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Moralizing Biology

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Abstract

In recent years, a proliferation of books about empathy, cooperation and pro-social behaviors (Brooks, 2011a) has significantly influenced the discourse of the life-sciences and reversed consolidated views of nature as a place only for competition and aggression. In this article I describe the recent contribution of three disciplines – moral psychology (Jonathan Haidt), primatology (Frans de Waal) and the neuroscience of morality – to the present transformation of biology and evolution into direct sources of moral phenomena, a process here named the ‘moralization of biology’. I conclude by addressing the ambivalent status of this constellation of authors, for whom today ‘morality comes naturally’: I explore both the attractiveness of their message, and the problematic epistemological assumptions of their research-programs in the light of new discoveries in developmental and molecular biology.

Keywords

altruism, developmental biology, Jonathan Haidt, human nature, moral brain, Frans de Waal

Introduction

In recent years, a proliferation of books about empathy, cooperation and pro-social behaviors (Brooks, 2011a) has significantly influenced the discourse of the life-sciences and reversed consolidated views of nature as a place only for competition, selfishness and aggression. Titles emphasizing the intrinsic morality or sociality¹ of our evolved nature have provoked a rethinking of the relationship between biology and the

¹For the notion of a natural morality see the recent volumes: Hauser, *Moral Minds* (2006); Gazzaniga, *The Ethical Brain* (2005); Verplaetse et al., *The Moral Brain* (2009); Haidt, *The Righteous Mind* (2012); Keltner, *Born to be Good* (2009); de Waal, *Good-Natured* (1996); Zak, *The Moral Molecule* (2012). For natural, innate sociality see: Goleman, *Social Intelligence* (2006); Brooks, *The Social Animal* (2011b); Nowak, *SuperCooperators* (2011); Keltner et al., *The Compassionate Instinct* (2010); de Waal, *The Age of Empathy* (2009).

moral phenomenon, as well as the emergence of new ideas of sociality, altruism and hope. The dismissal of the ‘dog-eat-dog’ view of nature and a new emphasis on the ‘bright side of biology’ (Nowak, 2011) have to be situated in important technical changes in the evolutionary literature since the 1970s. Take, for instance, this passage from Ghiselin’s classic (1974) *The Economy of Nature and the Evolution of Sex*:

The evolution of society fits the Darwinian paradigm in its most individualistic form. Nothing in it cries out to be otherwise explained. The economy of nature is competitive from beginning to end. What passes for cooperation turns out to be a mixture of opportunism and exploitation. Scratch an ‘altruist’, and watch a ‘hypocrite’ bleed. (Ghiselin, 1974: 247)

Now compare it with what the editors of a book titled *The Compassionate Instinct* write today:

We are witnessing a revolution in the scientific understanding of human nature. Where once science painted humans as self-seeking and warlike today scientists of many disciplines are uncovering the deep roots of human goodness. Empathy, gratitude, compassion, altruism, fairness, trust, and cooperation, once thought to be aberrations from the tooth-and-claw natural order of things, are now being revealed as core features of primate evolution. (Keltner et al., 2010: 5–6)

In addition to Ghiselin consider another classic from the 1970s:

Richard Dawkins' *The Selfish Gene* (2006[1976]: 4, 139), with its notion that 'anything that has evolved by natural selection should be selfish' and that 'we must teach our children altruism, for we cannot expect it to be part of their biological nature'. Again, compare this with a quotation from Frans de Waal's recent *The Age of Empathy* (2009: 5): 'we [humans] are group animals: highly cooperative, sensitive to injustice, sometimes warmongering, but mostly peace loving'.

Not by chance two references from the 1970s were selected here to stress the intellectual differences with the present understanding of the relationship between biology and altruism/morality. Evolutionary biologists in the 1970s were working within a theoretical framework marked by the dismissal of group theory (Williams, 1996[1966]), and the rise of 'inclusive fitness' (Hamilton, 1964), 'methodological individualism' (Ghiselin, 1974), the 'gene's eye view' (Dawkins, 2006[1976]) and the elaboration of theories of altruism (kin selection: Hamilton, 1964; reciprocal altruism: Trivers, 1971) that conceived it primarily as a disguised form of self-interest (or the genes' interest). In such a framework, a costly behavior (meaning: reducing reproductive fitness) like altruism was correctly said to be the 'central theoretical problem' of a newborn discipline like sociobiology (E. O. Wilson, 1975: 3). Clearly, it would be wrong to give the impression that these major tenets of evolutionary theory have all been turned upside-down now and certainly, beneath the most fashionable repackaging of biology in terms of altruism and ultra-sociality today, many things (especially at the conceptual level) remain continuous with the 1970s, as I will try to illustrate in the final section. On the other hand, however, it cannot be denied that, since the time of *The Selfish Gene*, a number of highly

visible technical changes in the evolutionary literature have occurred, and made room for the emergence of a different (or at least, broader) take on the relationship between biology and morality. A good analogy to explain continuities and discontinuities with the 1970s is to think in terms of *an increasingly widening circle* encompassing the possibility of altruism, cooperation and morality *within biology*. Taking as a starting point the above-mentioned 1970s' notions of selfishness and individualism as the only biologically plausible realities, and the subsequent explanation of altruism in terms of mere reciprocity or kin selection, then one can see a first attempt to enlarge this circle through the application of game theory and complex mathematical models to explain how cooperation can emerge and remain stable from a non-cooperative starting position (Axelrod and Hamilton, 1981; Axelrod, 1984; Axelrod and Dion, 1988); indeed, these accounts have expanded to such a point that, today, cooperation has been re-characterized as 'a third fundamental principle of evolution beside mutation and natural selection' (Nowak, 2006: 1563; Nowak, 2011). Parallel to these developments, a return to a more pluralistic view of natural selection has contributed significantly to the present scenario; this is the case in relation to the recent comeback of the notion of 'group selection', which was dismissed in the late 1960s because of its lack of rigour (Williams, 1996[1966]), and has today regained respectability (Sober and Wilson, 1998; Borrello, 2005; D. S. Wilson and E. O. Wilson, 2007), especially when conceived in cultural terms (Boyd et al., 2003). *Group selection*, *indirect reciprocity* and *network reciprocity*, along with the two previous notions of *kin selection* and *direct reciprocity*, have been recently described as the 5 basic mechanisms for the evolution of cooperation

(Nowak, 2006). A further contribution to a change of paradigm over the last decade has come from the work of experimental economists who have shown how, in ‘public goods’ games, unrelated people tend to exhibit high levels of cooperation, even in non-repeated interactions, as well as a propensity to punish norm-violators at their own cost, what is called ‘altruistic punishment’ (Fehr and Gächter, 2002; Fehr and Fischbacher, 2003; de Quervain et al., 2004). This array of experimental studies has shown how human altruism is a much broader phenomenon than would be expected according to theories of reciprocal altruism and reputation-based cooperation, and takes the form of so-called ‘strong reciprocity’ (Fischbacher and Gächter, 2002; Fehr and Fischbacher, 2003; Gintis, 2000; Bowles and Gintis, 2004). A final expansion of the circle of morality has come in recent years from the increasing number of studies emphasizing how altruism, helping behaviours and social networks can be ‘intrinsically beneficial’ to human health (Lozada et al., 2011; Brown et al., 2009; Cohen and Janicki-Deverts, 2009; Kok and Fredrickson, 2010), and how social cooperation (Rilling et al., 2002) and charitable donations are inherently rewarding experiences for the brain (Moll, Krueger et al., 2006).

All these technical innovations in evolutionary literature constitute the intellectual background upon which the present changes in the relationship between biology and morality are taking place. In a subtle but not irrelevant transformation of E. O. Wilson’s famous dictum ‘the time has come for ethics to be removed temporarily from the hands of philosophers and biologized’ (E. O. Wilson, 1975: 562), the sociobiological project of a ‘biologization of morality’² seems today

² Wilson dedicates to ethics a section of the final chapter of his *Sociobiology* but it is worth

increasingly transformed into a ‘moralization of biology’. By *moralization of biology* I here mean that in a significant fraction of the literature engaged today with biology and morality, some of the technical changes above mentioned, and other intellectual innovations that will be described next, are being reshaped and increasingly situated in a narrative for which biology becomes *an immediate source of goodness*. Far from being invoked as a justification for traditionally bleak views of human nature, the biology of the early 21st century becomes increasingly celebrated as the right place to look at when searching for the origin of pro-social and moral behaviours.

People familiar with a more skeptical view of morality and evolution may want to disagree at this point. First they would object that many of the technical changes described in this article *do not necessarily imply any slip* toward an idea of biology as a source of ‘goodness’.³ Second, they would remind us that, on the contrary, a very influential line of thought has concluded in favor of the idea of morality as a ‘collective illusion fobbed off on us by our genes’ (Ruse, 1991: 506); far from vindicating morality, evolutionism on this view contributes to a demystification of it (Joyce, 2001; Street, 2006). Third, the sceptics would object that there is a

remembering that the first chapter of his book is titled ‘The Morality of the Gene’. Beyond the names already mentioned in this article (like Wilson, Dawkins, Trivers, Hamilton and Ruse), the most important references of the period for a sociobiological elaboration of morality are: Barash (1977), Alexander (1979, 1987), Stent (1980). See Segerstråle (2001) for a general introduction to the sociobiology debate.

³ For instance, the evolutionary notion of cooperation is mainly developed as an intra-group notion and could technically be applied even to a cohort of Nazi soldiers who very cooperatively manage an extermination camp. Similarly, intergroup conflicts and warfare have been situated at the origin of our predisposition to behave altruistically in the attempt to explain why human altruism remains ‘parochial’, not expanding beyond the group boundary (Bowles, 2009). Also, it is worth noticing that in philosophically more refined appraisals of the concept of empathy the possibility that, at least in principle, empathy ‘can go awry’ rather than becoming the basis of pro-social behaviours is explicitly recognized. A torturer, or a businessman who wanted to defeat a rival, could both make use of ‘empathy’ for their own goals (Singer and Lamm, 2009).

tendentious confusion in my terminology, between two senses in which we can claim that humans are '*moral animals*'. In the first sense, being a moral animal means that 'the process of evolution has designed us to be social, friendly, benevolent' whereas in the second what is meant is that evolution has furnished us with a capacity 'to think in moral terms' and 'employ moral concepts' (Joyce, 2006: 3). For the sceptics, while not necessarily denying the first denotation (the human as an '*animal that is morally praiseworthy*'), it is only the second (the human as an '*animal that morally judges*') that has evolutionary significance. Finally, the sceptics will advance the usual warning that, when one comes to morality and nature, one cannot deduce an 'ought' from an 'is' as this amounts to committing the classical naturalistic fallacy.

In principle, these are all valid objections. However, I do not think that they exhaust all the possible variations that the notion of a biological morality may assume today, or that can be used as conclusive arguments against my case for a contemporary moralization of biology in a significant section of evolutionary writings. First, as philosopher Jesse Prinz has claimed (2007), the skeptical reading is not the only game in town. Starting from an evolutionary assumption, one might argue that a 'realist' interpretation of morality follows; that is, an interpretation that takes the moral phenomenon much more seriously and as 'truer' because it has been selected by evolution (see, for instance, Richards, 1986, 1987; Collier and Stingl, 1993; Rottschaefer and Martinsen, 1990). Second, though Joyce's preference for the notion of the human as an '*animal that morally judges*' is perfectly legitimate, a cartographer of the present scenario cannot but notice that it is instead the first horn of his distinction, the notion of the human as '*a morally praiseworthy*' animal,

by nature, that is more prevalent today (as I show below) – and the interesting intellectual question remains why it is so. Moreover, in spite of the ethical skepticism of authors like Ruse and Joyce, it must not be forgotten that, as historians have noticed (Bowler, 1986), evolutionary thought has always oscillated between a more utilitarian and a more romantic reading of morality and nature (Richards, 1987, 1999). The analysis I propose suggests that this second reading is coming again to the fore today, and in the final section I will explore some of the reasons for this intellectual shift. Finally, and more substantially, the apparently insuperable hiatus between ‘is’ and ‘ought’ is actually bridged, in the literature reviewed below, by the emergence of something that lies in-between descriptive and prescriptive statements: namely, a picture of human nature as *innately moral*, or, to use a classic nativist metaphor, made of marble with veins that incline to certain behaviors rather than others. Evolution, according to this view, has filled the first chapters of the book of human nature with a certain moral psychology that will favor, under normal conditions, not only a capacity to think in moral terms, but also a spontaneous inclination to display a vast range of pro-social and moral behaviors. The presence of this nativist vocabulary is one of the most visible features of the current reconceptualization of human nature in compassionate terms, and I will devote the final section to critiquing it.

To sum up, the intent of this article is twofold. First, I will delineate a preliminary profile for the constellation of authors who are circulating this revised picture of human morality, anchored solidly in its evolutionary and neurobiological foundations. In what follows I will describe three important contributions to this intellectual transformation:

the recent version of moral psychology offered by Jonathan Haidt; Frans de Waal's primatology; and the recently born field of the neuroscience of morality. Second, I will address the ambivalent status of this group of authors for whom today 'morality comes naturally'. I will focus both on the attractiveness of their message in terms of moralizing narratives and political hope, and the problematic epistemological assumptions that lie behind their research programs, especially in the light of the new findings in developmental and molecular biology.

Intuitions matter: The great shift in moral psychology

If the core notions of morality had remained what they were in the mainstream psychological literature of the second half of the 20th century, that is, mainly an affair regarding reason, socialization and the internalization of cultural norms, then little or no space at all would have been available for the current intense exchange between morality and biology. The crucial shift that has made a two-directional trading between nature and morality possible today has been the renewed emphasis on moral experience being the result of automatic, bodily processes. This has primarily occurred through a positioning of intuitions and emotions at the very core of moral judgement, in opposition to rationalistic views that saw them as irrelevant to ethical decision. Jonathan Haidt's *Social Intuitionist Model* (or SIM: Haidt, 2001, 2007, 2012) is perhaps the most accomplished representative of this new 'intuitionist' trend.

Haidt opens his very influential 'The Emotional Dog and Its Rational

Tail' (2001)⁴ with an exemplar story aimed to show how, in matters of morality, judgement is less 'a process of ratiocination and reflection' than something 'akin to aesthetic judgement' in which 'one sees or hears about a social event and one instantly feels approval or disapproval' (ibid.: 818). The story told by Haidt is the following: Julie and Mark are sister and brother; alone in a cabin near the beach on summer vacation, they decide to make love, just for one night, and without any risk of pregnancy as they use contraception.

They both enjoy making love, but they decide not to do it again. They keep that night as a special secret, which makes them feel even closer to each other. What do you think about that? Was it OK for them to make love? (2001: 814)

Haidt uses the way in which people respond to this scenario almost instantaneously, by feeling a 'quick flash of revulsion' and knowing 'intuitively that something is wrong' – in a 'I don't know, I can't explain it, I just know it's wrong' way – to build his model of moral psychology according to which 'quick, automated evaluations', under the form of 'intuitions', are the first cause of moral judgement. Moral intuition is a type of cognition but not reasoning Haidt claims, in an interpretation that clearly builds on Humean themes (2001: 814, 816). Whereas in a rationalistic view the central element in moral judgement would be a slow process of weighing up of the pros and cons of a certain dilemma,

⁴ Haidt has subsequently modified his 'emotion–cognition contrast', into a contrast between 'two kinds of different cognition': intuition and reasoning. 'Moral emotions', though remaining important, are for the last version of Haidt's model only 'one type of moral intuition, but most moral intuitions are more subtle; they don't rise to the level of emotions' (Haidt, 2012: 45). The intuition vs reasoning contrast is now framed by Haidt in terms of the elephant (automatic processes) and the rider metaphor, and Humean sentimentalism is transformed into an 'intuitionism'. Haidt has claimed that, in hindsight, 'The Emotional Dog' should have been called 'The Intuitive Dog' (ibid.: 48).

here moral evaluation is said to originate from fast, automatic processes ‘in which an evaluative feeling of good–bad or like–dislike appears in consciousness without any awareness of having gone through steps of search’ (Haidt, 2007: 998). The downplaying of the role of reasoning in this model is evident. For Haidt, moral reasoning within the individual is mainly a ‘post facto rationalization’ of what we have already experienced as gut feelings (2001: 817). From this perspective, more than as scientists or philosophers looking for truth, human beings appear like ‘intuitive lawyers’ or ‘politicians’ (Haidt, 2007: 999; 2012: 75) who are keen to justify what is already intuitively perceived. It is only in the social context, where people discuss their reasons and are responsive to the viewpoints of others, that moral reasoning becomes more important (Haidt and Bjorklund, 2007).

By focusing in particular on phenomena like ‘moral dumbfounding’ (the impossibility of offering a full rational justification for what is intuitively felt to be wrong), Haidt’s SIM aims to undermine rationalist models that have long dominated moral psychology:

Rationalist models made sense in the 1960s and 1970s. The cognitive revolution had opened up new ways of thinking about morality and moral development, and it was surely an advance to think about moral judgment as a form of information processing. But times have changed. Now we know (again) that most of cognition occurs automatically and outside of consciousness and that people cannot tell us how they really reached a judgment. Now we know that emotions are not as irrational, that reasoning is not as reliable, and that animals are not as amoral as we thought in the 1970s. Moral

emotions and intuitions drive moral reasoning, just as surely as a dog wags its tail [Haidt concludes]. (2001: 830)

What are the consequences of this shift for the position of morality in the sphere of knowledge? For Haidt this intuitionist turn is a vindication of E. O. Wilson's claim that morality, largely based on automatic, non-rational, evolutionary sources, can be more easily explained by *biologists than philosophers*. If the rationalist model of 'psychology forged its interdisciplinary links with philosophy and education' (2007: 998), Haidt's SIM favours a permanent channel of communication with scientific disciplines capable of studying how these automatic intuitions arise, focusing, for instance, on their evolutionary antecedents and neurobiological underpinnings. If moral judgement is no longer a matter of abstract, sophisticated reasoning, why should not one search for its predecessors in animal behaviors and the more ancient layers of our brain? After all, as Haidt remarks, these automatic processes from which moral intuitions spring are the same that have been 'running animal minds for 500 million years' (2012: 45). Following Haidt's intuitionist turn, morality leaves the shelves of philosophers and educators to reach the field of primatologists and neuroscientists.

Frans de Waal: Primatology and the evolutionary building blocks of human morality

Escaping Lorenz: From aggression to reconciliation

If Haidt's moral psychology is symptomatic of a shift in the conceptualization of morality without which no moralization of biology would be possible today, it is in the writings of the Dutch-born

primatologist Frans de Waal that one can find a true personification of this constellation of authors for whom today ‘morality comes naturally’. In an autobiographical passage of his 1996 *Good-Natured*, de Waal describes how, at the beginning of his career, he went to challenge ‘the funding floodgates for research on aggression’ that had been opened since the publication of Konrad Lorenz’s controversial *On Aggression*. While studying aggressive behaviours in long-tailed macaques, De Waal remembers:

What struck me most while sitting and waiting was how rarely these monkeys fought, even though they had a reputation for belligerence ... the *Gestalt* that gave me the key to my problem was an embrace and kiss between two chimpanzees shortly after a serious altercation. Since the embrace occurred between the chief opponents of the preceding fight, it struck me as a *reconciliation*. (1996: 163–4)

De Waal’s hugely influential research can be conceived of as a massive extension of this preliminary insight about reconciliation (de Waal and van Roosmalen, 1979) culminating in his exploration of conflict resolution and the study, more generally, of systems of reciprocity in primates. Upon this empirical work de Waal has elaborated his theoretical position, a full-frontal attack on what he has called the Veneer Theory of Morality, the idea – for de Waal iconically represented by Thomas Henry Huxley’s *Evolution and Ethics* (1893) – that morality is ‘a cultural overlay, a thin veneer hiding an otherwise selfish and brutish nature’ (2006: 10). De Waal is well aware of how this picture of morality,

which has been largely dominant in the writings of evolutionary biologists and science writers, is a profound betrayal of the Darwinian legacy, for Darwin himself understood the moral instinct as perfectly continuous with social instincts and emotional mechanisms of our evolved nature (Flack and de Waal, 2000). And it is exactly the Darwinian strategy to situate the origins of moral life entirely within the evolutionary framework that de Waal has tried to revive in his research-program: first, in terms of content, by expanding on Darwin's many observations of altruism and sympathy as phenomena not restricted to human life but very much present in the behaviors of many animal species; second, in terms of methodology, by looking at our closest evolutionary relatives to shed light on human higher faculties, according to a principle of 'evolutionary parsimony' for which it is wrong to create 'a double standard' of explanations for mechanisms that appear commonly shared by human and apes (1996: 64–5).

Exploring the foundations of the tower of morality

De Waal's contribution to the present reframing of the moral phenomenon has focused on the evolutionary antiquity of what he calls 'the building blocks of morality'. Drawing on different sources, from Aristotle to Westermarck and Kropotkin, for de Waal human beings are 'moral beings to the core' (2006: 56), born with a strong moral capacity designed by natural selection that 'has provided us with the psychological makeup, tendencies, and abilities to develop a compass for life's choices that takes the interests of the entire community into account' (ibid.: 58). De Waal's research has investigated at length these basic psychological tendencies, 'prerequisites' or 'antecedents' of

morality in primate life, contributing decisively to an already important literature on cooperation in animals (Dugatkin, 1997). Evidence for empathy and sympathetic concern in animals, the existence of group loyalty and helping tendencies in all species relying on cooperation, the presence of a system of reciprocity and a sense of social regularity in many primates, and even ‘inequity aversion’ (among brown capuchin monkeys: Brosnan and de Waal, 2003) have been for de Waal increasingly documented over the years but remain overlooked because of the exaggerated fear of anthropomorphism that characterizes research on animal emotions (2006: 24–5). For de Waal the several methods through which primates prevent and resolve within-group conflicts, from food-sharing to grooming, from peace-making to consolation, represent the ‘very building blocks of moral systems’ (1996: 3), evolutionarily ancient and pre-dating humanity. Far from being imposed by culture on an amoral natural substrate, human morality emerges from this reconstruction ‘firmly anchored’ (de Waal, 2006: 55) on these evolutionary building blocks. Differences in morality between humans and other animals are, for De Waal, only to be seen as differences of degree, not of kind. Following this Darwinian strategy, culture is seen by de Waal not as the ‘creator’ but ‘the modifier’ (Bonnie and de Waal, 2004: 214) of the ordinary bio-psychological mechanisms that occupy the first level, common to humans and animals, of the ‘tower of morality’ (2006). Along with this suggestive metaphor, de Waal proposes another image to convey his idea of the evolutionary antiquity of a human’s moral sense: a Russian doll ‘in which higher cognitive levels of empathy build upon a firm, hard-wired basis’ (2008: 287).⁵

⁵ As, for instance, the ‘Perception-Action Mechanism’ (PAM) that for Preston and de Waal underpins ‘phenomena like emotional contagion, cognitive empathy, guilt, and helping’ (2002: 4).

Even from this limited reconstruction, it is evident how De Waal's views have been crucial in the current two-directional movement for which morality is deeply relocated at 'the centre of our much-maligned nature' (1996: 218) and, in reverse, nature itself is increasingly reframed as a source of moral and pro-social behaviors. Although de Waal recognizes his debt to classical studies of kin selection (Hamilton) and reciprocal altruism (Trivers), his arguments for a morality firmly planted in the natural world appear much stronger, the result of a different way of understanding the interpenetration of the moral and the natural. Not by chance, de Waal's sources go well beyond the strict evolutionary tradition to include, for instance, the Confucian philosopher Mencius (372–289 BCE) with his belief in 'the immediacy and force of the sympathetic impulse' and his notion that 'humans tend toward the good as naturally as water flows downhill' (2006: 50–1).

The moral brain

Along with Haidt's moral psychology and de Waal's version of primatology, the third most relevant contribution to the current biological reframing of morality comes from neuroscience, and in particular the new emerging field of the neuroscience of morality, the study of the 'network of brain regions' (Moll, Zahn et al., 2005: 799) involved in moral cognition, emotions and judgement. The neuroscience of morality, which integrates insights from cognitive science, social psychology, evolutionary biology and anthropology, is a new discipline (the first fMRI study is dated 2001 [Greene, Sommerville et al., 2001]), but one with important historical roots, as the search for a 'moral brain' has characterized modernity from at least Gall's attempt to localize a

‘faculty of benevolence’ (Macmillan, 2000; Verplaetse, 2009). In the extremely variegated panorama of positions represented today within the frame of the neuroscience of morality – Moll, Zahn et al. (2005: 801–3) have recently counted 6 different approaches referring to this field – there are plausibly at least two shared conceptualizations that have profound consequences for the biologization of the moral phenomenon that is at stake in this article.

1 Validating the intuitionist turn

First, neuroscientific studies of morality have completed the revolution originating in Haidt’s SIM, offering a sort of *experimental validation* of the idea that automatic processes, often (but not always) emotionally laden, are at the center of moral experience (Greene and Haidt, 2002; Moll, de Oliveira-Souza, Eslinger et al., 2002; Greene, 2003). Although the roles of rationality and cognitive areas of the brain are certainly not omitted by neuro-studies of moral decision, many of the neuroscientific data have been used so far to claim that when one comes to matters of ethical deliberation, one should expect less from cold reasoning than from “‘gut feelings’” about what is right or wrong in particular cases’ (Greene, 2003: 847). As Joshua Greene, a co-author of the first fMRI study of moral judgement and a key-figure in the field, writes:

What turn-of-the-millennium science is telling us is that human moral judgment is not a pristine rational enterprise – that our moral judgments are driven by a hodgepodge of emotional dispositions, which themselves were shaped by a hodgepodge of evolutionary forces. (Greene, 2008: 72)

Though Greene is a proponent (Greene, 2003, 2008) of a ‘dual-process’ model, in which emotional and cognitive areas of the brain are in competition to deliver moral judgement and, philosophically speaking, he is very far from attributing epistemic authority to these kinds of affectively loaded ancestral intuitions (as ‘neural “is”’ is not ‘moral “ought”’: Greene, 2003) – his empirical work has nonetheless contributed robustly to shift attention from higher cognition areas to the ancient emotional mechanisms of the brain involved in moral decisions. Current experimental research further documenting how moral judgement can be affected by manipulation of emotional processes is extensive. From the study of utilitarian reactions in people with prefrontal cortex damage (Koenigs et al., 2007), to the ability of flashes of disgust to provoke more severe moral judgements in hypnotized people (Wheatley and Haidt, 2005), and finally the manipulation of moral responses through induction of positive affects (Valdesolo and De Steno, 2006), all these studies have further made the case for a stronger role of automatic, affective processes in moral judgement. In spite of Greene’s (2003) and Singer’s (2005) rejection of the normative value of these emotional responses, and the many words of caution coming from a number of moral philosophers (Joyce, 2008; Kahane and Shackel, 2008), it is undeniable that in other neuroscientific circles these emotional responses have been taken as much more reliable guides to moral behavior (Damasio, 2003: 147; see also Levy, 2007: 294–7). Such a re-collocation of the sources of morality into the automatic responses of our evolved nature is not without consequences on the image of nature itself. No longer seen as a passive recipient of a mostly rational moral thinking, built by education or socialization, or a neutral element at best

irrelevant to moral judgement, nature now becomes a powerful actor that *inclines* and *endows* human beings with a set of dispositions and tendencies. The renaissance of a nativist picture of the human as strongly inclined to certain moral and pro-social behaviors emerges, even more powerfully, from the exploration of a second critical notion coming from the emerging discipline of moral neuroscience.

2 The return of the moral sense

The notions that human beings are endowed not only with ‘a repertoire of emotions with a strong moral content’ but also with ‘a natural sense of fairness that permeates social perceptions and interactions’ (Moll, de Oliveira-Souza, Zahn et al., 2008b: 1; Moll, de Oliveira-Souza, Eslinger et al., 2002: 2730) seem central to most of the authors working on the neuroscience of morality. Underneath the different languages in which the moral brain is explored today, a recourse to a strong nativist language often associated with themes of the moral sense school⁶ seems to be one of the most powerful candidates to occupy the new territory of the neuroscience of morality, though this hegemony remains highly contested (Churchland, 2011). It is, however, the prevalence of this combination of sentimentalism and nativism that gives a moralizing flavour to much of the literature reviewed here. In Moll et al., for instance, this principle takes the form of what they call a ‘moral sensitivity’ (Moll, de Oliveira-Souza, Eslinger et al., 2002; Moll, de Oliveira-Souza, Krueger et al., 2005; Moll, de Oliveira-Souza and Zahn,

⁶ Explicit references to the philosophical framework of the ‘moral sense’/‘moral sentiments’ tradition appear, among the authors reviewed in this work, in de Waal (1996, 2006); Flack and de Waal (2000); Moll, de Oliveira-Souza and Zahn (2008a), Moll, de Oliveira-Souza, Zahn and Grafman (2008b); Haidt (2001); Greene (2008); Damasio (2003), although this latter emphasizes also the limitations of the ‘too optimistic’ Scottish Enlightenment view (2003: 319–20).

2008a; Moll, de Oliveira-Souza, Zahn et al., 2008b), a mechanism by which everyday events are automatically tagged with moral values (Moll, de Oliveira-Souza, Krueger et al., 2005: 803; Moll, de Oliveira-Souza, Zahn et al., 2008b: 5). Emerging from ‘a sophisticated integration of cognitive, emotional, and motivational mechanisms’ (Moll, de Oliveira-Souza and Zahn, 2008a: 161) this moral sensitivity is believed to guide ‘humans to quickly apprehend the moral implications of a social situation’ (ibid.: 165). In the writings of the French neuroscientist Jean-Pierre Changeux, this innate moral sensitivity becomes a ‘predisposition to ethical deliberation’ (Changeux in Changeux and Ricoeur, 2000: 179) that the human brain naturally exhibits. Just as our brains have neural predispositions and constraints that help us extract from the world a certain basic number of ‘natural’ colours (Changeux, 2004: 301), the same can be said at the level of morality: evolution has built into the human brain ‘not only a moral sense but also all the predispositions of moral evaluation necessary to ethical deliberation’ (Changeux in Changeux and Ricoeur, 2000: 190). Even for an author as overtly sceptical of the ethical authority of our automatic intuitions as Joshua Greene, the principle of an innate moral sensitivity remains at the forefront. The notion of ‘a powerful “moral sense”’ that compels us to engage (Greene, 2008: 60) is conceptualized either in the form of a ‘moral button’ (Greene, Cushman et al., 2009) inside our brain that gets pushed under certain circumstances of evolutionary significance, or as a ‘prepotent emotional response that drives people to say “no”’ in a scenario like the footbridge case (Greene, 2008: 45). The American neuroscientist Michael Gazzaniga has presented a stronger version of this principle: here Moll’s soft notion of an automatic tagging of everyday

experience in moral terms becomes the more audacious idea that the brain is ‘ethical’ (2005). For Gazzaniga, neuroscientific explorations are bringing to light today the existence of ‘a universal set of biological responses to moral dilemmas, a sort of ethics, built into our brains’. This ‘innate moral-ethics system’ is a natural product of ‘the brain’s automatic responses’ and takes the form of an evolved ‘universal moral compass’ capable of positively influencing our everyday decisions (2005: 55, 167–8). Finally, in what is arguably the most ambitious version of moral nativism, the *Universal Moral Grammar* (UMG) framework, the human brain is said to contain a ‘computationally complex “moral grammar”’ (Mikhail, 2008: 81), an unconscious mechanism that allows people to ‘evaluate a limitless variety of actions in terms of principles that dictate what is permissible, obligatory, or forbidden’ (Hauser, 2006: 36). In this explicit application to morality of the Chomskyan principles of linguistics, emotions still play a role, but a less important one than in other versions of moral psychology: here, rather than ‘generating a moral judgement’, emotions are conceived of only as weights reinforcing our intuitions (ibid.: 31). What remains common, however, between the UMG paradigm and other more emotion-oriented versions of moral psychology, is the nativist belief in a ‘moral instinct’ ‘that naturally grows within each child, designed to generate rapid judgements about what is morally right or wrong’. This ‘right impulse’ (ibid.: xvii, 419), on which moral judgement is automatically based, defines universally innate constraints for morality.

Attractiveness and ambiguity of the ‘morality-comes-naturally’ view

After the ‘rationalistic tangent’

The present repositioning of the moral phenomenon at the centre of human nature, and its emotional core in particular, signals an important intellectual shift, especially after the long prevalence in modernity of philosophical views that have dissociated morality from emotions, the body and intuitions. Such a challenge to the “‘two-hundred-year’” rationalistic tangent that has started after Hume’ (Haidt, 2012: 116) clearly emerges from the selection of authors reviewed in this article. Along with these positions, Antonio Damasio’s reappraisal of the role of gut feelings (*somatic markers*) as reliable guides of moral judgement (2006[1994]) could have been given a section itself, but nevertheless the collection of voices examined here adequately illustrates the present change in intellectual history. This turn cannot be underestimated and before moving to a critical review of its language it seems fair to concede it some merits. First, in the relationship between biology and social theory, it has to be recognized that, because of the present positive reassessment of altruism as a genuine evolutionary possibility, social scientists who now want to be in touch with biological facts are no longer confronted, as they were when the selfish-gene view was prevalent, with the ‘unattractive alternative’ of ‘either insulating a large part of human behaviour from biological explanation or . . . explaining all human behaviour in terms of individual self-interest’ (Sterelny and Griffiths, 1999: 12). The social sciences have started over at least two decades to appreciate the possibility of a different take on the relationship between altruism and biology, in which altruistic behaviours

are seen as an integral part of biological/social facts (Frank, 1988; Piliavin and Charng, 1990). Second, in the internal debates of moral philosophy, the present turn toward affect-laden intuitions certainly represents a healthy extension of what counts as the moral domain. New dimensions and sources that were removed from the rationalistic narrowing of morality are now included again (Haidt and Kesebir, 2010). Third, the emergence of more than two decades of empirical work on the affective basis of moral judgement has given us a solid body of evidence on the contributions of emotions to moral decision-making. Moral rationalism in the future will need to rethink some of its presuppositions and make room for this visceral, embodied dimension of moral experience.

A critique of the conceptual framework

However, while this sentimentalist component of morality seems a healthy message to take home, the conceptual framework in which many of these findings have been located by the three research programs examined in my cartography is much more questionable. I want now to come back to what I said at the beginning of this article; that is, that the sociobiological project of a biologization of morality launched by E. O. Wilson almost 40 years ago in his influential *Sociobiology* (1975) has increasingly been reversed today into a moralization of biology. How should we evaluate this reversal? Does the present constellation of authors reviewed here represent a break with the speculations of the 1970s? Is the view of an innately moral human nature the champion of a new biology compared with the time of E. O. Wilson and Dawkins? My conclusion has to be mixed: whereas in terms of *content* the constellation

of authors reviewed here represents a genuine break with the selfish-gene biology of the 1970s, in terms of *epistemological framework*, many things have remained continuous with the past. Rather than making a radical change, the authors reviewed here produce only a permutation of the vocabulary of biology of the 1970s:⁷ we have moved from the dark to the bright side of human nature, while preserving a ‘conceptual scaffolding’ (Meaney, 2001) that is increasingly out of touch with the new postgenomic (Stotz, 2006; Stotz, Bostanci et al., 2006; Stotz, 2008; Dupré, 2012), developmental (Pigliucci, 2001; West-Eberhard, 2003; Robert, 2004) and epigenetic view of biology (Jablonka and Lamb, 1995, 2005; Francis, 2012; Carey, 2012) that has made its way into the life-sciences since the beginning of this century. I do not mean to generalize or offer a caricature of the three programs being investigated. Each of these programs is different and needs analytic distinction and, in several places, there are undeniably efforts to make room for a more refined epistemology. However, in spite of these endeavours, Haidt’s moral psychology, de Waal’s primatology and the nativist version of the neuroscience of morality tend to remain caught *in a static view of ‘the biological’* that has become increasingly difficult to justify in the light of contemporary knowledge. Let us take, for instance, the nativist vocabulary that is so profusely used in these three programmes. Nativism has certainly been predominant in recent decades, especially in psychology and cognitive science (Carruthers et al., 2005–9), and it is not surprising therefore that a nativist wave has reached the field of morality today. However, other disciplines have been less impressed by

⁷ As confirmed, for instance, by the celebration of E. O. Wilson as a prophetic figure (2012: 32) who got the ‘big picture right’ (2007), in many of J. Haidt’s writings (cf. also the same adoption of the term ‘new synthesis’ as a title of one of his major articles: Haidt, 2007).

the results of this neo-nativist return. A ‘strong sceptical tradition’ (Griffiths, 2009) with roots in philosophy (Cowie, 1999; Prinz, 2012), ethology (Lehrman, 1953, 1970; Bateson, 1991; Bateson and Martin, 1999), and above all developmental biology (Oyama, 2000a[1985], 2000b; West and King, 1987; Bateson, 1991; Griffiths and Gray, 1994; Gottlieb, 1997; Griffiths, 2002; Moore, 2003; Oyama et al., 2001) has always been critical of many nativist assumptions. In these last few years, this skeptical approach has become increasingly important, making the use of the same concept of innateness deeply problematic. In the last decade philosophical critiques of innateness, for instance, have convincingly emphasized the irretrievable ambiguity of the term (Griffiths, 2002, 2009; Mameli and Bateson, 2006, 2007; Mameli, 2008; Linnquist et al., 2011) claiming that the notion of innateness ‘conflates different properties, properties that, according to best current biological and psychological knowledge, need to be kept distinct’ (Mameli and Bateson, 2011). In the most extensive study on the topic, Mameli and Bateson have analyzed 26 different candidates for a scientific definition of ‘innate’ (from ‘not learned’ to ‘genetically influenced’, from ‘heritable’ to ‘lacking plasticity’), finding all of them problematic and open to an abundance of counter-examples (Mameli and Bateson, 2006). Rather than a ‘cluster’ (a set of coherently co-occurring properties), the concept of innateness resembles what has been called a ‘clutter’ (Mameli, 2008), as it ‘conflates theoretically useful properties that scientists have found to be distinct’, exactly like what happened to the concept of jade in chemistry in the 19th century (Mameli and Bateson, 2011). Critiques inspired by recent advances in developmental biology and neuroscience have also shown how the ambiguity of the term renders

‘dubious any neat division of traits into those that are innate and those that are acquired through experience’ (Suhler and Churchland, 2011: 2105). Such a neat dichotomy appears to be the legacy of a vernacular, pre-scientific language, which seems to ‘come naturally’ to the human mind (the folk-biological concept of innateness: Griffiths, 2002; Bateson and Mameli, 2007; Griffiths et al., 2009), but which stands today ‘in the way of a genuine evolutionary understanding of human behavioural and psychological diversity’ (Linguist et al., 2011). In this context, many have suggested that the only possible outcome is to abandon the notion of innateness: there is too wide a gap between the nativist vocabulary and the new discoveries in developmental and molecular biology and neuroscience (Buller, 2006; Mameli and Papineau, 2006; Suhler and Churchland, 2011). Even authors who try to rescue the concept of innateness recognize the difficulty of this task and remain wary of the limitations of the concept (Samuels, 2002); others tend to suggest a critical and deflationary use of it, especially when applied to human behaviors (Shea, 2012). It goes beyond the scope of my article to analyze in detail the nativist/empiricist controversy in moral philosophy, a debate that in modern times goes back at least to Darwin and Mill. This debate is very much alive today (Joyce, 2013), as can also be seen in the intellectual contributions of the three research programs examined in this article, but it seems quite telling that an increasing number of authors who align themselves with the ‘Humean revival’ (Sterelny, 2010; Prinz, 2007, 2008, 2009, 2012) do not feel at ease with its neo-nativist framework and accept various versions of moral sentimentalism without embracing innateness or modularity, or at least only very modest versions of it (cf. also Griffiths, 1999; Nichols, 2002, 2004; Machery and

Mallon, 2010). Instead of revisiting these critiques, however, which often focus on the degree of innateness of moral or emotional predispositions, or the significance of framing morality in a modular language (Suhler and Churchland, 2011), I want to call attention to a problem that has become increasingly important in the last few years for a nativist epistemology. My argument is that, even in its mildest forms, as in the case of Gary Marcus' account of innateness (2004, 2005) whose conceptual framework Jon Haidt adopts for his SIM, the nativist vocabulary emerging from this and other programs relies on a view of the gene that is becoming *no longer plausible in contemporary biology*. Even in Marcus, who correctly avoids any talk of hard-wiring and fixity in favour of more plastic notions of pre-wiring and flexibility, the gene remains represented as an 'autonomous agent' (2004: 59), as something 'essential' (ibid.: 106) that 'guides', 'governs' and 'establishes' (2005: 31) developmental processes. In spite of the appreciable refinement of his analysis (Mameli and Papineau, 2006), the gene in Marcus' account remains more similar to a monarch, something that is ontologically, temporally and informationally privileged (or independent) over supposedly non-genetic factors, like experience or learning. His definition of innate as 'organized in advance of experience' (2004: 40) on which Haidt relies for his theory (Haidt and Joseph, 2007; Haidt, 2012) reflects exactly this primacy and the subordinate role of experience as a mere refinement of what is already created by genes (Lewkowicz, 2011). Such a pre-deflationary view of the gene squares poorly with the *context-dependent* view of the gene that is making its way into contemporary biology (Fox Keller, 2000; Oyama et al., 2001; Moss, 2003; Robert, 2004; Mameli, 2005; Griffiths and Stotz, 2007; Barnes and

Dupré, 2008; Parry and Dupré, 2010; Lewkowicz, 2011). The new conceptualization of the gene is dynamic and ‘perspectival’ (Moss, 2003); it addresses genes as ‘always determined by their cellular context’ (Mameli, 2005), ‘embedded inside cells and their complex chemical environments’ that are, in turn, embedded in organs, systems and societies (Lewkowicz, 2011). On this new post-genomic view, ‘the emergence of a new structure and/or function is due to bi-directional horizontal interactions’ (Lewkowicz, 2010), ‘the result of an immensely complex cascade of bottom-up and top-down co-acting influences’ (Karmiloff-Smith, 2009). This new conceptualization of the gene profoundly affects any residual idea of innateness, while extending the concept of biological inheritance (Mameli, 2005; Jablonka and Lamb, 2005). Genes are now seen as ‘catalysts’ more than ‘codes’ (Elman et al., 1996), ‘followers’ rather than ‘leaders’ (West-Eberhard, 2003), generated by interactions and not pre-existing developmental processes (Robert, 2004). ‘Genes-plus accounts of interaction’ (ibid., 2004) are no longer tenable, and constructions in which genes are seen to write autonomously ‘the first draft’ of the brain ‘during fetal development’, as Marcus (2004) and Haidt (2012) claim, are equally untenable. This supposedly purely genetic first draft that will be then revised in a second stage by experience looks more like a legacy of the past than an analysis informed by present knowledge. As Michael Meaney wrote almost 10 years ago at the dawn of the current epigenetic revival of which he is one of the recognized fathers: ‘There are no genetic factors that can be studied independently [*or “in advance of” to speak the language of Marcus (author’s note)*] of the environment, and there are no environmental factors that function independently of the genome. At no

point in life is the operation of the genome independent of the context in which it functions.’ Moreover, ‘environmental events occurring at a later stage of development ... can alter a developmental trajectory’ rendering insignificant linear regression studies of nature and nurture (2001). Such non-linearity and reversibility of developmental processes make the nativist requests for ‘primitives’ (Samuels), ‘starting points’ (Landau), ‘endowments’ (neuroscience of morality), ‘foundations’ (Haidt), or ‘building blocks’ (de Waal), meaningless for developmental theorists (Spencer et al., 2009; Lewkowicz, 2011). All the ‘stratigraphic’ models of the biological as the first layer (*stratum* in Latin) upon which socio-cultural processes are grounded (Oyama, 2000a[1985], 2000b; Daston, 2004) are undermined here. There is no ‘privilege of the origin’ or ‘privilege of the foundation’ in giving a biological (rather than a psychological) explanation, but just another interesting resource to use in a dynamic construct.

Biology moralized

However, why should the dichotomous framework, which sets up an opposition between biology as a solid bedrock and cultural/psychological processes, persist in the light of the new epistemology of the gene? Philosophers of biology have often attributed such persistence to the fact that scholars who usually ‘know better’ occasionally lapse into epistemologically outmoded views (Griffiths, 1999; Linquist et al., 2011), possibly confused by notions like innateness that permit unjustified inferences too easily (Griffiths, 2002). While this is certainly a plausible explanation it does not rule out a second one, namely that this outmoded epistemology still pays political dividends today, making it

inconvenient to let it go. I refer to the returns that this stratigraphic view of biology still yields today in terms of political hope and optimism. Take, for instance, this passage in Frans de Waal's *The Age of Empathy*: 'Biology constitutes our greatest hope,' de Waal writes, 'one can only shudder at the thought that the humanness of our societies would depend *on the whims of politics, culture, or religion*. Ideologies come and go, but human nature is here to stay' (2009: 45; emphases added). Here the nature–nurture dichotomy is *politically invested in a contraposition between a solid and wise biology, validated by evolution, and the transient and arbitrary character of cultural and political processes*, seen as superficial and even whimsical. The validating function of this view and its operationalization in terms of optimism are reasserted at the end of the book. After contrasting his biological view with the disillusionments engendered by the failures of past narratives of emancipation (from Marxism to feminism to individualism) de Waal uses the antiquity of evolution to offer a guarantee for the firm foundations of the new biological morality: empathy is not 'like a toupee put on our head yesterday', de Waal writes, with the risk 'that it might blow off tomorrow. Empathy is part of a heritage as ancient as the mammalian line' engaging 'brain areas that are more than a hundred million years old':

I derive great optimism from empathy's evolutionary antiquity [de Waal concludes]. [I]t makes it a robust trait that *will develop in virtually every human being* so that a society can count on it and try to foster and grow it. It is a human universal. (2009: 208–9; emphases added)

De Waal's passage is far from being *sui generis*. Similar descriptions in which biology is depicted as solid bedrock, a firmer layer and a universal resource on which 'society can count' to anchor an otherwise menaced morality (or sociality) are quite a common idiom in the literature reviewed here.⁸ It is the special status that biology enjoys in such a hierarchical view that favors the proliferation of narratives in which 'the biological' would constitute a sort of primary resource that can guide and even correct the pathologies of the social (Gazzaniga, 2005: 54, 84; see also Damasio's invocation of a 'congenital neurobiological wisdom' [2003: 79]). Therefore, in spite of the growing body of scholarship that has undermined such vestigial views of the nature–nurture opposition, a dichotomous epistemology remains highly appealing due to its capacity to offer a naturalistic agenda at a time when better political offers seem to be lacking. Along with the epistemological failure to recognize the complexities of the new biology, *hope* is therefore the second key-player in the persistence of this stratigraphic view of biology and the moralizing tone it radiates. As Kim Sterelny and Paul Griffiths have aptly remarked: 'hope has been rather too fecund a father to belief in the debates on evolutionary theories of human behavior. Too few of those involved seem to be able to resist ideology and moralising' (1999: 317). This moralizing vein of biologicistic writings has typically received little attention by sociologists and philosophers (for one exception: Kaye, 1986) but is, in my view, a great part of the contemporary appeal of the new conceptualization of our evolved nature as a safe harbour for pro-

⁸ See, for instance, the notion that neurobiological findings may constitute a firmer platform for a new universalist ethics that might be able to ease some of the 'conflicts that cultural differences are apt to generate' (Changeux and Ricoeur, 2000: 276). Similar universalist aspirations are all over the neuro-scientific literature; see, for instance: Moll, de Oliveira-Souza, Krueger et al., 2005; Changeux, 1991; Gazzaniga, 2005; Boella, 2008; Changeux et al., 2010.

social behaviors (Young, 2012). The extent and breadth of this moralization are deeply correlated with the simplistic epistemology of what I called the stratigraphic (or foundational) view of biology: E. O. Wilson moralized profusely in his *On Human Nature* (2004[1978]: in particular, the last chapter) as evolutionary psychologists did two decades later, and as today happens with de Waal or Gazzaniga. However, to the extent that the new postgenomic epistemology will become more and more established, it can be expected that this moralizing attitude will be made increasingly more difficult to sustain than in the past, possibly favouring the emergence of less normative, more contingent and pluralistic views of the biological.

Notes

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References

- Alexander, R. (1979) *Darwinism and Human Affairs*. Seattle: University of Washington Press. Alexander, R. (1987) *The Biology of Moral Systems*. New York: Aldine De Gruyter.
- Axelrod, R. (1984) *The Evolution of Cooperation*. New York: Basic Books.
- Axelrod, R. and Dion, D. (1988) ‘The Further Evolution of Cooperation’, *Science* 242: 1385–90. Axelrod, R. and Hamilton, W. D. (1981) ‘The Evolution of Cooperation’, *Science* 211: 1390–6. Barash, D.

- (1977) *Sociobiology and Behavior*. New York: Elsevier.
- Barnes, B. and Dupré, J. (2008) *Genomes and What to Make of Them*. Chicago, IL: University of Chicago Press.
- Bateson, P. (1991) 'Are there Principles of Behavioural Development?', in P. Bateson (ed.) *The Development and Integration of Behaviour: Essays in Honour of Robert Hinde*. Cambridge: Cambridge University Press, pp. 19–39.
- Bateson, P. and Mamei, M. (2007) 'The Innate and the Acquired: Useful Clusters or a Residual Distinction from Folk Biology?', *Developmental Psychobiology* 49: 818–31.
- Bateson, P. and Martin, P. (1999) *Design for a Life*. New York: Simon & Schuster.
- Boella, L. (2008) *Neuroetica. La morale prima della morale* [Neuroethics: Morality before Morality]. Milan: Cortina.
- Bonnie, K. E. and de Waal, F. B. M. (2004) 'Primate Social Reciprocity and the Origin of Gratitude', in R. A. Emmons and M. E. McCullough (eds) *Psychology of Gratitude*. Cary, NC: Oxford University Press.
- Borrello, M. (2005) 'The Rise, Fall and Resurrection of Group Selection', *Endeavour* 29: 43–7.
- Bowler, P. (1986) *Theories of Human Evolution: A Century of Debate, 1844–1944*. Baltimore, MD: Johns Hopkins University Press.
- Bowles, S. (2009) 'Did Warfare among Ancestral Hunter-Gatherers affect the Evolution of Human Social Behaviors?', *Science* 324: 1293–8.
- Bowles, S. and Gintis, H. (2004) 'The Evolution of Strong Reciprocity: Cooperation in Heterogeneous Populations', *Theoretical Population Biology* 65: 17–28.
- Boyd, R., Gintis, H., Bowles, S. and Richerson, P. J. (2003) 'The Evolution

of Altruistic Punishment’, *PNAS* 100: 3531–5.

Brooks, D. (2011a) ‘Nice Guys finish First’, *New York Times* (17 May): A27.

Brooks, D. (2011b) *The Social Animal: A Story of How Success Happens*.

London: Short Books. Brosnan, S. F. and de Waal, F. (2003) ‘Monkeys reject Unequal Pay’, *Nature* 425: 297–9.

Brown, S. L., Fredrickson, B. L., Wirth, M. M., Poulin, M. J., Meier, E. A., Heaphy, E. D., Cohen, M. D. and Schultheiss, O. C. (2009) ‘Social Closeness increases Salivary Progesterone in Humans’, *Hormones and Behavior* 56: 108–11.

Buller, D. (2006) *Adapting Minds: Evolutionary Psychology and the Persistent Quest for Human Nature*. Cambridge, MA: MIT Press.

Carey, N. (2012) *The Epigenetics Revolution: How Modern Biology is Rewriting Our Understanding of Genetics, Disease and Inheritance*. London: Icon Books.

Carruthers, P., Laurence, S. and Stich, S., eds (2005–9) *The Innate Mind*, 3 vols. Oxford: Oxford University Press.

Changeux, J.-P., ed. (1991) *Fondements Naturels de L’Ethique* [Natural Foundations of Ethics].

Paris: Odile Jacob.

Changeux, J. P. (2004) *The Physiology of Truth*. Cambridge, MA and London: Harvard University Press.

Changeux, J.-P., Damasio, A., Singer, W. and Christen, Y., eds (2010) *Neurobiology of Human Values*. Berlin: Springer.

Changeux, J. P. and Ricoeur, P. (2000) *What Makes Us Think?: A Neuroscientist and a Philosopher Argue about Ethics, Human Nature, and the Brain*. Princeton, NJ: Princeton University Press.

- Churchland, P. S. (2011) *Braintrust: What Neuroscience Tells Us about Morality*. Princeton, NJ: Princeton University Press.
- Cohen, S. and Janicki-Deverts, D. (2009) ‘Can We improve Our Physical Health by altering Our Social Networks?’, *Perspectives on Psychological Science* 4: 375–8.
- Collier, J. and Stingl, M. (1993) ‘Evolutionary Naturalism and the Objectivity of Morality’, *Biology and Philosophy* 8: 47–60.
- Cowie, F. (1999) *What’s Within? Nativism Reconsidered*. Oxford: Oxford University Press.
- Damasio, A. (2003) *Looking for Spinoza: Joy, Sorrow, and the Feeling Brain*. New York: Harcourt.
- Damasio, A. (2006[1994]) *Descartes’ Error: Emotion, Reason, and the Human Brain*. London: Vintage.
- Darwin, C. (1982[1871]) *The Descent of Man, and Selection in Relation to Sex*. Princeton, NJ: Princeton University Press.
- Daston, L. (2004) ‘The Morality of Natural Orders: The Power of Medea’, in G. B. Peterson (ed.) *The Tanner Lectures on Human Values*, vol. 24. Salt Lake City: University of Utah Press, pp. 371–92.
- Dawkins, R. (2006[1976]) *The Selfish Gene*. Oxford: Oxford University Press.
- de Quervain, D. J., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A. and Fehr, E. (2004) ‘The Neural Basis of Altruistic Punishment’, *Science* 305: 1254–8.
- de Waal, F. (1996) *Good-Natured: The Origins of Right and Wrong in Human and Other Animals*. Cambridge, MA: Harvard University Press.
- de Waal, F. (2006) *Primates and Philosophers: How Morality Evolved*, ed. S. Macedo and J. Ober Princeton, NJ: Princeton University Press.

- de Waal, F. (2008) 'Putting the Altruism back into Altruism: The Evolution of Empathy', *Annual Review of Psychology* 59: 279–300.
- de Waal, F. (2009) *The Age of Empathy: Nature's Lessons for a Kinder Society*. New York: Three Rivers Press.
- de Waal, F. and van Roosmalen, A. (1979) 'Reconciliation and Consolation among Chimpanzees', *Behavioral Ecology and Sociobiology* 5: 55–66.
- Dugatkin, L. A. (1997) *Cooperation Among Animals: An Evolutionary Perspective*. New York: Oxford University Press.
- Dupré, J. (2012) *Processes of Life: Essays in the Philosophy of Biology*. Oxford: Oxford University Press.
- Elman, J., Bates, E., Johnson, M., Karmiloff-Smith, A., Parisi, D. and Plunkett, K. (1996) *Rethinking Innateness: A Connectionist Perspective on Development*. Cambridge, MA: MIT Press.
- Fehr, E. and Fischbacher, U. (2003) 'The Nature of Human Altruism', *Nature* 425: 785–91. Fehr, E. and Gächter, S. (2002) 'Altruistic Punishment in Humans', *Nature* 415: 137–40.
- Fischbacher, U. and Gächter, S. (2002) 'Strong Reciprocity, Human Cooperation, and the Enforcement of Social Norms', *Human Nature* 13: 1–25.
- Flack, J. C. and de Waal, F. (2000) "'Any Animal Whatever'" Darwinian Building Blocks of Morality in Monkeys and Apes', *Journal of Consciousness Studies* 7: 1–29.
- Fox Keller, E. (2000) *The Century of the Gene*. Cambridge, MA: Harvard University Press.
- Francis, R. (2012) *Epigenetics: How Environment Shapes Our Genes*. New York: Barnes & Noble.

Frank, R. H. (1988) *Passions Within Reason: The Strategic Role of the Emotions*. New York: W. W. Norton.

Gazzaniga, M. S. (2005) *The Ethical Brain*. New York: Dana Press.

Ghiselin, M. (1974) *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.

Gintis, H. (2000) 'Strong Reciprocity and Human Sociality', *Journal of Theoretical Biology* 206: 169–79.

Goleman, D. (2006) *Social Intelligence: The New Science of Human Relationships*. London: Hutchinson.

Gottlieb, G. (1997) *Synthesizing Nature and Nurture: Prenatal Roots of Instinctive Behaviour*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Greene, J. D. (2003) 'From Neural "is" to Moral "ought": What are the Moral Implications of Neuroscientific Moral Psychology?', *Nature Reviews Neuroscience* 4: 847–50.

Greene, J. D. (2008) 'The Secret Joke of Kant's Soul', in W. Sinnott-Armstrong, Moral Psychology, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press, pp. 35–79.

Greene, J. D., Cushman, F. A., Stewart, L. E., Lowenberg, K., Nystrom, L. E. and Cohen, J. D. (2009) 'Pushing Moral Buttons: The Interaction between Personal Force and Intention in Moral Judgment', *Cognition* 111: 364–71.

Greene, J. and Haidt, J. (2002) 'How (and Where) does Moral Judgment work?', *Trends in Cognitive Sciences* 6: 517–23.

Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M. and Cohen, J. D. (2001) 'An fMRI Investigation of Emotional Engagement

in Moral Judgment’, *Science* 293: 2105–8.

Griffiths, P. E. (1999) *What Emotions Really Are: The Problem of Psychological Categories*. Chicago, IL: Chicago University Press.

Griffiths, P. E. (2002) ‘What is Innateness’, *The Monist* 85: 70–85.

Griffiths, P. E. (2009) ‘The Distinction between Innate and Acquired Characteristics’, in *Stanford Encyclopedia of Philosophy*. Stanford, CA: Metaphysics Research Laboratory, Stanford University, accessible @: <http://plato.stanford.edu/entries/innate-acquired/>

Griffiths, P. E. and Gray, R. D. (1994) ‘Developmental Systems and Evolutionary Explanation’,

Journal of Philosophy 6: 277–304.

Griffiths, P. E., Machery, E. and Linquist, S. (2009) ‘The Vernacular Concept of Innateness’, *Mind & Language* 24: 605–30.

Griffiths, P. E. and Stotz, K. (2007) ‘Gene’, in M. Ruse and D. Hull (eds) *Cambridge Companion to Philosophy of Biology*. Cambridge: Cambridge University Press, pp. 85–102.

Haidt, J. (2001) ‘The Emotional Dog and Its Rational Tail: a Social Intuitionist Approach to Moral Judgment’, *Psychological Review* 108: 814–34.

Haidt, J. (2007) ‘The New Synthesis in Moral Psychology’, *Science* 316: 998–1002.

Haidt, J. (2012) *The Righteous Mind: Why Good People Are Divided by Politics and Religion*.

New York: Allen Lane.

Haidt, J. and Bjorklund, F. (2007) ‘Social Intuitionists answer Six Questions about Morality’, in W. Sinnott-Armstrong (ed.) *Moral Psychology*, vol. 2, *The Cognitive Science of Morality*. Cambridge, MA:

MIT Press, pp. 181–217.

Haidt, J. and Joseph, C. (2007) ‘The Moral Mind: How 5 Sets of Innate Moral Intuitions guide the Development of Many Culture-Specific Virtues, and Perhaps Even Modules’, in P. Carruthers, S. Laurence and S. Stich (eds) *The Innate Mind*, vol. 3. Oxford: Oxford University Press, pp. 367–91. Haidt, J. and Kesebir, S. (2010) ‘Morality’, in S. T. Fiske, D. T. Gilbert and G. Lindzey (eds)

Handbook of Social Psychology. Oboken, NJ: Wiley, pp. 797–832.

Hamilton, W. D. (1964) ‘The Genetical Evolution of Social Behavior I and II’, *Journal of Theoretical Biology* 7: 1–52.

Hauser, M. (2006) *Moral Minds: How Nature Designed Our Universal Sense of Right and Wrong*. New York: HarperCollins.

Jablonka, E. and Lamb, M. J. (1995) *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. Oxford: Oxford University Press.

Jablonka, E. and Lamb, M. J. (2005) *Evolution in Four Dimensions*. Cambridge, MA: MIT Press.

Joyce, R. (2001) *The Myth of Morality*. Cambridge: Cambridge University Press.

Joyce, R. (2006) *The Evolution of Morality*. Cambridge, MA: MIT Press.

Joyce, R. (2008) ‘What Neuroscience can (and cannot) contribute to Metaethics’, in W. Sinnott-Armstrong, *Moral Psychology*, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press, pp. 371–94.

Joyce, R. (2013) ‘The Many Moral Nativisms’, in K. Sterelny, R. Joyce, B. Calcott and B. Fraser (eds) *Cooperation and its Evolution*. Cambridge, MA: MIT Press; penultimate draft read in press @:

http://www.victoria.ac.nz/staff/richard_joyce/acrobat/joyce_many.moral.nativisms.pdf

Kahane, G. and Shackel, N. (2008) 'Do Abnormal Responses show Utilitarian Bias?', *Nature* 452: section E5.

Karmiloff-Smith, A. (2009) 'Nativism versus Neuroconstructivism: Rethinking the Study of Developmental Disorders', *Developmental Psychology* 45: 56–63.

Kaye, H. L. (1986) *The Social Meaning of Modern Biology: From Social Darwinism to Sociobiology*. New Haven, CT: Yale University Press.

Keltner, D. (2009) *Born to Be Good: The Science of a Meaningful Life*. New York and London: Norton.

Keltner, D., Marsh, J. and Smith, J. A. (2010) *The Compassionate Instinct: The Science of Human Goodness*. New York: Norton.

Koenigs, M., Young, L., Adolphs, R., Tranel, D., Cushman, F., Hauser, M. and Damasio, A. (2007) 'Damage to the Prefrontal Cortex increases Utilitarian Moral Judgements', *Nature* 446: 908–11.

Kok, B. E. and Fredrickson, B. L. (2010) 'Upward Spirals of the Heart: Autonomic Flexibility, as Indexed by Vagal Tone, Reciprocally and Prospectively predicts Positive Emotions and Social Connectedness', *Biological Psychology* 85: 432–6.

Lehrman, D. S. (1953) 'Critique of Konrad Lorenz's Theory of instinctive Behavior', *Quarterly Review of Biology* 28: 337–63.

Lehrman, D. S. (1970) 'Semantic and Conceptual Issues in the Nature–Nurture Problem', in R. Aronson, E. Tobach, D. S. Lehrman and J. S. Rosenblatt (eds) *Development and Evolution of Behavior*. San Francisco, CA: Freeman, pp. 17–52.

Levy, N. (2007) *Neuroethics: Challenges for the 21st Century*. Cambridge:

- Cambridge University Press. Lewkowicz, D. J. (2010) 'Nature and Nurture in Perception', in *Sage Encyclopaedia of Perception*, ed. E. Goldstein Thousand Oaks, CA: Sage Publications, pp. 611–16.
- Lewkowicz, D. J. (2011) 'The Biological Implausibility of the Nature–Nurture Dichotomy & What It means for the Study of Infancy', *Infancy* 16: 331–67.
- Linquist, S., Machery, E., Griffiths, P. E. and Stotz, K. (2011) 'Exploring the Folk-biological Conception of Human Nature', *Philosophical Transactions of the Royal Society B* 366: 444–53.
- Lozada, M., D'Adamo, P. and Fuentes, M. A. (2011) 'Beneficial Effects of Human Altruism', *Journal of Theoretical Biology* 289: 12–16.
- Machery, E. and Mallon, R. (2010) 'Evolution of Morality', in J. M. Doris (ed.) *The Moral Psychology Handbook*. Oxford: Oxford University Press, pp. 3–46.
- Macmillan, M. (2000) *An Odd Kind of Fame: Stories of Phineas Gage*. Cambridge, MA: MIT Press.
- Mameli, M. (2005) 'The Inheritance of Features', *Philosophy of Biology* 20: 365–99.
- Mameli, M. (2008) 'On Innateness: The Clutter Hypothesis', *Journal of Philosophy* 55: 719–37.
- Mameli, M. and Bateson, P. P. G. (2006) 'Innateness and the Sciences', *Biology and Philosophy* 22: 155–88.
- Mameli, M. and Bateson, P. (2011) 'An Evaluation of the Concept of Innateness', *Philosophical Transactions of the Royal Society B* 366: 436–43.

- Mameli, M. and Papineau, D. (2006) 'The New Nativism: a Commentary on Gary Marcus's The Birth of the Mind', *Biology and Philosophy* 21: 559–73.
- Marcus, G. (2004) *The Birth of the Mind*. New York: Basic Books.
- Marcus, G. (2005) 'What Developmental Biology can tell Us about Innateness', in P. Carruthers, S. Laurence and S. Stich (eds) *The Innate Mind*, vol. 1. Oxford: Oxford University Press, pp. 23–33.
- Meaney, M. J. (2001) 'Nature, Nurture, and the Disunity of Knowledge', *Annals of the New York Academy of Sciences* 935: 50–61.
- Mikhail, J. (2008) 'Moral Cognition and Computational Theory', in W. Sinnott-Armstrong, *Moral Psychology*, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press, pp. 81–91.
- Moll, J., de Oliveira-Souza, R., Eslinger, P. J., Bramati, I. E., Mourao-Miranda, J., Andreiuolo, P. A. and Pessoa, L. (2002) 'The Neural Correlates of Moral Sensitivity: a Functional Magnetic Resonance Imaging Investigation of Basic and Moral Emotions', *Journal of Neuroscience* 22: 2730–6.
- Moll, J., de Oliveira-Souza, R. and Zahn, R. (2008a) 'The Neural Basis of Moral Cognition: Sentiments, Concepts, and Values', *Annals of the New York Academy of Sciences* 1124: 161–80.
- Moll, J., de Oliveira-Souza, R., Zahn, R. and Grafman, J. (2008b) 'The Cognitive Neuroscience of Moral Emotions', in W. Sinnott-Armstrong, *Moral Psychology*, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press, pp. 1–17.

- Moll, J., Krueger, F., Zahn, R., Pardini, M., Oliveira-Souza, R. and Grafman, J. (2006) 'Human Fronto-Mesolimbic Networks guide Decisions about Charitable Donation', *Proceedings of the National Academy of Sciences* 103: 15623–8.
- Moll, J., Zahn, R., de Oliveira-Souza, R., Krueger, F. and Grafman, J. (2005) 'The Neural Basis of Human Moral Cognition', *Nature Reviews Neuroscience* 6: 799–809.
- Moore, D. (2003) *The Dependent Gene: The Fallacy of 'Nature vs. Nurture'*. New York: Holt.
- Moss, L. (2003) *What Genes Can't Do*. Cambridge MA: MIT Press.
- Nichols, S. (2002) 'Norms with Feeling: Toward a Psychological Account of Moral Judgment', *Cognition* 84: 223–36.
- Nichols, S. (2004) *Sentimental Rules: On the Natural Foundations of Moral Judgment*. Oxford: Oxford University Press.
- Nowak, M. (2006) 'Five Rules for the Evolution of Cooperation', *Science* 314: 1560–3.
- Nowak, M. A. and with Highfield, R. (2011) *SuperCooperators: Evolution, Altruism and Human Behaviour, or, Why We Need Each Other to Succeed*. Edinburgh: Canongate.
- Oyama, S. (2000a[1985]) *The Ontogeny of Information: Developmental Systems and Evolution*. Durham, NC and London: Duke University Press.
- Oyama, S. (2000b) *Evolution's Eye: A Systems View of the Biology–Culture Divide*. Durham, NC and London: Duke University Press.
- Oyama, S, Griffiths, P. E. and Gray, R. D. (2001) *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge, MA: MIT Press.
- Parry, S. and Dupré, J. (2010) *Nature after the Genome*. Oxford: Wiley-

Blackwell.

Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: Johns Hopkins University Press.

Piliavin, J. and Charng, H.-W. (1990) 'Altruism: a Review of Recent Theory and Research',

Annual Review of Sociology 16: 27–65.

Preston, S. D. and de Waal, F. (2002) 'Empathy: Its Ultimate and Proximate Bases', *Behavioral and Brain Sciences* 25: 1–72.

Prinz, J. (2007) *The Emotional Construction of Morals*. Oxford: Oxford University Press.

Prinz, J. (2008) 'Is Morality Innate?', in W. Sinnott-Armstrong (ed.) *Moral Psychology*, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press.

Prinz, J. (2009) 'Against Moral Nativism', in D. Murphy and M. Bishop (eds) *Stich and His Critics*. Oxford: Blackwell, pp. 167–89.

Prinz, J. (2012) *Beyond Human Nature*. New York: Penguin/Norton.

Richards, R. (1986) 'A Defence of Evolutionary Ethics', *Biology and Philosophy* 1: 265–93. Richards, R. (1987) *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*.

Chicago, IL: University of Chicago Press.

Richards, R. (1999) 'Darwin's Romantic Biology: The Foundation of His Evolutionary Ethics', in

J. Maienschein and M. Ruse (eds) *Biology and the Foundations of Ethics*. Cambridge: Cambridge University Press, pp. 113–53.

Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S. and Kilts, C. D. (2002) 'A Neural Basis for Social Cooperation', *Neuron* 35: 395–405.

Robert, J. S. (2004) *Embryology, Epigenesis and Evolution: Taking Development Seriously*.

Cambridge: Cambridge University Press.

Rottschaefer, W. A. and Martinsen, D. (1990) 'Really taking Darwin Seriously: an Alternative to Michael Ruse's Darwinian Metaethics', *Biology and Philosophy* 5: 149–73.

Ruse, M. (1991) 'The Significance of Evolution', in P. Singer (ed.) *A Companion to Ethics*.

Oxford: Blackwell, pp. 500–10.

Samuels, R. (2002) 'Nativism in Cognitive Science', *Mind and Language* 17: 233–65. Segerstråle, U. C. (2001) *Defenders of the Truth: The Sociobiology Debate*. Oxford: Oxford

University Press.

Shea, N. (2012) 'Genetic Representation explains the Cluster of Innateness-related Properties',

Mind & Language 27: 466–93.

Singer, P. (2005) 'Ethics and Intuitions', *The Journal of Ethics* 9: 331–52.

Singer, T. and Lamm, C. (2009) 'The Social Neuroscience of Empathy', *Annals of the New York Academy of Sciences* 1156: 81–96.

Sinnott-Armstrong, W. (2008) *Moral Psychology*, vol. 3, *The Neuroscience of Morality: Emotion, Brain Disorders and Development*. Cambridge, MA: MIT Press.

Sober, E. and Wilson, D. S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.

Spencer, J. P., et al (2009) 'Short Arms and talking Eggs: Why We should No Longer abide the Nativist–Empiricist Debate', *Child Development*

Perspectives 3(2): 79–87.

Stent, G. S. ed (1980) *Morality as a Biological Phenomenon: The Presuppositions of Sociobiological Research*. Berkeley: University of California Press.

Sterelny, K. (2010) ‘Moral Nativism: a Sceptical Response’, *Mind & Language* 25: 279–97. Sterelny, K. and Griffiths, P. (1999) *Sex and Death: An Introduction to Philosophy of Biology*.

Chicago, IL: University of Chicago Press.

Stotz, K. (2006) ‘With Genes like That, Who needs an Environment? Postgenomics’ Argument for the Ontogeny of Information’, *Philosophy of Science* 73: 905–17.

Stotz, K. (2008) ‘The Ingredients for a Postgenomic Synthesis of Nature and Nurture’, *Philosophical Psychology* 21: 359–81.

Stotz, K., Bostanci, A. and Griffiths, P. E. (2006) ‘Tracking the Shift to “Post-Genomics”’, *Community Genetics* 9: 190–6.

Street, S. (2006) ‘A Darwinian Dilemma for Realist Theories of Value’, *Philosophical Studies* 127: 109–66.

Suhler, C. L. and Churchland, P. (2011) ‘Can Innate, Modular “Foundations” explain Morality? Challenges for Haidt’s Moral Foundations’, *Theory Journal of Cognitive Neuroscience* 23: 2103–16.

Trivers, R. (1971) ‘The Evolution of Reciprocal Altruism’, *Quarterly Review of Biology* 46: 35–57.

Valdesolo, P. and De Steno, D. (2006) ‘Manipulations of Emotional Context shape Moral Judgment’, *Psychological Science* 17: 476–7.

Verplaetse, J. (2009) *Localizing the Moral Sense: Neuroscience and the Search for the Cerebral Seat of Morality, 1800–1930*. Dordrecht:

Springer.

- Verplaetse, J., De Schrijver, J., Vanneste, S. and Braeckman, J., eds (2009) *The Moral Brain: Essays on the Evolutionary and Neuroscientific Aspects of Morality*. Dordrecht: Springer.
- West, M. J. and King, A. P. (1987) 'Settling Nature and Nurture into an Ontogenetic Niche', *Developmental Psychobiology* 20: 549–62.
- West-Eberhard, M. J. (2003) *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.
- Wheatley, T. and Haidt, J. (2005) 'Hypnotic Disgust makes Moral Judgments More Severe', *Psychological Science* 16: 780–4.
- Williams, G. C. (1996[1966]) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, NJ: Princeton University Press.
- Wilson, D. S. and Wilson, E. O. (2007) 'Rethinking the Theoretical Foundation of Sociobiology', *Quarterly Review of Biology* 82: 327–48.
- Wilson, E. O. (1975) *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.
- Wilson, E. O. (1978) *On Human Nature*. Cambridge, MA: Harvard University Press.
- Young, A. (2012) 'The Social Brain and the Myth of Empathy', *Science in Context* 25: 401–24.
- Zak, P. (2012) *The Moral Molecule: The Source of Love and Prosperity*. New York: Penguin.