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What Modern Sports Competitions Can Tell Us About Human Nature

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Abstract
To fully understand human behavior, it seems inevitable to approach it from an evolutionary perspective. However, much of human behavior has been overwritten by culture and society, thus allowing little insight into how it might have evolved amid natural and sexual selection. Here, I argue that sports competitions, although a cultural phenomenon in themselves, strip away many of the cultural layers and reveal more primary, rudimentary aspects of human behavior. Fortunately, because they are ubiquitous, meticulously recorded, and often quantified in great detail, sports competitions provide a plethora of usable data. In this article I provide an evolutionary account of the cross-cultural existence and popularity of sports by reviewing evidence of four functional hypotheses that regard the omnipresence of sports as a by-product of fitness-related adaptations (skill acquisition and development, status seeking, courtship display, and coalition formation). Then I outline how the growing body of sports data and documentation can be exploited for increasing our understanding of human nature (e.g., on conflict and cooperation, lateral preferences, territoriality, and nonverbal communication). The article concludes by giving guidelines for future cross-disciplinary research to advance the understanding of how evolution has shaped human behavior.

Keywords
sport, evolution, competition, cooperation

The goal of numerous scientific disciplines is to understand human behavior. However, much of human behavior that is understood to date occurs in front of a computer screen in low-stress, artificial situations that involve pressing a button. Although this approach allows us to control all variables—which is an important factor in good scientific research—it is limited in understanding human behavior that evolved to be adaptive in our natural environment. In this article, I argue that competitive sports can be a promising research field for enhancing our understanding of human nature because they are incredibly popular across all nations and cultures. As a result of their popularity, sports provide a large amount of usable data, and several global companies have emerged in recent years that have specialized in collecting sports data.

In this article, I first provide an evolutionary account of the cross-cultural existence and popularity of sports by reviewing evidence suggesting that they can be considered a by-product of fitness-related adaptations (Deaner, Balish, & Lombardo, 2016; De Block & Dewitte, 2009; Lombardo, 2012). In the second part of the article, I show how the growing body of sports data and documentation can be exploited for increasing our understanding of human nature by using the tools of evolutionary psychology (Buss, 2005; Ketelaar & Ellis, 2000). More specifically, *evolutionary functional analysis* (Tooby & Cosmides, 1992) is introduced as a methodological approach for testing evolutionary hypotheses in sports that has led to important insights on the evolutionary origins of certain behavioral tendencies in humans.

Defining Sport

Although definitions of sport vary (e.g., Lombardo, 2012), it is often described to include all forms of competitive physical activity or games that, through casual

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or organized participation, aim to use, maintain, or improve physical ability and skills, providing enjoyment to participants and sometimes entertainment for spectators (Council of Europe, 2001). According to the International Olympic Committee, the only sports that can be included in the Olympic Games are those based on physical athleticism or physical dexterity. In line with the inclusion criteria of the Olympic Committee (see also Deaner et al., 2016 for a similar argument), I exclude noncompetitive physical activities (i.e., exercise) and strategic games that mainly depend on chance (e.g., board games) and decision making (e.g., chess) for the purpose of this article.

An Evolutionary Perspective on Human Behavior in Sports

William James (1892), one of the founding fathers of the field of scientific psychology, already urged scientists in this newly emerging field of investigation to adopt principles of the established natural sciences by identifying a set of guiding theoretical assumptions. This proposal was followed up half a century later by Kurt Lewin (1935, 1951), who stated that psychological researchers should start by setting up an axiom system from which to derive theorems and correlates and subsequently subject these to experimental tests. The emerging subfield of evolutionary psychology within psychology can be considered a response to the proposals of James and Lewin by adopting evolutionary theory as a grand metatheory for setting up an overarching axiom system that allows the derivation of empirical hypotheses and integrating existing findings across different domains (Buss, 2005; Ketelaar & Ellis, 2000). In line with the observation that scientists widely disagree about what constitutes a theory (Gigerenzer, 1998), it is important to note that evolutionary psychology should not be regarded as a theory or a model but is better described as a set of metatheoretical assumptions that give guidance to scientists on how to approach conceptual and empirical research on psychological phenomena (Buss, 2005; Ketelaar & Ellis, 2000).

The typical approach of evolutionary psychology begins with identifying specific categories of fitness-relevant behavior (e.g., coalition formation) and how this can be regarded as an adaptive solution for solving a fitness-relevant problem (e.g., avoiding social exclusion and thereby facilitating self-protection and resource acquisition). In this respect, evolutionary approaches always begin with the tacit assumption that observable behavior ultimately serves some function (i.e., is adaptive). Evolutionary theory assumes that the ultimate function of behavior is reproduction (the passing on of genes to the next generation). However, reproductive fitness is not equivalent to a (conscious or unconscious) psychological goal state. From an evolutionary perspective, behavior can be considered adaptive if a set of behaviors (and the mechanisms that produce them) increased reproductive fitness in the past—in a proximal or distal manner. How exactly an animal behaves depends on the design of its brain and body, as these attributes determine how information about the environment and its own states is processed. In this respect, evolutionary psychologists distinguish between proximate and distal causation of behavior. Proximate mechanisms refer to cognitive and motivational states that the brain entertains in a given situation, whereas distal mechanisms refer to stable traits of a species (e.g., a vegetarian diet). Behaviors that are adaptive in evolutionary terms (i.e., increase reproductive fitness) are usually driven by more proximate goals, motives, or needs (Neuberg, Kenrick, & Schaller, 2010). Further, it is important to note that observable behavior is not always directly related to reproductive fitness, as evolutionary adaptations are not perfect. Although it is convenient to speak of the natural selection of behaviors, this statement is misleading because natural selection can select only for the mechanisms producing behavior (Tooby & Cosmides, 1992).

There is considerable overlap in the literature on the recurring problems and opportunities early humans were assumed to face (e.g., Bugental, 2000; Kenrick, Li, & Butner, 2003; Neuberg et al., 2010). Similar to most other animals, humans have to solve problems of self-protection from predators and human rivals, the avoidance of diseases, mate attraction and retention, and the rearing of offspring. In addition, like other social animals, humans have to solve problems related to group life: coalition formation, cooperation, the exchange of resources, competition, status seeking, and navigating hierarchies. All of these broad classes of problems can be further divided into hierarchical subproblems (for more detail, see Neuberg et al., 2010). For the purpose of this article I mainly focus on social adaptations of humans because reproductive fitness was substantially enhanced by group life (e.g., Baumeister & Leary, 1995; M. B. Brewer & Caporael, 2006; Campbell, 1982; Leakey & Lewin, 1977).

On the (Cultural) Evolution of Sports

The universality of sports, particularly for men and boys (Deaner et al., 2016), across different cultures might indicate that sports have evolutionary origins (Brown, 1991; Sharp, Coatsworth, Darling, Cumsille, & Ranieri, 2007; Stubbe, Boomsma, & de Geus, 2005). Despite its immense popularity and cross-cultural occurrence, sports most likely do not qualify as an innate capacity

of humans; instead, sports have been proposed to be one of the cultural activities invented for their adaptive utility (De Block & Dewitte, 2009; Lombardo, 2012). Humans inherit behavior through two routes: genes and culture (dual inheritance theory; Boyd & Richerson, 1985; Richerson & Boyd, 2005). Dual inheritance theory is best described as a culture-gene coevolutionary model that rests on the premise that human behavior is shaped by a dynamic interaction between culture and genes. From this it follows that genes affect cultural evolution by influencing psychological predispositions for learning, whereas culture creates ecological situations in which genes are selected for their adaptive utility in the cultural environment. In this regard the nature versus nurture debate has been criticized for assuming an oversimplified dichotomy in explaining the cross-cultural occurrence of sports (Sands & Sands, 2010).

Given the multidisciplinary nature of sports, it is probable that a variety of theoretical perspectives will help to explain the cross-cultural existence of sports. For the purpose of this article I will focus on four functional hypotheses (for more detail, see Deaner et al., 2016) that attempt to explain why humans have evolved dispositions to participate in and watch sports and how this interest in sports might have supported an increasing reproductive fitness (however distal this relationship might have been). Note that these functional hypotheses do not suggest that an interest in sports should be considered an adaptation per se (i.e., that it solves a specific fitness-related problem); instead, they assume that sports should be considered a by-product of other adaptations, including motivational drives and capacities to develop adaptive skills, to compete for status and mates, and to monitor the abilities of others to form beneficial coalitions (Deaner et al., 2016; De Block & Dewitte, 2009; Lombardo, 2012). These functional hypotheses can be considered complementary to one another and are not mutually exclusive.

Skill acquisition and development

From an evolutionary perspective, sports probably originated as a cultural activity invented to develop and practice war- and hunting-relevant skills such as throwing (Deaner et al., 2016; Winegard & Deaner, 2010). Therefore, it seems feasible that humans might have evolved an adaptive urge to engage in sports when they do not feel the pressure to strive to fulfill basic human needs such as foraging and hunting. The tendency of humans, and especially children, to play and engage in sports might be considered an adaptive strategy for developing stable, fitness-related skills. In this regard it has been suggested that humans might have evolved a motivational drive to play and engage in sports similar to the urge of a bird to head south when the temperature begins to drop or a hamster to run in a wheel when kept in a cage (Sands & Sands, 2010).

Today, top-level sports can be considered a showcase scenario for demonstrating the immense skills and degree of specialization humans can achieve with experience and practice. Watching top-level athletes such as Simone Biles, Lindsey Vonn, LeBron James, Rodger Federer, Kelly Slater, or Lionel Messi perform seemingly impossible maneuvers and skills in their respective sports is awe-inspiring. However, participating in sports is beneficial not only in acquiring domain-specific skills (Starkes & Ericsson, 2003) but also in acquiring and developing general skills that are important in other areas of life (e.g., following rules; Eccles, Barber, Stone, & Hunt, 2003; Videon, 2002). Evolutionary theory has suggested that the prolonged developmental and nurturing phase of humans compared with other species has substantially contributed to the success of the human species because this phase, for example, allowed for acquiring extremely high levels of skills and specialization (e.g., in the area of tool use; see Sterelny, 2012 for a review). This prolonged nurturing and developmental phase enabled humans to specialize in certain tasks and acquire incredible levels of expertise that were useful in exploiting the environment to facilitate survival and reproductive success.

Although the skills discussed in sports mostly relate to warfare and (social) hunting (Chick, Loy, & Miracle, 1997), sports have further been suggested to help the development of a broad range of physical and social skills (Chick, 2010). That sports are well suited for developing skills that were useful for warfare and hunting has high face validity (Lombardo, 2012), but sports have also been associated with the development of a moral code and collaborative skills (Ewing & Seefeldt, 1996). Several lines of research provide evidence for the skill acquisition and development hypothesis. First, it has been suggested that children's natural tendency to play is a precursor to sports (Pellegrini, Blatchford, Kato, & Baines, 2004), and play behavior has been shown to enhance both social and motor competencies (Graham & Burghardt, 2010). Play behavior has fascinated researchers for centuries, but it remains controversial, and there is considerable disagreement about the functions of play (Sands & Sands, 2010). Because play is not identical to the definition of sport used for the purpose of this article, this controversy is beyond the scope of this review. However, play and sports are assumed to show considerable overlap, and engagement in these activities might have facilitated learning adaptive skills.

A common distinction in the skill acquisition literature assumes two main categories of learning processes:

explicit learning and implicit learning (Masters & Maxwell, 2004). Explicit learning is typically defined as rule-based learning that depends on working memory to consciously encode declarative knowledge, whereas implicit learning is commonly described as a more automatic (procedural) learning process in which perceived patterns are encoded mostly nonconsciously. It has been suggested that skills learned implicitly may be more resilient under duress because the phylogenetically older implicit learning system may be less prone to error than the phylogenetically younger explicit learning system (Reber, 1992). "We have inherited motor processes from our pre-declarative ancestors that have potential to be both resilient to fatigue and to the passage of time" (Poolton, Masters, & Maxwell, 2007, p. 466). Playing sports has been shown to be an excellent context for implicit learning (e.g., Memmert et al., 2015).

In line with the definition of innateness as "organized in advance of experience" (Marcus, 2004), it is plausible that humans are innately predisposed to enjoy engaging in play and in sports because this has proven a beneficial context for skill acquisition and development. Because the most popular sports mostly depend on war- and hunting-relevant skills such as running, tackling, throwing, kicking, and dodging opponents and projectiles (Winegard & Deaner, 2010), it seems likely that sports originally served as arenas for practicing and developing these skills. However, sports remained incredible popular in modern cultures in which hunting and combat were not as central to human reproductive fitness. Therefore, it is unlikely that the skill acquisition and development hypothesis is sufficient for explaining the cross-cultural existence of sports.

Status seeking

From a Darwinian perspective (De Block & Dewitte, 2009), sports may be seen as one of the cultural activities invented to promote the acquisition of status: "And acquiring status is—on average, in the long run, and in the ancestral environment to which our species is adapted—beneficial to an individual's reproductive success" (p. 4). Boxing legend Muhammad Ali is often quoted as stating that he hated every minute of training but motivated himself by telling himself, "Don't quit. Suffer now and live the rest of your life as a champion." This quote serves to highlight a central motivational drive of humans that helps athletes overcome the strenuous sacrifices involved in competitive sports: the drive for acquiring status and prestige. Acquiring and communicating status can be considered a fundamental human motive (Anderson, Hildreth, & Howland, 2015) that is assumed to have evolved as an adaptive cognitive strategy that helps organize group life by establishing and maintaining status hierarchies (Sidanius & Pratto, 1999). Following the outlined theoretical approach of first identifying a fitness-relevant behavior (i.e., status seeking) and subsequently outlining how this can be considered an adaptive solution to solve a fitness-relevant problem (i.e., avoiding social exclusion and facilitating resource acquisition) in enhancing the ultimate evolutionary goal of reproductive success, I now outline evidence showing how the sports context serves the adaptive function of communicating status.

Because unrestrained physical fights, combat, and warfare pose the risk of physical harm and death to competitors, sports have been suggested to be a culturally invented arena for publicly displaying desirable qualities such as strength, endurance, bravery, and fighting ability (Deaner et al., 2012; Faurie, Pontier, & Raymond, 2004; Lombardo, 2012). In this respect, athletes (especially boys and men) can display their qualities and gain in status by competing in sports without having to fear fatal consequences. In support of this hypothesis, studies in modern societies have shown that sporting success is linked to the attainment of status by children (Chase & Dummer, 1992; Chase & Machida, 2011), adolescents (Holland & Andre, 1994; Thirer & Wright, 1985), and adults (Földesi, 2004; Sohi & Yusuff, 1987). Similar findings have been reported in historical societies (Golden, 2008). For example, in ancient Greece an *Olympionike*, or champion in the Olympic Games, enjoyed the highest possible social status and was even entitled to dining at state expense (Potter, 2012).

Further support for the status-seeking hypothesis can be found in a recent line of investigation showing that athletes display nonverbal signals that are associated with social status during and after sports competitions. Olympic athletes have been shown to display unique behaviors after winning that communicate supremacy (Matsumoto & Hwang, 2012). The fact that congenitally blind athletes showed similar victorious expressions that could not have been learned through cultural transmission suggests an innate basis of communicating status after successful physical performance (Tracy & Matsumoto, 2008). A related line of investigation in sports has shown that the nonverbal behaviors of athletes occurring during competition can be reliably interpreted as cues as to who is currently leading and who is trailing (Furley & Schweizer, 2014a). Observers of sports competitions also rated leading athletes as more dominant, more proud, and more confident than trailing athletes without being aware of the score (Furley & Schweizer, 2016a). Dominance, pride, and confidence have been linked to high social status and support the idea of sports as a culturally invented indicator of social

status. In further support, a recent study using event-related brain potentials (Furley, Schnuerch, & Gibbons, 2016) showed enhanced attentional orienting toward leading compared with trailing athletes, indicating that subtle signs of athletic supremacy are reliably differentiated in the human brain. This finding indicates that humans have evolved a neural receptivity toward signals associated with high status and superiority.

Because the desire for status can be considered a fundamental human motive, our perceptual-cognitive system seems to have become particularly attuned to status cues (see Anderson et al., 2015; Schmid Mast & Hall, 2004). This reasoning is supported by empirical research showing that observers can distinguish between leading and trailing athletes under very challenging conditions (Furley & Schweizer, 2016a), and even young children (Furley & Schweizer, 2014a) and children with autism spectrum disorder (Ryan, Furley, & Mulhall, 2016) were able to do this when watching short video clips of athletes during competition. Efficient perception of status displays probably serves adaptive functions at the level of individual goal attainment (McArthur & Baron, 1983; Zebrowitz & Collins, 1997): for example, who should be avoided in a confrontational situation, who would be a good ally or mate, or whom one should attend to for behavioral guidance and imitation. In this respect, the prestige bias predicts that humans have the tendency to attend and copy the behaviors of the most successful individuals, as this appears to be an adaptive mechanism (De Block & Dewitte, 2009). In line with this proposal, children and adolescents frequently choose the most successful athletes as their heroes and role models (Lockwood & Kunda, 1997), and boys increase status displays at puberty, which is also when successful sports performance results in greater popularity with girls (Weisfeld, 1994). This brings us to the next functional hypothesis for the cross-cultural occurrence of sports: sports as a culturally invented context for courtship display. Although this hypothesis shows considerable overlap with the status-seeking hypothesis, there are some important differences involving the gender of sports participants and spectators (Deaner et al., 2016).

Courtship display

Darwin (1871/1981) pointed out that the evolutionary goal of reproductive success explained the fancy ornaments and costly armaments found both in the animal kingdom and in human culture. In this regard, it has been suggested (De Block & Dewitte, 2009; Lombardo, 2012) that sports may be seen as one of the cultural phenomena invented to communicate mate quality. There are remarkable similarities between human game play and animal courtship rituals (Huizinga, 1955) in that both are competitive and ornamental (do not have direct utility or usefulness; Caillois, 1961). "Each sport could be viewed as a system for amplifying minor differences in physical fitness into easily perceivable status differences, to make sexual choice easier and more accurate. In this sense, sports are culturally invented indicators of physical fitness" (Miller, 1999, p. 253).

Thus, modern sports competitions may be interpreted as a stage for displaying fitness-related attributes and in turn providing access to desirable mates. If performance in competitive sports can signal phenotypic quality and heritable fitness to potential partners, then one would expect to find evidence for this in today's life of modern sports contests. Several lines of research provide support for this "courtship-display hypothesis."

An integral part of sports competitions is that they can differentiate between the abilities and skills of the competitors. Research has demonstrated that many athletic abilities are heritable (Tucker & Collins, 2012) and correlated with "good gene traits" such as fluctuating asymmetry (Longman, Stock, & Wells, 2011), second-to-fourth-digit ratio (Hönekopp & Schuster, 2010), and facial attractiveness (e.g., Postma, 2014; K. M. Williams, Park, & Wieling, 2010). Therefore, it may come as no surprise that athletes indeed have more sexual partners than nonathletes (Faurie et al., 2004; Llaurens, Raymond, & Faurie, 2009). The fact that student athletes have more sexual partners fits the evolutionary theorizing of sports but might alternatively reflect differences in sexual motivation or personality between the two groups. However, athletes are also rated as sexually more attractive (Miller, Sabo, Farrell, Barnes, & Melnick, 1998; Schulte-Hostedde, Eys, & Johnson, 2008). In addition, experiments show that women desire a man more if he is described as an athlete (G. Brewer & Howarth, 2012; Schulte-Hostedde et al., 2008).

Further, important gender differences in sports participation, motivation to engage in sports, and interest in sports have been proposed in regard to the courtship ritual hypothesis that differentiates this hypothesis from the status-seeking hypothesis. In this respect, it is important to note that "there has never been a time, from the dawn of our civilization to the present, when women have been as involved in sports, as participants or spectators, as men have" (Guttman, 1991, p. 1). This statement is supported by a growing body of studies in large contemporary societies suggesting a consistent, possibly universal, sex difference in sports participation (Deaner & Smith, 2013). Of further relevance, men were almost four times as likely to list a competitive sport rather than a noncompetitive activity as their most common physical activity, and this sex difference was

statistically significant across all 37 countries analyzed (Apostolou, 2014a; see also Apostolou, 2014b).

Similar evidence exists for sex differences in sports spectatorship (Deaner et al., 2016). In general, research suggests that females have less interest in sports and not merely fewer opportunities for engagement. In addition, the motivation for sports engagement seems to differ between men and women in terms of competitiveness and risk-taking. Moreover, Deaner et al. (2016) suggest that the status argumentation outlined above applies mainly to male athletes, whereas the courtship argumentation is better suited to explain females' interest in watching male sports. Considering that differential reproduction is at the heart of natural selection, it seems feasible that traits associated with sporting success constitute honest signals of mate quality. This reasoning is supported by the finding that females show a preference for athletic physique (Dixon, Halliwell, East, Wignarajah, & Anderson, 2003; Li & Kenrick, 2006). Further support for this reasoning stems from evidence showing that females rated men that played competitive sports in an aggressive manner as the most desirable partners for both short-term and long-term relationships (compared with not playing sports, playing sports on a casual basis, and playing sports competitively in a nonaggressive manner; G. Brewer & Howarth, 2012). On a related note, research has demonstrated that when women were asked about regrets in their lives, they indicated that they wished they had tried harder to avoid getting involved in poor mate choices, whereas men wished that they had slept with more partners (Roese et al., 2006). In this respect, watching male sports contests might represent a means for women to achieve their desired goal of avoiding poor mate choices.

Coalition formation

Billions of people watch sports on television or at the large arenas and stadiums especially built for these events. People even seem to be prepared to sacrifice large amounts of their free time and money in monitoring and supporting sports teams, which seems paradoxical from a rational economic perspective because they do not realize any material benefit from their investment (Winegard & Deaner, 2010). However, recent research is starting to shed light on this phenomenon by suggesting that sports fandom is a by-product of evolved coalitional tendencies in humans. In line with the evolutionary framework, being a fan of a sports team probably reflects an adaptive solution to the fitness-relevant problem of avoiding social exclusion by binding individuals into groups and thereby facilitating resource acquisition. In support of this hypothesis, research demonstrates various benefits of being a fan of a sports team such as heightened feelings of connectedness, increased popularity, and elevated self-esteem, particularly when the supported team is successful (Branscombe & Wann, 1991; Cialdini et al., 1976; Wann, 2006). Further research shows that sports fandom binds individuals of the team and ally fans together (Wann & Dolan, 1994; Wann et al., 2006). These empirical findings support the claim that instances of modern group behavior such as sports fandom can be understood as an adaptive solution to the fitness-related problem of intergroup rivalries and warfare (Johnson & van Vugt, 2009; McDonald, Navarrete, & Van Vugt, 2012; van Vugt, De Cremer, & Janssen, 2007; Winegard & Deaner, 2010) because warfare has been a recurring challenge in human evolutionary history (Gat, 2006).

There is some overlap between the status-seeking argument and coalition formation hypothesis of sports, and these two lines of reasoning can be considered complementary (Lombardo, 2012) because the success of a certain team (Cialdini et al., 1976; Wann, 1996) or players (Melnick & Wann, 2011) influences the likelihood of becoming a fan of that team or player. All else being equal, people will probably prefer to ally with successful teams or players (e.g., forming a coalition with a champion archer), which can be considered an adaptive strategy (Deaner et al., 2016). This might partially explain why the most popular sports mostly depend on war-relevant skills (Winegard & Deaner, 2010).

Despite this overlap between the status-seeking and coalitional hypotheses, these hypotheses might also be seen as conflicting because of the competitive gist of the status-seeking (and courtship) hypotheses and the cooperative gist of the coalitional hypothesis. These seemingly contradictory hypotheses might be reconciled by the aphorism that "we are 90 percent chimp and 10 percent bee" (Haidt, 2012, p. 217), which suggests that human nature was produced by selection pressures working at two levels: the level of the individual and the level of the group. Although most evolutionary theorists have argued against group selection, recent work has produced compelling arguments for some occasions when groups, instead of individuals, can be the vehicle of selection (Nowak, Tarnita, & Wilson, 2010; Wilson & Sober, 1994). According to multilevel selection theory (Wilson & Wilson, 2008), the selective pressures of evolution operate cohesively to maximize fitness at different levels: The lowest level is the genes, then the cells, then the organism level, and finally the group level. For the purpose of this article, it is important to point out that individuals compete first and foremost with individuals within groups

(individuals as a vehicle of selection). Hence, modern humans are the descendants of primates that excelled at this competition, resulting in the selfish, competitive side of human nature that has been outlined under the sections "Status Seeking" and "Courtship Display." However, at the same time, groups competed with other groups, and this competition favored team players. Arguably, the most cohesive groups were more likely to beat groups of selfish individualists. Most of human nature was probably shaped by natural selection operating at the level of the individual, but not all, as we seem to have a few group-related adaptations too, as can be seen, for example, when our self merges into a large crowd of cheering sports fans in a stadium (Haidt, 2012; Nowak et al., 2010; Wilson & Wilson, 2008).

Evolutionary Research in the Context of Sports

Although a growing body of evolutionary-based empirical research supports the functional hypotheses of skill acquisition, status seeking, courtship display, and coalition formation, the predictions of these broad hypotheses should be sharpened in future investigation by precisely specifying their boundary conditions and subjecting these conditions to empirical tests (Ketellar & Ellis, 2000). In this respect, future research should continue to work toward the overarching goal of providing high-resolution models of the evolved mechanisms that shape human nature (Tooby & Cosmides, 2005). Fortunately, the widespread documentation and quantification of diverse sports competitions enables researchers to use these large databases to test precise predictions and further separate and integrate the functional hypotheses, as exemplified by the research of Deaner et al. (2012; see also Deaner, 2013), who have demonstrated robust gender differences in competitiveness and status seeking that have led to separating the courtship hypothesis from the status-seeking hypothesis.

The next part of the article moves on from providing an evolutionary account of the cross-cultural existence of sports to demonstrating how the context of sports can be instrumentally used to answer further questions on human nature. Because much of human behavior has been overwritten by culture and society, sports competitions strip away many of the cultural layers and therefore have the potential to reveal more rudimentary aspects of human behavior. Further, I am not aware of any other field of human behavior that is as quantified and documented as sports are: "Sport measures outcome with a finality of judgment that scientific papers would not pass" (Walsh, 2014, p. 860). I initially outline a methodological guideline of how sports data and documentation can be used to test evolutionary hypotheses. I then illustrate two detailed examples of how this approach has been successfully implemented in sports. I conclude by reviewing insights that have arisen so far.

How can sports data be used to advance understanding of human nature?

The step-by-step method that has been proposed to test evolutionary hypotheses about human behavior has been termed evolutionary functional analysis (Tooby & Cosmides, 1992). This approach always starts with the following basic if-then reasoning: If humans were confronted with such-and-such adaptive problem in their *environment of evolutionary adaptedness* (EEA), then modern humans should have evolved such-and-such proximate behavioral control mechanism. The EEA has been defined as the "composite of environmental properties of the most recent segment of a species' evolution that encompasses the period during which its modern collection of adaptations assumed their present form" (Tooby & Cosmides, 1990, p. 388). For the EEA of the human species the composite of environmental circumstances is typically reconstructed from assumptions about human hunter-gatherer life during the Pleistocene era. If evidence for a proximate mechanism is found in an experiment among modern humans, then scientists conclude that this must be an adaptation. Hence, the first step involves precisely specifying the adaptive problem human ancestors were confronted with. In the second step the psychological mechanisms have to be described that evolved to solve the identified adaptive problem. Because these proposed psychological mechanisms usually cannot be observed directly, the third step requires rigorous observation and experimentation on human behavior to identify physiological or behavioral variables, or both, associated with the proposed psychological mechanism.

Evolutionary functional analysis can be described as reverse engineering because it attempts to reconstruct the mind's design on the basis of contemporary data and assumptions of the problems the mind must have solved during the EEA. This kind of reverse engineering is a highly challenging endeavor and faces problems at all three steps of the method (Buller, 2006). Perhaps the biggest challenge of evolutionary functional analyses is the fact that it is very difficult to observe and collect behavioral data that allow inferences about an evolved psychological mechanism because cultural constraints and learning can potentially "disguise" behavioral outcomes of an evolved psychological mechanism. In this respect, modern sports competitions have been

argued to reveal more rudimentary forms of human behavior (Lombardo, 2012) and, importantly, offer abundant data that can be either (a) extracted from televised recordings or (b) documented and published as a consequence of the increasing quantification and popularity of sports data (e.g., Rein & Memmert, 2016).

Two studies on conflict, cooperation, and touching behavior in sports have been selected to highlight the utility of evolutionary functional analysis on sports data, as both conflict and cooperation are assumed to be important adaptive problems and opportunities human ancestors faced. Therefore, humans should have evolved psychological mechanisms that regulate behaviors associated with conflict and cooperation. However, modern cultural conventions arguably complicate the observation and experimentation on representative instances of conflict and cooperation in humans today.

Conflict, cooperation, and touch in sports

Regarding the first step of evolutionary functional analysis, human ancestors were assumed to face the adaptive problem of intragroup competition (i.e., competing with members of the same sex for mates and resources; e.g., Buller, 2006; Neuberg et al., 2010). However, and somewhat conflicting, the *male warrior hypothesis* proposes that male humans also faced the adaptive problem of being maximally effective in intragroup cooperation because success in intergroup contests has been vital in human evolution (Benenson & Wrangham, 2016). Stated differently, men need to bond with other men to go to war together (Koski, 2016). Further, a precondition of functioning social life is that conflicts (if unavoidable) must be resolved and the damage mitigated in groups living together. Note that this should be more pronounced among men compared with women (Benenson & Wrangham, 2016). Regarding the second step, male humans should have evolved a psychological mechanism that regulates intragroup competition and cooperation. Hence, when a conflict occurs among humans, males should show behavioral evidence of a psychological mechanism that attempts to reconcile the future relationship with the competitor soon after the conflict is over. Following the third step of evolutionary functional analysis, high-level sports matches were sampled (see supplementary material in Benenson and Wrangham (2016) on avoiding sampling bias) as a "proxy for intragroup conflict, because they occur within a large organization and constitute seminaturalistic, standardized, aggressive, and intense confrontations" (p. 2208). The authors subsequently extracted fine-scaled postconflict affiliation variables via a standardized coding procedure from the recorded sports (tennis, table tennis, badminton, and boxing) matches. Results confirmed the hypothesis across three types of racket sports and boxing and showed a consistent pattern of longer-duration postmatch affiliation (e.g., shaking hands) in men compared with women. Of further interest, men also touched each other more often than women using additional friendly behavior (e.g., pats on the shoulder).

Together with previous studies (de Waal, 2000; Tabak, McCullough, Luna, Bono, & Berry, 2012), these results provide converging evidence that males seem to be equipped with a psychological mechanism that predisposes them to be more willing than females to repair their relationship after a conflict via friendly behavior toward the opponent. The study is well suited to illustrate how important variables can be extracted from readily available video recordings of sports contests to shed light on psychological mechanisms regulating conflict, cooperation, and touching behavior, "as sports contests involve emotionally and physically demanding confrontational investment from the contestants, yet are standardized so that many confounding factors can be excluded and different nationalities can be included" (Koski, 2016, p. 761).

A related study on cooperation, touch, and performance in basketball (Kraus, Huang, & Keltner, 2010) further illustrates the utility of evolutionary functional analysis on a combination of sports data extracted from video recordings and performance data provided online by the National Basketball Association (NBA). Similar to the intragroup cooperation reasoning in the Benenson and Wrangham (2016) study, Kraus et al. (2010) tested whether the proposed effect of physical touch can indeed be considered a behavioral indicator of an evolved psychological mechanism that solves the adaptive problem of increasing intragroup cooperation. By coding tactile communication and cooperation in video recordings of all 30 NBA teams and correlating these variables with performance indicators available from statistical websites of the 2008–2009 NBA season, the study provides evidence that touch behavior was associated with better basketball performance, even after controlling for several confounding variables. The effect of higher levels of touch on enhanced team performance was mediated by increased cooperative behavior between teammates. Hence, these findings provide additional support for the hypothesis that touch can be considered adaptive behavior among humans that most likely evolved as a solution to the adaptive problem of facilitating intragroup cooperation, as success in intergroup conflicts has been vital in human evolution (Benenson & Wrangham, 2016; Koski, 2016).

These two studies highlight how evolutionary functional analysis can serve to formulate hypotheses that can be tested in the context of sports (see also Balish, Eys, & Schulte-Hostedde, 2013). In the next sections, I review further evolutionary research that has adopted this approach to advance evolutionary understanding of the occurrence of lateral preferences in humans on territoriality and the home game advantage and on nonverbal communication.

Laterality

Humans have lateral preferences because we predominantly use either side of the body to carry out specific tasks. Although human handedness can be considered the most prominent example in which such lateral preference can be observed (McManus, 2002), the preferred stance orientation, for example, when fighting in a confrontational situation, is another instance of lateral preference (Loffing & Hagemann, 2015; Raymond, Pontier, Dufour, & Møller, 1996). Left-handedness (approximately 10%–13% in humans) has not changed in prevalence since the Neolithic (Raymond et al., 1996), even though it seems associated with reduced fitness in some areas: for example, lighter body weight, shorter height, and lower life expectancy (for a review, see Coren, 1992; but see Benbow, 1986 on potential fitness benefits of left-handedness). The persistence of left-handers today seems to imply fitness-related advantages in other areas of life. Note that selection pressures were not only driven by the physical environment of humans but also by the social environment (Buller, 2006). In this respect the *fighting hypothesis* was proposed. This hypothesis suggests that left-oriented athletes are underrepresented in the overall population, and therefore it is less common to be confronted with this orientation in a fight (Ghirlanda, Frasnelli, & Vallortigara, 2009; Ghirlanda & Vallortigara, 2004). Hence, an opponent will have less experience in this situation and will be less able to anticipate punches and defend himself. Accordingly, *frequency-dependent selection* (i.e., evolution favors a particular ratio of certain traits within a species instead of a trait being an adaptation per se) will give relatively rarer left-handers a competitive advantage in confrontational contests; accordingly, it has been suggested as an evolutionary mechanism ensuring the stable maintenance of lateral preference polymorphism in humans (Loffing, 2017; Raymond et al., 1996).

An overrepresentation of left-handers in interactive sports (Loffing, Sölter, & Hagemann, 2014) and specifically in boxing (Loffing & Hagemann, 2015; Raymond et al., 1996) supports this hypothesis, although evidence for this hypothesis is mixed (Baker & Schorer, 2013; Loffing & Hagemann, 2015). The ambiguity in findings regarding the fighting hypothesis across interactive sports might be reconciled by including time pressure (i.e., the amount of time athletes have to respond to an opponent's action) of the sports context as a moderating variable, as the prevalence of left-handers was higher in a large-scale analysis in sports that was characterized by high time pressure (e.g., table tennis) compared with sports in which the time pressure was not as high (e.g., tennis; Loffing, 2017). Because humans in close-range fights are under particular time pressure, and success in hand-to-hand fighting has been important in human evolution (e.g., Lombardo, 2012), the outcome of these fights might have contributed to the maintenance of left-handedness in humans.

Territoriality and home game advantage

Athletes and sports teams playing at home are, on average, more successful than teams playing away. This home advantage is backed up by a large body of research (see Allen & Jones, 2014 for a recent review). Although the home advantage is not unequivocal (see Baumeister & Steinhilber, 1984; Wallace, Baumeister, & Vohs, 2005 on potential disadvantages of playing at home) and is more prevalent in some analyses compared with others (Jones, 2013), "there are no sports in which athletes or teams are more successful away from their home venue" (Allen & Jones, 2014, p. 48).

The "classical model" of the home advantage assumes four main factors that contribute to the advantage: the support of the home audience, travel fatigue of the away team, familiarity with the home venue, and rules or referee decisions that might favor the home team (Allen & Jones, 2014). Although the classical model has not incorporated evolutionary theory in explaining how these four factors might lead to performance advantages, recently an evolutionary-based territoriality model of the home advantage has been proposed that assumes (part of) the home advantage to be a manifestation of a natural protective physiological and behavioral responses to protect one's territory (Neave & Wolfson, 2003).

Given the limited resources and space on earth, most animals show a natural protective response to territorial incursion that can be considered an evolved response tendency intended to secure one's perceived territory (Sobolewski, Brown, & Mitani, 2012). Although it is "virtually undisputed that humans exhibit territoriality, at the national, family home, or temporary (my-seat-in-the-bus) level . . . the question remains how meaningful the similarities are to animal territoriality" (Edney, 1974, p. 961). Even though human territoriality is considered

an important topic, "no particular paradigm characterizes this topic, and as yet there is no standard set of principles that can be reliably applied to problems in the area" (Edney, 1974, p. 959). Surprisingly, this has hardly changed over 40 years later. In this regard, Neave and Wolfson (2003; see also Carré, Muir, Belanger, & Putnam, 2006) have shown that the field of competitive sports seems a fruitful paradigm for investigating human territoriality because humans sometimes show a similar territorial response to animals and that this can be observed in the context of competitive sports. In partial support of this theorizing, they found that testosterone concentrations were considerably higher before home games compared with away games and neutral training sessions in a sample of association football (soccer) players. Allen and Jones (2014) assume that this territoriality response (including higher levels of testosterone) contributes to the home advantage by increasing risk-taking behavior, improving metabolic rates of muscles, and enhancing spatial ability (Jones, Bray, & Olivier, 2005).

A recent study (Furley, Schweizer, & Memmert, 2018) points to a further mechanism as to how the territoriality response might contribute to the home advantage by providing evidence that elite and amateur soccer players change their nonverbal behavior before the game depending on game location and that these changes can be reliably recognized by observers. Observers on average rated soccer players higher on assertiveness, dominance, and aggression when playing at home compared with playing away. This effect was even more pronounced in amateur soccer players not playing in front of a large supportive audience. The behavioral dimensions of assertiveness, dominance, and aggression have all been linked to territoriality in the past (see Mazur, 2005 for a review). Signaling territoriality of home-playing athletes might contribute to the home advantage. For example, home-playing athletes may enter the playing field more erect and perform their warm-up routines more assertively and dominantly and thereby intimidate their opponents. In initial support of this idea, previous research has demonstrated that certain preperformance nonverbal displays affect prospective confidence levels and outcome expectations of athletes (e.g., Furley & Dicks, 2012; Furley, Dicks, & Memmert, 2012) and that this has the potential to affect subsequent behavior and performance (Furley, Dicks, Stendtke, & Memmert, 2012).

I acknowledge that the territoriality hypothesis in explaining the home advantage has not received sufficient empirical support and is speculative at present. I hope that this overview of initial studies on territoriality in sports stimulates future empirical investigation into this topic and that the outlined evolutionary functional approach provides a useful framework for conducting this research. In this respect, new technological developments that track physiological and behavioral data during competition are likely to provide new insights on territoriality in sports.

Nonverbal communication

Sports commentators frequently refer to the body language of athletes and their nonverbal communication (Furley & Schweizer, 2014a). Despite the fact that nonverbal communication is often described colloquially as "body language," it can generally be defined as any communicative act not expressed in words (Watzlawick, Beavin, & Jackson, 1967). Evolutionary theory has argued that the organization in groups brings adaptive benefits to animals but requires efficient communication among the individual group members. Therefore, humans have evolved the capacity to automatically display nonverbal behavior expressive of certain internal states (e.g., emotions or behavioral intentions) and to automatically interpret and adequately respond to these states (Matsumoto, Frank, & Hwang, 2013 for a review). This theorizing has been tested in the context of sports and has provided evidence that athletes, coaches, and officials are constantly sending out nonverbal signals depending on their internal states and on the current situation that are accurately interpreted by observers. For example, observers of sports competitions can reliably assess who is leading or trailing without being aware of the current score (Furley & Schweizer, 2014a, 2014b, 2016a). Researchers have attributed this finding to the evolutionary past of primates by arguing that, among primates, sending submissive or shameful signals when losing an antagonistic encounter increased the chances of avoiding further potentially life-threatening attacks (de Waal, 2007). Likewise, sending dominant or proud signals helps primates save valuable resources by communicating superiority over an opponent (Archer, 2006).

A further study providing evidence that internal states (e.g., emotions) can "leak" through via nonverbal expressions, even if people are trying to mask their true feelings, comes from soccer refereeing (Furley & Schweizer, 2016b). In a multiexperimental study, the nonverbal behavior of professional referees was rated as significantly less confident by observers when communicating relatively ambiguous decisions compared with relatively unambiguous decisions. As research has shown that professional referees are motivated to project impressions of confidence via body language and facial expressions (Cunningham, Simmons, Mascarenhas, & Redhead, 2014), the findings show that even trained professionals have difficulty deliberately

controlling their body language in a desired way. In this respect, "it appears that social communication has been chosen by natural selection to be of greater survival value than disguising our intentions and feelings, so much so that we even have ways of unintentionally 'outing' ourselves to others" (Cozolino, 2006, p. 24).

A related study analyzed acoustic nonverbal behavior of athletes in recordings of competitive tennis matches and tested whether the nonverbal vocalizations of tennis players (tennis grunts) during professional tennis competitions contain adaptively relevant perceptual cues similar to nonhuman vocalizations (Raine, Pisanski, & Reby, 2017). The results revealed that tennis grunts conveyed cues to a player's gender and the outcome of the competition. Together with the studies on body language in sports, these findings suggest that human behavior in confrontational situations such as sports is influenced by a complex interplay of nonverbal signals that are constantly transmitted by the individuals interacting with each other. Although evolutionary-motivated studies on nonverbal communication in sports have mainly failed to investigate performance effects of nonverbal behavior, a recent study indicated a relationship between certain preperformance facial expressions and performance in combat sports (Kraus & Chen, 2013). More specifically, this study tested whether smiles before a physical confrontation are a nonverbal signal of reduced hostility, physical dominance, and aggression. If this were the case, fighters who smile more intensely in prefight photographs should perform worse in a fight compared with fighters who do not smile or smile less intensely. Results supported the hypothesis, as increased smile intensity before an Ultimate Fighting Championship match was associated with poorer performance by the fighter showing the smile and better performance by his opponent.

Limitations and recommendations for future evolutionary research in sports

Throughout the article I have argued and demonstrated that the context of sports can be useful in testing evolutionary-based hypotheses. However, evolutionary psychology is frequently challenged to avoid "just so stories" in which plausible explanations are made up in a post hoc fashion of how certain traits or behaviors might once have been adaptive (Ketelaar & Ellis, 2000). An important prerequisite for the success of evolutionary functional analysis on sports data is that evolutionary hypotheses are formulated a priori to data analyses, and it is therefore advisable to follow the open science recommendations (e.g., Open Science Collaboration, 2017; Pashler & Wagenmakers, 2012), including the preregistration of hypotheses and analyses plans. Concerning the formulation of hypotheses, I consider the approach of Ketelaar and Ellis (2000) as fruitful in transforming evolutionary just so stories into theoretical evidence. Their approach is derived from Kurt Lewin's proposal (1935, 1951) that psychologists should attempt to become more like natural scientists by starting by setting up an axiom system from which to derive theorems and correlates and subsequently subject these to experimental tests. According to Ketelaar and Ellis (2000; see also Buss, 1995), the axiom system in psychology should be *basic metatheoretical assumptions of evolutionary theory*. Below these metatheoretical assumptions are *middle-level theories* that elaborate on the basic assumptions of the metatheory into specific domains. From these middle-level theories, *hypotheses* and *specific predictions* can be derived, as specified in the approach of evolutionary functional analysis. Metaphorically speaking, this approach has the benefit of seeing a map of the entire forest as opposed to details of one part of the tree. Because it has been argued that the ratio of theory to data is too high in evolutionary psychology (Ketelaar & Ellis, 2000), I have outlined how the abundant data provided by the ubiquitous, meticulously recorded sports competitions can be a useful context for testing evolutionary hypotheses in modern society.

According to Buller's (2006) critique of evolutionary psychology, the challenging goal of evolutionary functional analysis is to discover the Darwinian algorithms that are executed by evolved cognitive modules. Cognitive modules have been described as "mental organs" (Pinker, 1997, 2003; Sperber & Hirschfeld, 2004) that process sensory information in a certain manner and in turn causally elicit behavior. A Darwinian algorithm can be defined by a set of decision rules that transform a representation of an adaptive problem into a solution to that adaptive problem: "A Darwinian Algorithm must generate behavior that was adaptive in the EEA and, importantly, it must generate the full range of behavior that we actually observe humans to perform in modern environments, even when that behavior is maladaptive" (Buller, 2006, p. 70). This suggestion is analogous to Darwin's (1871/1981) strategy of providing evidence for phylogenetic evolution by natural selection by demonstrating the existence of "rudimentary, atrophied, or aborted organs" (p. 255) that no longer serve an adaptive function (i.e., vestiges of adaptations). Hence, a promising avenue for future evolutionary research in the context of sports might be to search for behaviors that could be considered adaptive in the EEA of humans but are no longer adaptive today.

Although our ancestral environments share some similar features to today's environment (e.g., families, threats from out-groups), there are also major differences. Sports-related research has indicated potential downsides of phylogenetically adaptive yet outdated behavioral tendencies. For example, sending submissive cues seems adaptive in primates when losing a fight because this helps to avoid further attacks, but it seems unlikely that leading athletes will go easy on trailing athletes as a result of submissive behavior. On the contrary, recent research suggests that when leading athletes perceive nonverbal behavior associated with defeat in their competitors, the leaders' self-confidence is enhanced (Furley & Schweizer, 2014b). Enhanced confidence is likely to affect performance (e. g., Furley, Moll, & Memmert, 2015) and, in turn, might end in a vicious circle for the trailing athletes: for example, when things are going badly for a particular athlete during competition, this might show in his/her nonverbal behavior, causing an opponent to perform better and the athlete worse. Likewise, professional sports referees are motivated to communicate decisions confidently (Cunningham et al., 2014). Nevertheless, their body language has been shown to reveal signs of insecurity when communicating difficult decisions (Furley & Schweizer, 2016b). This behavioral tendency is likely due to the fitness-enhancing adaptation of outing internal states such as emotions to group members.

Another example of a negative effect of behavior that was considered adaptive in our ancestral past is sports fan rivalries or hooligans in modern society. Although identifying with a sports team or club (either as a player or fan) can be considered a consequence of an adaptive mechanism of binding individuals into larger groups (e.g., to satisfy the need to belong; Baumeister & Leary, 1995), it has nowadays been shown to also provoke intergroup rivalries and aggressive acts (Wann, Haynes, McLean, & Pullen, 2003), even resulting in negative health outcomes (Wilbert-Lampen et al., 2008). Following these examples, it seems likely that other maladaptive behaviors that are observable in sports (e.g., arguing with the referee, losing one's temper, or cheating/doping) can be considered by-products of evolved adaptations.

Another potentially fruitful avenue for future evolutionary research in sports could be on evolutionary stable behavioral strategies (Smith, 1979) in social interactions. Evolutionary biologists have started to treat behavioral strategies of interacting animals (e.g., when to fight or when to defer to a combatant) as phenotypes and have successfully used the mathematical modeling of game theory to predict evolutionary beneficial strategies (Smith, 1979). This approach requires a large quantity of in situ observations of social interactions, and initial research has suggested that, for example, soccer penalty kicks can be exploited to test predictions derived from game theory in humans (Misirlisoy & Haggard, 2014; but see Braun & Schmidt, 2015). Because the findings from this approach are rather inconclusive to date, I will not go into detail, but I consider this approach useful to test novel hypotheses derived from game theory in sports interaction that might result in useful applied recommendations: for example, when competing athletes should change their dominant response strategies to become less predictable to their opponents or the frequency of using deceptive behavior so that the opponent does not easily recognize it as deception.

Conclusion

Evolutionary psychology is fundamentally interdisciplinary and has led to a variety of important new insights and explanations across various fields. Within this article I have reviewed empirical evidence showing that the cross-cultural existence and popularity of sports can be considered a by-product of other adaptations, including internal capacities to learn and develop skills, to compete for status and mates, and to form beneficial coalitions with other individuals and groups. In addition, the large databases of sports recordings and data have proven useful in enhancing the understanding of cooperation and conflict in groups, lateral preferences or handedness in humans, territoriality, and nonverbal behavior in confrontational and cooperative contexts. It is my hope that this review will encourage further evolutionary investigation in the context of sports because sports can be a useful natural laboratory for testing hypotheses and specific predictions about our ancestral past that have the potential to reveal evolutionary aspects of human behavior more clearly than psychological testing involving computer-based responses.

In addition, the field of sports science has recently been criticized for lacking a suitable overarching theoretical framework (Glazier, 2017). This criticism has resulted in a lively debate as to which field(s) this theoretical framework can be derived from given the multidisciplinary nature of sports science (Button & Croft, 2017; Cardinale, 2017; Cobley, Sanders, Halaki, & O'Dwyer, 2017; Hackfort, 2017; Lopez-Felip & Turvey, 2017; Rein, Perl, & Memmert, 2017; Sands, 2017; Seifert, Araújo, Komar, & Davids, 2017; Williams & Ward, 2017). In this respect, the outlined evolutionary framework might be helpful in resolving this debate.

Both sports and Darwin's theory of evolution have fascinated people for many years. Although a simple one-to-one correspondence between genetic adaptions

and behavior is hard to find and is complicated by cultural learning, this article shows that important insights can emerge from using the tools of evolutionary psychology on sports data.

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