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The Promises of a Naturalistic Approach: How Cultural Evolution Theory Can Inform (Evolutionary) Economics

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Abstract
Humans are an ecologically extremely successful species. Underlying this achievement is our evolved unique adaptation for culture. Moreover, humans' cultural capacity initiated a process of gene-culture coevolution that lead to a plethora of behavioral and cognitive dispositions on which cultural adaptation to challenging environments via cultural evolution rests. These characteristics of human cognition are highly relevant to any discipline dealing with human behavior. This article presents these outcomes of human phylogeny and discusses this naturalistic perspective's implications for (evolutionary) economics. Moreover, some fruitful applications of cultural evolution theory to the explanation of economic phenomena are provided.

Keywords
Economic theory development – Cultural evolution theory – Learning mechanisms – Human behavior in economic contexts

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> "… a theory of behavior and cognition suitable for evolutionary economics needs to recognize the evolving cultural context of economic behavior and cognition."
>
> Richard R. Nelson (2016, p. 737)

1. Introduction

Humans are an ecologically extremely successful species. We have been capable of living and thriving in a broad range of habitats around the globe. Inuits, to give an example, have created a vast body of cultural know-how about how to survive and adapt in the Artic – an ecologically very challenging habitat. For instance, to hunt a seal in this environment, they know how to find their well-hidden breathing holes in the ice (example drawn from Henrich, 2016, ch. 3). The area around it must be covered by snow since otherwise the animals will detect hunters approaching. Next, Inuit hunters skillfully open the hole, smell it to verify that it is still in use, and assess the shape of the hole with a special piece of caribou antler to ascertain the precise location and dimensions of the breathing hole beneath the ice without otherwise disturbing it. This is important to know where to thrust the harpoon later. They then cover the hole with snow again leaving a small gap at the top that is capped with a specifically constructed down indicator. If the seal enters its breathing hole, the indicator moves, and the hunter must be capable of blindly throwing the harpoon into the hole using all his weight. The harpoon must have a particular length, a detachable tip tethered with a strong braid of sinew line, and a rear spike made of extra-hard polar bear bone. What is more, Inuits know how to cook a hunted seal (before the meat goes off) by starting a fire (in the Artic!) in a lamp made from soapstone, burning oil from seal blubber and using a wick out of a particular species of moss.

Our species' remarkable ecological success that exemplarily shows up in the Inuit case calls for an identification of its behavioral and cognitive underpinnings. An answer to this question is highly relevant to any discipline dealing with human behavior – including economics – for we would expect it to reveal basic features of our cognition. So, is our outstanding adaptive performance arising from a far superior – as compared to other primates – form of well-informed individual decision-making that draws on a powerful general-purpose brain structure as economists may argue? Are individuals in this process really aware of all options open to them for preference-satisfaction to then pick the inter-temporary utility-maximizing variant out of this set? Is that the way we deal with the world's complexity? In fact, the scientifically sound answer to this question is that the successful human cultural adaptation to various challenging environments depends predominantly upon our unique pro-sociality: it is collective culture that

enables the accumulation of skills, knowledge, and patterns of behavior far more complex than any individual could invent in her lifetime (see Henrich and McElreath, 2003; Caldwell and Millen, 2008; Henrich, 2016).[1]

Human cultural adaptation, therefore, is enabled by learned behavior developed over years with investment and exchange from other individuals (McElreath, 2016). Culturally transmitted information accumulates over generations, such that knowledge gets refined and more and more complex – the so-called "ratchet effect" that not only underlies Inuit hunting strategies but also modern technology and institutional arrangements (e.g., Herrmann *et al.*, 2007). These phenomena's knowledge bases are created by group members', organizations', and professional peers' lengthy cultural learning processes and are acquired by individuals only as they are part of this broader, communicating community (see Nelson, 2016). At the root of our adaptive success lies our capacity for culture based on unique features of social cognition (see Tomasello, 1999b). Hence, cultural – including economic – evolution rests on and is constrained by foundations laid before by natural selection in the course of human phylogeny (see Witt, 1999; Cordes, 2006, 2015; Gowdy, 2008). Evolved cognitive devices and dispositions as well as wants and learning mechanisms define the cognitive and physiological basis on which cultural evolution is predicated. Below, we show how gene-culture coevolution (GCC) explains many crucial aspects of these cognitive foundations, including an unmatched degree of prosociality and cooperation, cultural learning skills, and biases in cultural transmission.

Our perspective contrasts sharply with the idea that human agents primarily arrive at their behavioral options by doing perfectly informed isolated utility-maximizing calculations. While standard economic theory can account for phenomena such as other-regarding preferences, cooperation, or affective states of agents, it does so in an *ad hoc* manner by just adding further parameters to the utility function and thus to the process of rational decision-making. It is, however, silent about some much deeper influences of culture on human behavior and choice: preference systems are a result of cultural transmission forces (e.g., through socialization) and subject to continuous change via cultural learning (see Section 4). Preferences are culturally generated. What is more, also causal beliefs about possible outcomes of behavior – as another crucial ingredient of rational decision-making – are emanating from cultural learning and are acquired "pre-rationally" (also Collier, 2016). As to humans' prosocial dispositions and their affective underpinnings, the recognition of cultural evolution in combination with genetic inheritance (gene-culture coevolution, see below) provides sound explanations of their evolutionary origins and exact behavioral effects. Thereby,

[1] Culture is considered to be all of the information that individuals acquire from others by a variety of social learning processes including teaching and imitation (see Boyd and Richerson, 1985).

it substantiates these ingredients to a more encompassing behavioral model by drawing on interdisciplinary scientific evidence (see Section 2). This also holds for psychological characteristics that potentially lead to non-utility maximizing, non-rational behaviors, such as a norm following psychology or various biases in cultural learning that may make us adopt maladaptive cultural traits (for details, again see below).

As shown in this article and supported by, among others, anthropological evidence, rational decision-making is not the core feature of humans' immense ecological success and its cognitive foundations. Rather, it is culture including social interaction and various learning mechanisms that is the defining feature of humankind (see Brewer *et al.*, 2017) – much more than it is the case with rational choice-based behaviors. This insight, which directly follows from facts delivered by, for example, cognitive sciences, evolutionary biology, neurosciences, anthropology, and evolutionary psychology, should affect the way we do economics. In this article, we therefore call for a naturalistic approach to economics that does justice to *Homo sapiens* and this agent's evolved cognitive and behavioral traits and that contributes to more realistic models of human behavior in economic contexts. We also indicate the potential of an application of these insights to economic theory building including formal models of cultural evolution.

The article is organized as follows. In Section 2, we discuss the fundamental human adaptation for culture and how GCC has subsequently led to further unique biological, social, and behavioral dispositions in the case of humans. Next, Section 3 describes cultural learning mechanisms and various systematic biases in cultural transmission that can also be incorporated into formal models of cultural evolution. Section 4 presents some promising applications of naturalistic thinking and models of cultural evolution to (evolutionary) economics. Finally, Section 5 concludes.

2. Who we are: humans as cultural beings and the results of gene-culture coevolution

As a cultural species, we are able to attentively observe and learn from other people by inferring our models' underlying intentions, motivations, beliefs, strategies, and preferences. This skill also enables us to engage in effective instructive teaching, the flip side of cultural learning. According to Tomasello *et al.* (2005; also Tomasello, 1999a; Tomasello and Rakoczy, 2003; Herrmann *et al.*, 2007), the crucial human adaptation for culture that prepared the cognitive stage for these capabilities is our capacity to understand others as intentional beings like the self (also Cordes, 2004). This perspective-taking competence made possible a differentiation between intentions and behavioral means employed by role models to achieve certain goals. Thus, putting oneself into the shoes of others is a prerequisite for our extraordinarily powerful cultural learning mechanisms. Cultural evolution is then a consequence of genetically evolved

psychological adaptations for learning from other people. As shown below, further refinement processes of these dispositions due to recursive gene-culture interactions made us ever more powerful social learners in the course of human evolution. What is more, while instances of frugal cultural learning are frequent in non-human nature, it is only humans who realize a "ratchet effect" in cultural evolution giving rise to cumulative cultural development and adaptation.[2]

As a kind of side effect, this capacity for culture gave rise to very idiosyncratic human behaviors: it constitutes the basis for empathy, i.e., the understanding of affective states of others by vicariously taking their position (e.g., Singer and Fehr, 2005; Bernhardt and Singer, 2012). Moreover, our mind-reading skills also facilitate the development of sophisticated "theories of mind", another distinctively human competence (Herrmann *et al.*, 2007). Others' emotions, therefore, shape our own motives toward them and deliver the motivational underpinnings of many seemingly "irrational" behaviors, such as helping behavior or the preference for particular social norms of fairness (e.g., the "golden rule", see Cordes and Schubert, 2007). Hence, other-regarding sociocognitive features of humans enable both, the cultural "ratchet effect" and prosocial, altruistic acts, which do not necessarily accord with assumptions of individual, selfish utility maximization – a first important deviation from the standard model of economic behavior.

Once cultural adaptation became the cornerstone of our species' success about two million years ago, the main selection pressure on genes led to improving our psychological skills to acquire, store, process, and organize the cultural knowledge increasingly available in our social environment (see Richerson and Boyd, 2005; Mesoudi *et al.*, 2006; Henrich, 2016).[3] Subsequently, more sophisticated learning capacities facilitated more complex cultural adaptations that then again called for even better learning skills. In this context, less skilled cultural learners would have been at a strong selective disadvantage (social and natural) vis-à-vis competing learners in a group because they would not have acquired the same repertoire of behaviors, norms, skills, and know-how. Hence, enhanced cultural learning abilities gave rise to a close interaction between an accumulating body of cultural knowledge and genetic evolution, a process that has shaped our cognitive setup in very particular ways. This coevolutionary process between genes and culture – gene-culture coevolution (GCC) –

[2] Dean *et al.* (2012) demonstrate how sociocognitive processes of imitation, instruction, and prosociality, which are only observed in humans but not in other primates, enable cumulative cultural evolution.

[3] For a review of theories of cultural evolution including criticisms and controversies, see Mesoudi (2016). This article also discusses some open questions in the field of GCC.

created many important features of the psyche of modern humans also relevant in contemporary behavior in economic contexts.[4] Below, in Section 3, we discuss several cognitive dispositions, especially manifold learning biases in cultural transmission, which resulted from GCC in the past, while Section 4 applies these insights to economic theorizing.

In combination with cultural group selection, GCC also explains the phylogenetic origins of further uniquely human inclinations toward non-selfish, prosocial behaviors. Examples are cooperation in groups (including non-kins) and altruistic punishment of deviators, behavioral traits that are irrational from the point of view of fitness- or utility-maximizing individuals, but welfare-enhancing at the group-level (Soltis *et al.*, 1995; Boyd and Richerson, 2002; Richerson and Boyd, 2005; Sober and Wilson, 1998). Groups with prosocial norms had an advantage over other, competing groups in cultural group selection. The cultural environments in these relatively more successful groups favored agents exhibiting prosocial behaviors including cooperation and altruistic punishment. As a consequence, phenotypes with genetic dispositions for such behaviors fitting well into these group cultures do better than others and disseminate. In line with this idea, evidence from the neurosciences shows that there is an evolved neurological foundation on which some of these prosocial behaviors rest (see Fehr and Gächter, 2002; Rilling *et al.*, 2002; Reuter *et al.*, 2011). They are rewarded by specific dopamine-releasing brain structures. These neuronal dispositions are at odds with a behavioral model merely putting individual utility-maximizing center stage. Moreover, Tomasello (2009, p. 43) suggests the strong emotional reactions of “shame” and “guilt” as good examples of outcomes of the coevolutionary process between biology and humans’ specific cultural environments, namely groups that reward or sanction certain behaviors (also Durham, 1991). One can hardly argue that these affective motivational underpinnings of human behavior always lead to rational, individual welfare-enhancing behaviors, although originally these have been adaptive as to living and acting in certain cultural group contexts.

Norm psychology is another important feature of human cognition evolved by means of GCC (see McElreath *et al.*, 2003; Chudek and Henrich, 2010; Henrich, 2016, ch. 11). It has been caused at the genetic level by the enforcement of social norms in group culture contexts. Phenotypes endowed with a propensity to obey norms enjoyed a relative advantage in these settings. This psychological disposition was of great adaptive value for it enabled the stabilization and maintenance of cooperation and other prosocial norms at the group level. However, due to this cognitive disposition,

[4] Other important products of GCC are anatomical changes of hands, shoulders, and elbows due to increasingly complex weapons and tools, changes in throat anatomy and brain structures because of language, and extended childhood and adolescence to take advantage of cultural knowledge (Henrich, 2016, ch. 5).

cultural evolution can also produce social norms that tend to be stable even if they neither serve the group nor the individual. Norm psychology can also support maladaptive traits by inducing the following of norms for their own sake (also Durham, 1991). This may even be against an agent's self-interest. Moreover, culture often comprises – causally opaque – adaptive repertoires accumulated over generations that are not understood by individuals. For this reason, complex cultural adaptations and GCC have favored individuals who frequently rely on pure faith in cultural transmission rather than on applying causal models, personal experiences, or rational thinking (see Henrich, 2016, ch. 7). Again, we observe seemingly irrational human cognitive traits that only make (adaptive) sense when seen through a cultural evolution lens.

Detailed evidence on the concrete outcomes of GCC is amassing (see Herrmann *et al.*, 2007; Henrich, 2016). Rapid progress in molecular genetics and genomics provides data to produce rich empirical support for GCC (e.g., Ross and Richerson, 2014). Chiao and Blizinsky (2010), to give a detailed account, describe the intriguing GCC between cultural values of individualism-collectivism and allelic frequency of the serotonin transporter functional polymorphism. Geographical regions, they show, characterized by cultural collectivism exhibit a greater prevalence of S allele carriers of this polymorphism, which is associated with increased negative emotions, depression, attentional bias to negative information, and fear conditioning. Their argument is that collectivistic cultural norms have evolved to serve as an adaptive, "anti-psychopathology" function, creating an environmental niche that reduces exposure to, for example, chronic life stress or affective disorders for genetically susceptible group members. Mediation analyses indicate that increased frequency of S allele carriers predicts decreased anxiety and mood disorder prevalence owing to increased collectivistic cultural values. This leads to genetic selection of the S allele within collectivistic cultures. Indeed, evidence shows that historical prevalence of the S allele predicts cultural variability in individualism-collectivism. Since this genetic disposition also gives rise to affective attentional biases, it influences information processing mechanisms and the storage and transmission of cultural values by favoring, for example, collectivistic cultural norms of conformity and interdependence. Genes and cultures interact, therefore, in both directions. On the other hand, carriers of the L allele of this gene exhibit positive cognitive bias to individualistic thinking, such as self-expression and autonomy.[5]

[5] The cultural dimensions of "individualism" and "collectivism" have repeatedly been shown to be of great importance when it comes to explaining economic phenomena, such as economic performance of societies (Greif, 1994), economic growth and innovative activity (Gorodnichenko and Roland, 2011), or organizational development (Cordes *et al.*, 2017).

As shown in this Section, starting from our unique social-cognitive adaptation for culture, GCC led to the further selection for phenotypes that could use cultural information available in their social environments. Improved cultural learning skills would have permitted a greater accumulation of cultural know-how and further driven genetic evolution to increase cultural learning abilities. Cultural evolution initiated a process that drove, partly in combination with cultural group selection forces, genetic evolution to make us powerful social learners, prosocial group members, and cooperative, docile rule followers. These capacities and traits represent the very essence of our specific cognitive setup and our unmatched ecological success. For any scientific discipline dedicated to explaining real-world human behavior, these findings provide a very rich source of naturalistic insights on our nature that can and should inform theory development and empirical work.

3. What we need: models of cultural evolution incorporating cultural learning mechanisms

As shown above, evolutionary theory explains the origins of cultural evolution in human phylogeny and its interactions with genetic evolution (GCC). It also fosters the understanding of the lasting influence of evolved cognitive devices that participate in generating human behavior. Moreover, GCC drove the emergence of specialized cognitive abilities including cultural learning biases that guide the tapping of cultural knowledge in an individual's social environment. These cause people to acquire some cultural traits rather than others. By selectively attending to certain types of cultural content, individuals most effectively acquire valuable cultural knowledge. These biologically evolved foundations of learning and reasoning enable cumulative cultural evolution and also directly facilitate and affect economic evolution as part of this all-encompassing process (see Witt, 2003, p. 15f; Cordes, 2015). Thus, if we want to deal with cultural beings when doing economics, rational choice models based on individual decision-making are not going to do the whole job. Instead, we need to apply cultural evolution theory including its formal tools to grasp important facets of human behavior in economic contexts.

Models of cultural evolution allow one to deduce the group-level consequences of individual-level psychologies, decision rules, and behaviors (e.g., Henrich and Boyd, 2002; McElreath and Boyd, 2007; van den Bergh and Gowdy, 2009; Hoppitt and Laland, 2013; also Rice, 2004). Many of these models involve deriving recursion equations in discrete or continuous time that allow us to predict the frequency of a certain cultural trait in a population in the next stage of the cultural evolutionary process given its frequency in the present stage (see, as points of origin, Cavalli-Sforza and

Feldman, 1981; Boyd and Richerson, 1985).[6] Cultural learning processes may also be captured by, for example, models of sexual selection stemming from population genetics (e.g., Boyd and Richerson, 1985; Schubert and Cordes, 2013), replicator dynamics (e.g., Metcalfe, 1988; Henrich, 2001), evolutionary game theory (e.g., McElreath and Boyd, 2007), or Price equation-based approaches (e.g., Beheim and Baldini, 2012; Klarl *et al.*, 2018). Moreover, drawing on earlier work in cultural evolution theory (see Feldman and Cavalli-Sforza, 1975), Cordes *et al.* (2017) introduce another modeling technique: they depict group-bound learning and socialization drawing on cultural transmission matrices within a Markovian formal framework. Thus, formal tools of cultural evolution theory offer a plethora of fruitful ways to analyze evolving cultures and behaviors of human agents as cultural beings. Furthermore, these rigorous, quantitative forms of analysis are open to empirical testing. We will discuss some of these contributions at greater detail in the next section.

All these models of cultural evolution describe the changing frequencies and values of cultural traits in populations of interacting agents due to cultural transmission mechanisms including general, for example, group-bound, learning forces and particular learning biases (also Norenzayan and Heine, 2005; Mesoudi and O'Brian, 2008; Hoppitt and Laland, 2013). Because of these biases, humans do not arbitrarily copy cultural traits exhibited within their social environments. Instead, evolved and/or learned cognitive biases take effect in cultural transmission by affecting the probability of adopting certain kinds of cultural traits and corresponding behaviors.[7] These biases are a way how real-world human beings tap the rich cultural knowledge available to them and heuristically cope with the great amount of choice options and behaviors open to them. They guide attention and economize on scarce cognitive resources. Moreover, many of these learning biases are outcomes of GCC that has led to the evolution of phenotypes capable of effectively using cultural information (see above).

As to the biases that may be included in these formal models, the conformity bias is a prominent one. It represents a fast and frugal strategy to figure out well-adapted kinds of behavior in a complex cultural setting by drawing on the frequency with which certain behaviors are shown by agents in this particular cultural context

[6] A cultural trait is defined as an idea, norm, belief, attitude, habit, or value that is acquired by social learning and that influences an individual's behavior (e.g., Bisin and Verdier, 2001; Henrich *et al.*, 2008). Cultural traits have long been used in anthropology as units of transmission that reflect behavioral characteristics of individuals or groups (e.g., O'Brian *et al.*, 2010).

[7] Reliance on cultural learning as well as the weighting of biases is itself tuned by both own experience and observation of others. Moreover, social learners may combine the learning heuristics described.

(e.g., Aronson *et al.*, 2002; Kameda and Diasuke, 2002; Cialdini and Goldstein, 2004; Corriveau and Harris, 2010). Agents are, therefore, more likely to pick the behavioral variant that is modeled by the majority of group members, i.e., they discriminate against behaviors that are rare among peers. Conformity explains many aspects of group behavior including nonlinear behavioral changes in groups, such as threshold phenomena (e.g., Cordes *et al.*, 2010). Self-similarity along dimensions such as sex, dialect, or ethnicity is another simple bias that allows to determine cultural contents worthwhile and safe being copied in complex cultural environments (e.g., Shutts *et al.*, 2009) and that lends itself to formalization. Both biases can, however, also lead to the adoption and spreading of maladaptive, "irrational" cultural traits (see below).

Further important cultural learning biases that have been formalized in cultural evolution theory are the role model bias or prestige-based biases (e.g., Cordes *et al.*, 2008). Humans are prone to adopting behaviors exhibited by successful or prestigious individuals. For instance, seeking prestige drives much human behavior causing a certain number of prestigious role models to exist in every human group (see Henrich, 2016, ch. 8). Evidence from psychology and anthropology shows that the adoption of cultural traits is frequently conditioned by observable attributes of individuals exhibiting the trait (e.g., Rogers, 1983; Harrington Jr., 1999; Labov, 2001; Henrich and Broesch, 2011; Atkisson *et al.*, 2012; Chudek *et al.*, 2012).[8] Suicide, to provide a very telling example, is role model and prestige biased: when celebrities commit suicide, there is a subsequent spike in suicide rates (e.g., Jonas, 1992).[9] Moreover, the cultural transmission of suicide is also subject to self-similarity biases: individuals who kill themselves soon after celebrities tend to match their models on sex, age, and ethnicity. This demonstrates how potent our cultural learning abilities are: we can even acquire practices that natural selection would have eliminated under most conditions for they are not in our self-interest or that of our genes (also Henrich, 2016, ch. 4).

Other biases active in cultural transmission and suited as potential ingredients to formal approaches to cultural evolution comprise payoff-based biases (e.g., Boyd and Richerson, 1985; Henrich, 2001; McElreath *et al.*, 2008), biases arising from cultural dimensions acquired via socialization (see Chiao and Blizinsky, 2010; Cordes *et al.*, 2017), or kinship-based biases (e.g., Henrich and Broesch, 2011). What is more, direct biases in cultural as well as individual learning make people preferentially adopt cultural traits based on their contents (e.g., Richerson and Boyd, 2005). Due to certain evolved cognitive predispositions that increase the inherent attractiveness of particular traits, directly-biased people learn some cultural traits rather than others. Examples are

[8] Role model bias may also depend on demonstrator performance, the number of demonstrators, or the consensus among demonstrators (see Morgan *et al.*, 2012).

[9] In social-psychology, this phenomenon is called the "Werther effect".

deeply-rooted preferences for prosocial behaviors such as cooperation or altruistic punishment (see Reuter *et al.*, 2011; Fehr and Gächter, 2002), Veblen's (1899) instinct-based concerns about status that translates into a preference for status-signaling goods (also Ng's (2003) "materialistic bias" or Frank's (2008) interest in "relative position"), or religious and "folkbiological" contents that spread easily due to "cognitive tracks" (see Sperber, 1990; Boyer, 1999; Henrich, 2016, ch. 5).

4. What we gain: promising applications of naturalistic thinking and cultural evolution theory in economics

This section presents some concrete existing applications of naturalistic thinking and cultural evolution theory to economic phenomena that all indicate the great explanatory potential of such a research agenda.

4.1. Earlier naturalistic, Darwin-inspired approaches to economics

First naturalistic, Darwin-inspired approaches to economics were the instinct- and habit-based theories of human agency delivered by American Institutionalism during the second half of the nineteenth century (e.g., Veblen, 1898, 1914; Clark, 1918a, 1918b; Commons, 1920; Rutherford, 2000; Asso and Fiorito, 2004; Cordes, 2015). These institutionalists enabled cross-fertilization between contemporary economics, evolutionary biology, and psychology. They argued that human behavior responds to two kinds of determinants: the basic drive of instinctive factors and the drive to conform to habits. Mitchell (1910), for instance, claimed human activities to be governed by instincts and habits as well as imitation and suggestibility. Humans' intellectual apparatus then is the instrument by which instincts and habits seek their satisfaction. American Institutionalists understood human instincts as evolved, innate cognitive features that determine what agents perceive, pay attention to, experience as an emotional excitement, as well as the impulses to act on objects in a particular manner (e.g., McDougall, 1910). Thereby, many of these dispositions are functionally similar to the cognitive biases of modern cultural evolution theory. The formation and dissemination of habits, on the other hand, is influenced by instinctive proclivities as well as institutional settings and relies on sophisticated forms of evolved cultural learning capacities (e.g., Veblen, 1914, p. 7) – an early recognition of our species' fundamental adaptation for culture. Moreover, the assumption of deeply-rooted motivations to stick to established habits is in line with effects attributed to norm psychology as a result of GCC.

American Institutionalists suggested a great variety of instincts as results of human phylogeny (e.g., Veblen, 1914; Clark, 1918a; McDougall, 1920, 1924): the instincts of fear, repulsion, curiosity, anger, self-abasement, self-assertion, and

parental care as well as acquisitive, constructive instincts, such as the "instinct of workmanship". Also some social, gregarious instincts, such as the "parental bent" that aims at the welfare of the family, clan, or group including non-relatives (!), belonged to this catalogue of cognitive traits. It therefore also comprised some prosocial behavioral features whose evolutionary origins are explained by modern GCC (see above). What is more, these institutionalists explicitly saw individual economic actors as operating within cultural contexts that, through the institutions they engender, strongly influence their behaviors (also Mazzoleni and Nelson, 2013). A modern naturalistic approach based on contemporary knowledge on humans' cognitive dispositions as well as cultural evolution theory can substantiate many of American Institutionalists' notions of instincts and habit transmission mechanisms, thereby operationalizing them for further analysis. This would avoid *ad hoc* justifications for any kind of human behavior simply by adding one new instinct or learning channel to an existing set, a criticism that has been frequently raised against this strand of economic research.

Also F. A. Hayek – as a representative of the Austrian School – took a naturalistic stance on important issues by assuming a core set of human instincts that evolved in the "primitive tribal societies of prehistory" (Hayek, 1960, 1979; also Hodgson, 2007; Cordes, 2015). Following Hayek, innate behavioral dispositions can be assumed to have great influence on the evolution of institutions. He stated that frugal forms of social behavior, values, and attitudes became genetically fixed during human phylogeny. His conception of instincts starts from his notion of social rules: a stratification of rules of conduct rests on genetically inherited "instinctive" drives that are determined by "physiological structure". This system of layered rules also includes – culturally transmitted – traditions of the past and a thin layer of deliberately added "made" rules. However, Hayek did not specify the exact contents of humans' innate instincts and how their working keeps influencing institutional evolution. Instead, he just claimed that instincts are "tamed and checked" by the rules of conduct and institutions of civilized society. Moreover, Hayek shared a strong interest in theories of cultural evolution with Thorstein Veblen, a prominent representative of American Institutionalism. They both emphasized the unique human capability for cultural adaptations through cultural learning. In addition, they both paid extraordinary attention to group-regarding proclivities – phylogenetic outcomes of GCC. Furthermore, Hayek argued that an inherent part of human nature includes the welfare of others – an aspect of human empathy and pro-sociality (see above) – as a condition for individual happiness. Finally, he also embarked on the idea of a process of cultural group selection in institutional development favoring cooperative group cultures (Hayek, 1988).

Neo-Schumpeterians within the evolutionary economics camp draw on selectionist models analogous to phylogenetic biological evolution to scrutinize innovation dynamics and frequently combine these with aspects of cultural transmission. Nelson and Winter (1982), for example, reproduce the results of the

neoclassical (Solowian) growth model in a formal approach that includes competition via innovation and imitation based on observational learning. Metcalfe (1988, 1994) analyzes the diffusion of innovation in an economy with the help of a replicator dynamic that also includes cultural learning among consumers about product features as a form of selection (also Witt and Cordes, 2007).

A naturalistically inspired theory of economic change that includes aspects of cultural evolution has also been brought forward by Douglass North (2005). His approach puts unique human cognition center stage: the driving forces of economic evolution are, he argued, human intentionality, beliefs, cognitive learning, and knowledge creation, including its subsequent dissemination via cultural learning mechanisms. Moreover, Denzau and North (1994) have provided a conceptual link between human cognition and the evolution of institutions: categories and mental models are based on individual and collective learning processes, i.e., evolved capabilities of social cognition contribute to the design and the cultural passing on of mental frameworks and finally corresponding societal institutions.

4.2. Cultural transmission mechanisms and changing preferences

As shown by more recent work, naturalistic insights and cultural evolution theory are especially well-suited to grasp the mechanisms underlying changes in human wants, i.e., to account for the empirical fact that our preferences are neither fixed nor homogenous (e.g., Elster, 1982; Sen, 1977; Bisin and Verdier, 2000; Schubert, 2012). Rather, agents permanently learn new ones or modify existing ones, thereby being subject to deep cultural influences (see Winter, 2014; Hoff and Stiglitz, 2016). This observation represents a central challenge for neoclassical theory that necessarily relies on given sets of stable preferences in utility maximization as fixed “measuring rods”. Economists have to come to terms with the fact that preferences are fundamentally shaped by cultural environments and that social interactions are, therefore, crucial determinants of economic outcomes. A naturalistic concept of wants presented by Ulrich Witt (2001, 2003) inspired by modern behavioral theory and cognitive psychology explains the origins and development of innate as well as learned wants people pursue (also Ruprecht, 2005; Lades, 2013; Chai, 2017). Starting from an individual’s set of innate wants this repertoire is extended by processes of non-cognitive (via conditioning) and cognitive learning of acquired wants. In this context, cognitive learning forces include various cultural transmission mechanisms and biases as discussed above. Changing consumption patterns in the course of economic development and satiation phenomena that also impact on long-term economic growth rates can be fruitfully tackled by this approach.[10] This concept explains aspects of

[10] Satiation phenomena are rarely accounted for in neoclassical approaches.

human consumption behavior that elude treatment by rational choice models comprising agents endowed with constant preferences.

Moreover, Witt (2017) connects preferences over actions to the motivational forces driving actions, whereby the latter are entertained by naturalistic insights from biology, behavioral science, and psychology. Again, this enables the explanation of changing consumption patterns (e.g., with rising income) induced by systematically changing motivational forces underlying consumption acts. Witt argues that wants that are hard to satiate, such as status, social recognition, or positive self-image, account for a growing share in consumption in developed economies. Moreover, the continuous updating of wants due to cultural preference learning processes prevents certain forms of consumption motivation from ever vanishing (also Lades, 2013). This naturalistic theory of consumption also addresses normative and (adverse) welfare implications as to, for example, the call for continual consumption growth – prominent in traditional economics – in the face of difficult to satiate wants due to cultural learning dynamics (also Schubert and Cordes, 2013; Chai, 2017). In another contribution to this field, Woersdorfer (2010) shows how the demand for washing machines and other tools that meet the human want for cleanliness are strongly governed by culturally transmitted social norms prevalent in the agents' environment. Norm psychology as a result of GCC enters the picture here.

Also formal models of cultural evolution theory have been fruitfully applied in the field of endogenously changing preferences to fill this lacuna in economic theory. Schubert and Cordes (2013) present a model of population-based preference learning via cultural transmission: the continuous updating of individuals' consumption preferences by processes of cultural learning biased by a sample of role models prevents them from reaching consumption levels that would satisfy a certain non-changing preference level. As a consequence, agents permanently feel deprived and unsatisfied, a state that motivates them to permanently strive for ever higher levels of consumption. The authors argue that such a "run-away" preference learning process leads to welfare losses at the individual and societal level. Moreover, agents' preferences lose their function as reliable "measuring rods" of economic outcomes. Again, based on a mathematical model of cultural evolution and applied to the field of ecological economics, Cordes and Schwesinger (2014) show how the cultural acquisition of "green preferences" by agents via conformist, role model, and also directly-biased individual, hedonistic learning can pave the ground for the diffusion of environmentally-benign technologies (also Buenstorf and Cordes, 2008; Pahl-Wostl *et al.*, 2008; Welsch and Kühling, 2009). In this model, preference acquisition processes may even override relative cost disadvantages between competing technologies or consumption behaviors (also Røpke, 1999; Woersdorfer and Kaus, 2011). The combination of individual and cultural preference learning with more traditional economic considerations involving cost-based competition arrives at particular

recommendations as to environmental policy instruments promoting the diffusion of sustainable technologies (also Gowdy, 2008).

4.3. Naturalistic approaches in organization theory

Furthermore, naturalistic approaches that scrutinize the role of firms and other organizations in economic development have delivered a substantial body of research. They often explicitly include evolved cognitive dispositions of human agents and some are combined with formal tools from cultural evolution theory. Among other things, these avenues account for (changing) motivational underpinnings of human behavior within organizations, the evolution of firm cultures, firm performance, and organizational development (e.g., Boyd and Richerson, 1980; Witt, 1998, 2000; Langlois, 2003; Nicholson and White, 2006; Winter, 2014). For instance, based on a formal model of the evolution of a firm's culture, Cordes *et al.* (2008; also Cordes *et al.*, 2011) show that what successful organizations do better than markets – besides economizing on transaction costs – is to establish a cooperative regime among its employees that "crowds in" desirable behavior based on humans' unique evolved group-regarding social predispositions (resulting from GCC).[11] These behaviors go beyond the self-regarding, opportunistic concerns emphasized in the traditional theory of the firm. In these models, the agents' acquisition of different behaviors including pro-social ones is determined by learning biases, such as the role model bias, taking effect in cultural transmission within organizations. This naturalistic contribution to the theory of the firm also demonstrates how entrepreneurs and other business leaders can take advantage of the role model bias and actively shape behavior within a firm. As prominent, potentially prestigious role models in cultural learning they affect firm performance, culture, and growth – a cognitive and cultural evolutionary dimension neglected in both transaction cost economics and the theory of the firm more general (also, Langlois, 1998; Witt, 2007; Witt and Schwesinger, 2013).

Based on anthropological, social-psychological, and economic evidence on the effects of increasing group size on group performance, Cordes *et al.* (2014) scrutinize the role of evolving firm cultures in triggering spinoffs via growth crises in firm development due to behavioral changes in growing groups. Within the proposed model of cultural evolution, the – often rather sudden – occurrence of organizational growth crises is crucially influenced by conformist transmission among culturally interacting members of an organization. In small firms, it may initially stabilize a cooperative corporate culture based on humans' prosociality that is especially successful in dynamic, nascent business environments. Later, conformism can spur the

[11] For industry-level effects of evolving firm cultures and corresponding organizational performance see Cordes *et al.* (2010).

dissemination of opportunistic behavior once its frequency has surpassed a critical threshold in the course of success-driven increases in firm size and corresponding changes in group culture and employees' behaviors. Growth crisis than cause the exodus of personnel – well-trained in the previously cooperative firm culture – founding own firms and affecting a whole industry's or region's economic performance (see, Christensen, 1993; Buenstorf and Fornahl, 2009). Cordes *et al.* (2015) present a model that again features a critical organizational size triggering growth crises. Together with other processes, such as firm exit and entry, systematically appearing growth crises at the firm level produce several empirically well-established (right-skewed) shapes of firm size distributions (including power law and lognormal distributions). In both approaches, aspects of our group-bound psychology, which evolved via GCC in our past and which affect current processes of organizational development, are related to economic phenomena at the firm and industry level.

Cultural learning is also underlying group-bound socialization processes. Drawing on an approach introduced to cultural evolution theory by Feldman and Cavalli-Sforza (1975), Cordes *et al.* (2017; also Lundan *et al.*, 2017) suggest a Markovian model of cultural evolution that depicts the development of cultural distance within and between groups or organizational units by capturing the socialization dynamics taking place within these entities. This is done with the help of cultural transmission matrices. The approach facilitates to assess alternative organizational governance structures in terms of the socialization processes they enable that entail different intraorganizational transaction costs due to cultural distance within or between units. Characteristics that define an organization's socialization governance structure include shared or divided social experiences in (sub-) groups, the assignment and influence of role models, group sizes, the cultural background of employees, specific cultural dimensions, such as collectivism and individualism, and the implementation of certain cultures in business units. Thus, the authors argue, organizations have the capacity to capture transactional benefits arising from the governance of socialization experiences as a feature of cultural evolution.

4.4. Further cultural forces as determinants of economic outcomes

Cultural forces are important determinants of many economic outcomes that are not explicable by rational choice theory in a convincing – non-tautological – way: a sense of collective identity fostering altruistic acts toward an organization's members (e.g., McElreath *et al.*, 2003; Cordes *et al.*, 2008), a culture of honor that causes agents to behave in ways preventing mutually beneficial conventions from emerging in social interactions (e.g., Richerson and Boyd, 2005, ch. 5; Vance, 2017), priming a certain cultural context before (economic) decision-making (e.g., Hoff and Stiglitz, 2016), or engaging in transactional relationships based on culturally established trust regimes (e.g., Nooteboom, 1996). Beaman *et al.* (2012) provide empirical field evidence for a

very significant role model effect in cultural transmission: if women are enabled by law to take respected roles or leadership positions in local populations, villagers in India start to appreciate higher educational attainments for females, thereby strongly affecting their later economic status. Similarly, La Ferrara *et al.* (2012) show how exposure to soap operas in which women had few children reduced fertility rates in Brazil. Cultural dimensions, such as individualism and collectivism as results of socialization based on cultural transmission mechanisms, even explain long-run economic growth paths of nations: more individualist cultures generate more innovation, higher productivity, and higher growth rates than countries with a more collectivist culture (see Gorodnichenko and Roland, 2011). Moreover, analyses of differential institutional performance have been based upon cultural dimensions of this kind (e.g., Greif, 1994).

Chiao and Blizinsky (2010) show how affection-based direct biases in attention and cognition that result from GCC (see above) influence the transmission of cultural values of individualism and collectivism: carriers of a certain allele are more likely to engage in narrow thinking, perceive negative information, and consider dependency, whereas carriers of another allele of the same gene show greater willingness to take risks, self-express, and pay attention to positive information. Biases in cultural learning also emanate from socialization: Kitayama and Park (2010) provide evidence form neuroscience showing that people in Western cultures keep their personal self highly accessible in reasoning and place greater value on it, which gives rise to attention biases as to individual goals and desires as well as socially disengaging emotions. On the other hand, Eastern cultures bias attention toward aspects of interdependency, holism, and social goals and socially engaging emotions. Mesoudi *et al.* (2014) demonstrate how agents in Western populations – as opposed to members of Eastern cultures – under-utilize social information in lab experiments due to a too strong reliance on asocial learning, which happens because of cultural biases toward individualism. Moreover, the authors found higher copying frequencies in females than male participants. It is culture in combination with evolved or learned cognitive dispositions that explain these important differences in agents' perceiving, learning, and acting. Of course, they are also relevant in economic decision-making. Again, these cognitive and cultural forces effective in human reasoning do not automatically lead to "optimal" behaviors.

4.5. The spreading of maladaptive cultural traits

Consequently, while the evolved human capacity for culture surely was of great adaptive value in reproduction and survival of our species, this does not imply that cultural transmission always promotes the diffusion of well-adapted, welfare-enhancing cultural traits or rational, utility-maximizing behaviors in the sense of the *Homo economicus* model prominent among economists. Rather, the channels of cultural

transmission may be hijacked by pretty maladaptive ideas and strategies that do not necessarily serve an individual's (objective) interests. Conformity bias and norm psychology, for example, can sometimes foster the spreading or stabilization of cultural variants in groups that do not contribute to overall welfare of its members. Humans' strong reliance on cultural information as a means of ecological adaptation, therefore, also facilitates the spreading of behaviors that appear "strange" in the eye of a scientific, external observer (see Brown and Richerson, 2014). This holds especially true in modern societies where selection pressures are weak at most. Mass media, for example, exposes us to many influential, prestigious role models whose behaviors are not suited to increase our personal wellbeing – a situation in which a role model bias in our psychology makes us susceptible to maladaptive cultural contents.

In fact, there is a large anthropological literature describing how maladaptive cultural contents can spread to the disadvantage of actors (for references see Richerson and Boyd, 2005; Henrich *et al.*, 2008): for instance, Diamond (2005) describes how the Norse failed to survive in Greenland because of sticking to maladaptive cultural traits, such as pastoralism, cattle raising, and food taboos (no fish!). Moreover, due to issues of cultural distance, the Norse refused to learn from Inuit how to use abundant food resources available in that habitat. Agents, Diamond argues, have been socialized in certain cultures and this prevented them from considering any – potentially rational – solution to Greenland's problems. Modern demographic transition, to provide another example, can partly be attributed to the sharp increase in the ratio of non-kin to kin in social networks, leading to the dissemination of fertility-limiting cultural information between unrelated peers (see Newson *et al.*, 2007). This is maladaptive from the perspective of the selfish, fitness maximizing gene and seems to be at odds with a rational choice process as to the number of children an individual should bring up in order to maximize utility. Obviously, humans frequently miss rational predictions due to their unique and powerful adaptation for culture.

5. Conclusions

Culture is not a variable upon which economists have traditionally focused. This is a severe scientific shortcoming since culture and its transmission are the defining features of *Homo sapiens*: we strongly depend on culturally transmitted information. Humans are uniquely adapted for culture, a capacity that rendered us an ecologically very successful species. It is collective culture based on evolved special skills of social-cultural cognition that supports complex forms of human collaboration, such as tool-use and hunting (remember the Inuits!) as well as modern technology, consumption behaviors, organizations, and institutions. As cultural beings, humans are not just social, but "ultra-social" (see Herrmann *et al.*, 2007). Moreover, when accepting the outstanding role of culture in human evolution, we must also pay attention to subsequent processes of gene-culture coevolution (GCC) and their cognitive and finally

behavioral results. Cultural evolution has been a primary driver of humans' genetic evolution. Many uniquely human cognitive, affective, and moral capacities, such as other-regarding concerns including cooperation, identification, group membership, and fairness, as well as various cultural learning mechanisms, originated from the evolutionary dynamics of GCC. These dispositions go far beyond the self-regarding concerns of agents focused upon in mainstream economics.

While, cultural systems are capable of innovative adaptive response to changes in conditions and are often smart and ecologically highly successful, they are not approaching something like optimality. In real-world settings, optimal behavior is mostly impossible. Instead, limits to our cognitive resources in the face of a – especially interactionally – complex world induce individuals to adopt culturally transmitted behaviors using simple heuristics and other learning mechanisms. Therefore, cultural learning strategies that are studied by cultural evolutionists can – and often do – lead to the acquisition of maladaptive information. Thus, these potent cultural systems are not based on rational decision-making but rely on the unique human capacity of learning-based cumulative cultural evolution. Furthermore, as culture is continuously and actively evolving in historical time, the assumption that a population of economic agents is always (or ever) at an optimal equilibrium along this trajectory is implausible.

Given the strong human dependency upon cultural transmission, economists – as social scientists – have to do justice to the fact that also the bulk of agents' behavioral repertoires, choice sets, utility functions, and preferences are set up and changed via cultural learning forces. Their perception, cognition, and, finally, decision-making are heavily affected by their (varying) cultural environments and do not necessarily meet the requirements of rational choice. Hence, taking serious our anthropological knowledge about human phylogeny, we see that it was not *Homo economicus* that resulted from this evolutionary process. Rather, an agent has evolved that heavily relies upon information in her cultural environment plus individual learning, deliberation, and creativity that "fuel" cumulative cultural evolution. This should have profound implications for any behavioral model used in economics since any explanation of human economic behavior that fails to take cultural evolutionary processes into account will provide only an incomplete understanding. Consequently, the naturalistic approach to human behavior suggested in this article does not draw on full blown optimization as the all-embracing benchmark of economic theorizing. Rather, it takes the nature of human actors as it is described by the sciences as the origin of theory development and inspiration for new directions in empirical work. Cultural evolution theory including naturalistic insights may, therefore, also serve as a synthetic concept for the behavioral sciences (also Gintis, 2007).

As shown, a naturalistic approach to economics that does justice to the fact that human beings are evolved as a highly cultural species can explain real-world economic phenomena as a dimension of cultural evolution based on and influenced as well as

constrained by humans' evolved cognitive capacities. We have presented existing fruitful applications of naturalistic thinking – partly combined with formal models of cultural evolution – in the fields of changing preferences, consumption behavior, theory of the firm, and industrial dynamics, among others. In this context, it is important to note that the behavioral model based on a naturalistic avenue does not represent yet another deviation from the standard rational choice model as is often the case with contributions to bounded rationality. For instance, experiments in behavioral economics are predominantly motivated by identifying contexts in which quasi-rational individual actors systematically exhibit seemingly inconsistent, faulty choices due to agents' limited cognitive abilities (a.k.a. the "neoclassical repair project"). However, violations of the rational actor model, which may also be subsumed under the so-called "anomalies" of behavioral economics, such as following "wrong" role models, "bad" norms, "irrelevant" cultural frames, "maladaptive" habits, or "badly informed" majorities, seem to constitute the very core of humans' unique cultural capacities. Therefore, naturalistic and cultural evolutionary approaches look at these powerful cultural transmission mechanisms that make up essential parts of human cognition and then elaborate on their deep behavioral and finally economic implications. Ignoring these cultural skills and the cultural contexts of individuals blinds economic analysis to important influences and phenomena in which it should be interested.

Compliance with Ethical Standards:

The author declares that he has no conflict of interest.

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