the pair of ants controlling both the speed and course of the run (Franks and Richardson 2006). In honeybees, leading individuals (scouts) recruit followers using 'dances' that inform proximate colony members on the location of new nest sites when moving home (Riley et al. 2005). More active forms of leadership are also found in species operating in much smaller social groups. Ravens with information about the location of high-quality food sources lead others through a series of acrobatic display flights. Knowledgeable dolphins use visual displays to influence the behaviors of an entire group. Finally, in non-human primates, leaders use vocal and visual signals to initiate collective movement (De Waal 2006). In addition, leadership decision rules can either be despotic or democratic. In some species, for instance those with a clear dominance hierarchy, followers accept the decision of a specific despotic individual on a regular basis, whereas in others, almost any individual can attract followers. In the case of these more democratic forms of leadership, it can be achieved via a majority vote or when a threshold number of followers agrees with a potential leader proposal (Conradt and Roper 2005).

Contrasting human with non-human leadership styles, we see that human leadership styles are more variable, from weak and passive forms of leadership to active and coercive styles. Signaling mechanisms to attract followers are very well developed in humans. Humans use facial expressions, gazes, gestures, rituals and language to attract followers. Furthermore, human leadership is often formalized, in that individuals occupy roles whereby their primary task is to lead others. Oftentimes these consistent leaders employ coercive tactics to get others to follow, such as a manager in the workplace who can demand that subordinates improve their efficiency. Finally, there is considerable evidence that humans are capable of both democratic and despotic leadership styles. Democratic decision making was evident throughout much of early human evolution, where our ancestors lived in relatively egalitarian hunter-gatherer societies (Boehm 1999; Dunbar 1993), whereas despotic leadership is more evident in the non-human primates as well as in episodes of relatively recent human history (e.g., modern dictatorships). It seems that humans are capable of organizing themselves in any way they want, depending on conditions, and further research is needed to find out which leader structures emerge under which conditions (Van Vugt 2009).

In sum, leadership in animal groups can be accidental, passive and weak or strong, coercive and formalized. It seems that humans are highly plastic in the way they organize leadership in groups, from accidental leaders who find themselves at the head of a group, to more consistent, even institutionalized leaders whose primary task it is to get individuals to follow and punish if they fail. Furthermore, depending on socio-environmental conditions such as time pressures and inter- or intra-group conflicts, human groups can revert to either more despotic or more democratic forms of leadership.

Ontogenetic Development of Leadership

The adaptive benefits of leadership hint at the possibility of the presence of various evolved cognitive and neurobiological mechanisms supporting leadership across animal species. An adaptationist analysis suggests that organisms may have specialized mechanisms for (1) identifying situations as requiring coordination, (2) assessing the costs and benefits of following another individual versus going alone, (3) identifying the trade-offs involved in following different individuals, (4) assessing the goals and intentions of different potential leaders, (5) selecting an appropriate individual to follow, (6) getting them to lead, and (7) staying close to the individual leader while following them (Van Vugt and Kurzban 2007). It is likely that these mechanisms are supported by specific neurological mechanisms, and the more complex and variable the forms of leadership that animals display the more sophisticated this neurological machinery will be.

Human leadership is in many ways the same but in some ways very different from that in other animals. Humans use facial expressions, gazing, gestures, rituals, and language to attract followers. Humans also create social institutions and develop rules and laws to induce followership. What specific neurological mechanisms make this possible? Building on the child developmental research by Mike Tomasello and colleagues (2005), I would like to suggest that one of the things that makes human leadership so different is that humans have the capacity for shared intentionality, meaning *the ability to share psychological states with each other for the purposes of engaging in collaborative action.*

Gaze Following

Shared intentionality sets humans apart from other animals, including the non-human primates. It opens up new ways to lead and follow, thus contributing to the genetic and cultural elaboration of leadership to the extent that human leaders can coordinate the actions of millions of individuals in dispersed fission-fusion societies. One of the primary building blocks for the ontogenetic development of leadership is gaze following. Eye gaze following is a powerful cue in various social species (Zuberbuehler 2008). Monitoring and following the gaze of others can provide useful information about threats and opportunities in the environment of an individual. Developmentally, it is one of the earliest manifestations of leadership and followership, as it is already seen in human babies as early as 3 months old. Other animals follow the eye gaze of conspecifics, too, to know what they are looking at. For instance, chimpanzees follow the gaze to external locations and then they check back to see if there is anything interesting. Human infants go far beyond this capacity, however. A 1-year-old human infant does not just follow the gaze of others but also actively shares attention with others. It has been suggested that humans have so much white around their eyes (compared to other animals) to allow them to coordinate their activities better through gaze following: the cooperative eyes hypothesis.

Research into Leadership and Gaze Following. One of the experimental paradigms used in cognitive neuroscience to track gaze following is the gaze cuing paradigm. Cognitive scientists typically use a gaze cuing task to study the influence of gaze on attention. In such tasks, a central face is presented whose diverted gaze is either directed toward the target stimulus (valid cue) or away from the target stimulus (invalid cue). The results typically show that participants respond faster and with fewer errors to a validly cued target than to an invalidly cued target. This is known as the 'gaze cuing effect.' Note that this effect occurs despite the fact that the gaze direction does not actually predict the location of the target stimulus.

The gaze cuing task is ideally suited to test evolutionary hypotheses about leadership and followership. Here we report the results of a gaze cuing experiment that was conducted at the VU University Amsterdam, in collaboration with Garian Ohlsen and Dr. Wieske van Zoest, and published recently in PlOS-One (Ohlsen et al. 2013). The experiment examined if humans are biased to follow the gaze of dominant individuals. Some studies have found that cues associated with social status and dominance influence the gaze cuing effect. A study in primates showed

that macaque monkeys follow the gaze of dominant monkeys more than of non-dominant monkeys. Comparable results have been found in human populations. People selectively attend more to individuals rated as high in status, and they especially look at their eye regions. Other research has shown that the gaze cuing effect is stronger when participants look at a face of an individual being described as high in status. Social status in humans may be conveyed through facial features like dominance, trustworthiness or competence.

The aim of the study was to investigate whether certain facial features of dominance would affect gaze cuing. Informed by an evolutionary psychological perspective, the idea is that it might be evolutionary adaptive to follow dominant-looking individuals specifically in times of danger, when dominant individuals may provide protection and safety. We hypothesized that, if we primed individuals with threat cues, they would influence gaze cuing only with dominant-looking but not with non-dominant looking faces. Earlier research already showed that people have a stronger preference to follow dominant-looking (masculine) leaders in war and non-dominant-looking (feminine) leaders in peace (Spisak et al. 2012). Building on this work, we predicted that facial cues of dominance enhanced gaze cuing but only under conditions of emotional threat.

The procedure was as follows. Prior to the gaze cue task, participants were primed with emotional pictures signifying no threat or pictures signifying threat to induce either a safe or dangerous condition, respectively. We used pictures from the International Affective Picture System (IAPS) database: 20 pictures denoted threat (e.g., pictures of road accidents, combat situations, physical attacks) and 20 denoted no threat (e.g., pictures of smiling babies, couples holding hands). This gaze cuing task was similar to the one employed in many previous studies. Participants were instructed to focus their attention on the centrally presented fixation point that was visible for 500 ms. After the fixation cue, depending on condition, a non-dominant-looking female face or a dominant-looking male face appeared with a straight-ahead gaze for 1,000 ms. This face was subsequently replaced with exactly the same face with a gaze directed either to the left, right or straight ahead (control condition, no change). The peripherally located target ('L' or 'T') appeared 200 or 800 ms (SOA) after the presentation of the second face, and its location was unrelated to the gaze direction of the face stimulus. Figure 1 provides an example of the trial sequence and a picture of the dominant-looking male and non-dominant-looking female faces used as gaze cues. The first results were that the dominant male face was indeed rated as more masculine and dominant than the female face and that, in the threat condition, participants felt more negative than in the no-threat condition. Furthermore, the gaze cuing results showed that the gaze cue effect was significantly larger for the dominant male face than the non-dominant female face, yet only in the threat condition and at short viewing times. In the threat condition, the non-dominant female face no longer elicited a gaze cuing effect. The main results are plotted in Fig. 3. This research thus suggests that there is a highly automatic bias to follow dominant-looking faces, especially in times of danger and crisis. This finding has implications for our thinking about the ontogenetic development of leadership in humans.

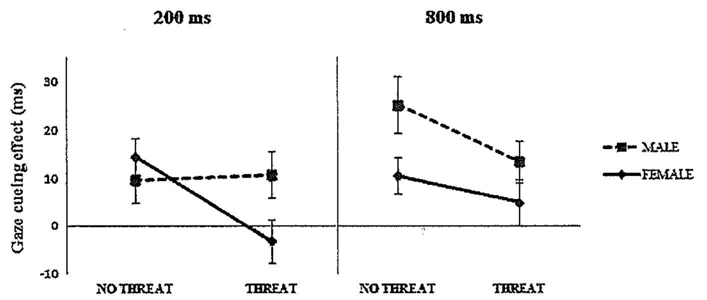

Fig. 3 Gaze cueing effect is absent for female faces when participants are primed with threat pictures (<200 milliseconds; Ohlsen et al. 2013)

Pointing and Gesturing

A second building block for the development of leadership in humans is the capacity for gesturing and pointing. Human infants gesture to communicate, for example, by pointing. These gestures depend fundamentally on shared intentionality because they involve both a shared understanding and cooperative intention. For instance, if children play a hiding-finding game and one child points to a bucket, the other infant will likely infer that he is pointing to inform her of the location of the hidden object. When children are 9 months of age, they already begin to direct others' attention to objects by gesturing. When they are 1-year-old, they point to inform others of things they do not know – in effect sharing information with them – even when there is no benefit to themselves. Leadership through gesturing is rare among other animals. For instance, chimpanzees and other great apes do not generally point, even though they sometimes point to things they want humans to fetch for them. Because they lack shared intentionality, when they observe a pointing gesture they do not understand its underlying cooperative intention. Another highly social species that understands human pointing are dogs, which have co-evolved with humans for the past 30,000 years. Research on canines suggests that the ability to understand human pointing is an instinct and does not require any training (Hare and Tomasello 2005).

Teaching and Instructed Learning

The third cognitive building block underlying the development of leadership in humans, which sets them apart from other species, is teaching. Human infants more readily imitate the actions of adults, and they sometimes do this with the apparent motivation to coordinate their actions with adults. In addition, human adults quite often teach youngsters things by demonstrating what they should do, which the youngsters then respond to by imitating. Interestingly, when adults instruct their children in this way, infants copy the particular actions the adults used and they do so more often than when adults do not actively teach. Human infants also sometimes reverse roles, where they redirect the actions back to the demonstrator.

This form of leadership through teaching is unheard of in non-human animals. For instance, chimpanzees do not engage in imitative learning and adults do not demonstrate things for youngsters. What seems to be lacking is a collaborative mindset whereby the adult builds up an active collaborative relationship with the infant. Of course, active goal-directed social learning through instructed teaching opens up new opportunities for leading and following in humans.

Research into Leadership and Mimicry. One of the neurological mechanisms underlying leadership through teaching is behavioral mimicry. Mimicry is the automatic imitation of the manner in which another person expresses him/herself (Chartrand and Bargh 1999). This includes motor activities such as gestures and postures, vocal signals such as pitch and volume, facial expressions, and language use. Behavioral mimicry is a human universal; it occurs spontaneously, from a very young age, and has been observed in various social species, suggesting that it has important adaptive benefits for group-living species. It has been hypothesized that, through mimicry, humans learn new skills and strategies that are important for their survival and reproductive success (Henrich and Gil-White 2001).

Our present research, conducted with Wouter Wolf and Dr. Claire Ashton-James at the VU University, has examined the role of behavioral mimicry in the effectiveness of leaders to attract followership. Based on the leadership literature, we distinguished between two sources of influence: dominance and prestige. Dominance is based on the ability of an individual to threaten and harm. It is a classic form of influence in species with dominance hierarchies such as non-human primates. Prestige is influence of an individual that is based on his ability to help followers achieve their goals. Competence, expertise, experience and prosociality are aspects of prestige that may give individuals leadership status in humans.

In one study, we showed student participants a clip of one of their professors. First they pre-rated their professor on various aspects of prestige ("Students respect and admire him/her") and dominance ("He/she often tries to get his/her own way regardless of what students may want"). Next, they watched a 3-min video of their professor responding to interview questions. The video was presented without sound because it might influence perceptions of the professor's prestige and dominance. During the pre-recorded interview, the professor enacted a variety of gestures (face touching, head scratching, hair touching, nose wiping). Participants' mimicry of these gestures was recorded by the video camera and was later coded by three research assistants who were blind to any of the participant answers that categorized the video based on either the absence or the presence of mimicry in the video. As predicted, we found that students mimicked their professor more to the extent that they perceived him/her to be a prestige-based leader.

In the next study, we wanted to see if mimicry as a form of followership was strategically motivated or not. We conducted an experiment in which we trained a confederate to be either dominant (e.g., directive) or prestigious (e.g., knowledgeable) while they were leading an individual during a problem-solving task.

In addition, in one condition participants received five Euros for their participation in this study, whereas in the other condition they were told that the leader would decide how much they would get for their participation in the study. We then looked at the extent to which the participant mimicked the leader. As in the previous study, we found that participants mimicked a leader who exhibited prestige more than a leader who exhibited dominance. However, when they could gain financially from affiliation with the leader, they mimicked the dominant leader to the same extent as the prestigious leader.

From these two studies, we conclude that the mimicry of prestige-based leaders is relatively unconditional, whereas the mimicry of dominance-based leaders is more strategic. Also, the mimicry paradigm offers a novel way of studying the implicit influence of leaders on followership, thus offering a great way of testing evolutionary hypotheses about leadership and followership.

Enforcing Social Norms

A fourth and final phase in the development of leadership in humans is its role in promoting cooperation and enforcing social norms. Teaching can channel social learning in ways that benefit individuals and groups but, if there is conflict of interests, then – as we have seen in chimpanzees – collaboration breaks down. An additional function of leadership in humans is to achieve not just coordination but also cooperation by solving the free rider problem. Specific individual leaders may be willing to bear the costs of punishment in return for access to status, resources or reproduction. Our research shows that high levels of cooperation can be achieved with just a single designated punisher (O'Gorman et al. 2009). This capacity is also seen in some non-human species where dominant individuals play a role in enforcing cooperation but they do this entirely to benefit themselves. Yet having a sense of shared intentionality allows leaders to enforce cooperative norms through coercion and punishment because it benefits the group rather than themselves. In support of this finding, a recent study showed that individuals who altruistically punished received greater status in their group and were more likely to be seen as leaders (Barclay 2006).

A Short (Speculative) Evolutionary History of Leadership

The previous information allows us to speculate on the evolutionary history of leadership in humans (King et al. 2009; Van Vugt and Ahuja 2010). As shown, human leaders not only initiate coordination but they also motivate, inspire, plan, organize, direct, monitor, punish, and maintain social cohesion. They may lead democratically and despotically, may lead from the front and from the back, and may lead small groups and groups involving millions of people. How did this all

come about? Although there are clearly aspects of leadership that we share with many other organisms, the expansion of the human brain and (not coincidentally) the size of human groups have led to a unique evolutionary history of leadership (Dunbar 1993). I suggest the following evolutionary transitions. First, leadership emerged in animal groups as a mechanism to solve simple coordination problems such as group movement. Second, leadership was enacted primarily by (socially) dominant individuals in species with dominance hierarchies, such as the non-human primates. Third, dominance was attenuated in egalitarian hunter-gatherer societies so that leadership could be enacted by prestigious individuals with a specific personality, knowledge or motivation to foster cooperation in group activities such as hunting, warfare and peacekeeping. Fourth, living in highly cooperative groups selected for the development of sophisticated cognitive mechanisms (e.g., theory of mind, shared intentionality, language) that increased the scale and scope of leadership dramatically. Fifth and finally, interactions in large, complex fission-fusion societies paved the way for the cultural evolution of the formalized (and sometimes hereditary) leadership structures with designated leaders and followers that we see in modern-day organizations such as nations, states and companies.

An Integrative Agenda on Leadership Research in Biology, Psychology, and Neuroscience

Let me conclude with a list of exciting research findings on leadership from evolution-inspired research programs, using a diverse range of methodologies from mathematical models to primate studies, and from archival data to social neuroscience experiments. Although not one of these findings tells a definitive story about the evolution of leadership and followership, together they all point to the possibility of specialized neurological and cognitive mechanisms in both humans and non-humans for solving coordination problems through leadership. These data thus support many different hypotheses from evolutionary leadership theory (Van Vugt and Ahuja 2010).

1. Mathematical models show that, in groups in which information is distributed among many individuals, democratic leadership works better than despotic leadership (Conradt and Roper 2005).
2. A social psychological experiment shows that individuals with high testosterone levels perform better on intellectual tasks when assigned to high-status (leadership) positions, whereas low testosterone individuals perform better on a cognitive tasks in a low-status position (Josephs et al. 2006).
3. An fMRI experiment shows that when a receiver gets an unfair offer from the allocator (leader) in an ultimatum game, it elicits brain activity in areas related to emotion (anterior insula), suggesting that emotions play a role in deciding whether to follow a leader (Sanfey 2007).

4. Archival data from chiefdoms, kingdoms and empires show that their leaders have greater reproductive success than ordinary individuals, suggesting selection for dominance (Betzig 1986).
5. Swarming experiments with humans show that, with just a few informed individuals, large groups can coordinate their activities efficiently (Dyer et al. 2009).
6. Experiments with capuchin monkeys show that they respond negatively to unfair outcome allocations from (human) experimenters, suggesting an early evolutionary origin of injustice aversion in interacting with leaders (Brosnan et al. 2009).
7. Observations from hunter-gatherer societies suggest that they have a host of different leveling mechanisms to keep leaders in check, varying from gossip and ridicule to exclusion and assassination (Boehm 1999).
8. Survey findings show that men in top management positions in Western societies have more sexual liaisons than men in lower-ranked functions in the organization (Perusse 1993).
9. When men and women watch someone who behaves unfairly in an ultimatum game being punished, there is activation in the reward regions of the brain, yet only for men, and this is accompanied by feelings of revenge (Singer et al. 2006).
10. Individuals with leadership roles in organizations have reduced levels of cortisol (the stress hormone), suggesting that high-status positions yield personal health benefits (Sherman et al. 2012).

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Using Awake A ... to Understand Neural Circui ... es Ranging from Mater...

Craig F. Ferris

Ab ... , in awake animals
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spects of breast feed-
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Imaging Awake Animals

Awake animal imaging is a relatively new and interesting methodological approach to understanding the neurobiology of emotions. How do we know an animal is content, hungry, afraid, angry, or hurt? While there have been many experimental approaches used to address these questions, the most informative to date have been the traditional experimental and ethological observations of animal behavior. We observe an animal's behavior under well-controlled laboratory conditions or in their

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