Ten years ago E.O. Wilson, the Harvard entomologist, wrote a remarkably ambitious book called Consilience: The Unity of Knowledge, in which he predicted that the ever-accelerating insights of evolutionary biology would drive a fundamental convergence of the social and natural sciences. This essay is considerably less ambitious. I’d like to report on the really rather remarkable inroads into the law, and into the legal academy, made by post-Darwinian evolutionary thinking—thinking that is itself deeply resonant with the now well-entrenched law and economics movement. This resonance is beginning to shed light on the mysteries of human behavior, and therefore on the mysteries of human institutions, including law.

One point of clarification before I begin my survey. Most readers, when they see the phrase “law and biology,” probably think of the legal implications of medical advances, including issues like the patentability of genes, the use of fMRI and other brain imagining techniques to detect lying, or privacy and ethical issues related to the sequencing of the human genome. I label this constellation of issues “the law of
biology,” and although much exciting work is being done in this area, this is not what I mean, or most law and biology scholars mean, by the phrase “law and biology.”

Instead, what this discipline focuses on is the biology of law, that is, what an evolutionary perspective might say about human nature and the foundations of law. What is law? What is right and wrong? What is intentionality, when does a person act without intentionality, and when, despite acting intentionally, should a person’s acts be excused by the law? Are these entirely cultural constructs, as the proponents of the Standard Social Science Model have been trying to convince us for a hundred years? Or might there be universal evolutionary components wired into our brains that cause us to share a sense of right and wrong about core issues, a sense of blameworthiness and a sense of justice?²

Law and biology in this foundational sense is an interdiscipline whose time has most definitely come. Scientists, economists, lawyers and judges now regularly meet at interdisciplinary conferences, including the annual conferences held by the Gruter Institute for Law and Behavioral Research³ and by the Society for Evolutionary Analysis in Law (“S.E.A.L.”).⁴ Papers on law and biology are beginning to crack the most prestigious of scientific journals, including Nature, Science and the Royal Society’s Philosophical Transactions.⁵ The 2007 annual conference of the American Association

² Students in my law and biology class are often surprised to see that the first five sections cover philosophy, genetics, evolution, economics and neuroscience before we even begin to touch, at least expressly, on the legal implications of these perspectives.

³ See http://www.gruterinstitute.org/

⁴ See http://law.vanderbilt.edu/seal/

⁵ See, e.g., Bettina Rockenbach & Manfred Milinski, The Efficient Interaction of Indirect Reciprocity and Costly Punishment, 444 Nature 718 (December 7, 2006); Ernst Fehr & Simon Gachter, Altruistic Punishment in Humans, 415 Nature 137 (January 10, 2002); Samuel Bowles, Group Competition, Reproductive Leveling and the Evolution of Human Altruism, 314 Science 1569 (December 8, 2006);
for the Advancement of Science included a presentation titled “Does Neuroscience Challenge Moral and Legal Notions of Responsibility?” In October 2007, the MacArthur Foundation announced a $10 million three-year grant to fund The Law and Neuroscience Project, an interdisciplinary endeavor populated by neuroscientists, philosophers, legal theorists and judges.6

The discipline is also gaining a foothold in the nation’s law schools, where courses in law and biology have been or are being taught in at least a dozen law schools, including Colorado, Maryland, Pittsburgh, UCLA, Vanderbilt, Vermont, Washington and Yale. Law review articles mentioning the topic, which annually numbered in the handful as late as 1985, have sky-rocketed to more than 300.7

What in the world, reasonable readers might well ask, does biology, or economics for that matter, have to do with the law? The answer, most broadly, is that all three disciplines deal with the problems of how individuals make choices, how those choices affect society, and how, if at all, society’s institutions should react to those choices.


6 http://www.lawandneuroscienceproject.org/


The Convergence of Economics and Biology

Economics is the study of human behavior, admittedly often in a pricing context, and of the manner in which individual decisions accumulate into markets. Ever since Aristotle and Xenophon, humans have been puzzled by two economic mysteries: what is the nature of property and what is price? That is, do individuals have the right to “own” property, and what exactly are the indicia of such ownership? When they decide to sell their property does it have an intrinsic value? If not, then what is price?

Church thinkers in the middle ages continued to struggle with the morality of property ownership, principally over the question of whether the Church itself could own property. They also had fierce debates over price, and in particular over the theological meaning of “fair” interest rates. Two of the most important medieval schools of scholastic thought—the Dominicans and the Franciscans—arose largely over disagreements about the morality of Church property and the nature of price.8

At least in the West, post-feudal systems largely resolved the issue of the morality of property ownership, although of course innumerable issues continue to reside inside the question of the nature of ownership, to the chagrin of all first-year students of property law.

As for price, it took Adam Smith and his Scottish Enlightenment colleagues to solve its essential mystery (and, alas, Marx to re-confound it), and to put to rest the ancient notion that goods have any intrinsic value. Classical economics assumed people were self-interested in a rather narrow sense—that we all make decisions to maximize our net economic interest. Willing sellers and willing buyers agree to a price that reflects

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8 See generally JANET COLEMAN, A HISTORY OF POLITICAL THOUGHT FROM THE MIDDLE AGES TO THE RENAISSANCE 77-79 (Blackwell 2000).
nothing more than their own desires, which themselves are the products of their own calculations, albeit based on imperfect information, about maximizing their economic self-interest. The accumulation of all those somewhat arbitrary and largely unpredictable self-interests—what Smith called “the invisible hand”—produces markets that are fairly predictable using the tools of classical macro-economics.

But this *Homo economicus* view of the human species has always ridden a little uneasy, even with some classical economists, who sensed that the notion of “self-interest” might be much more complicated than maximizing the value of goods a person can accumulate. It doesn’t take more than a few moments of reflection to know that people often forego economic gain for other interests, including things like job satisfaction and commitment to family. The stereotype of the starving artist is resonant with us because it reminds us of the essential truth that there is much more to life than maximizing economic gain.

Indeed, even in situations in which these other externalities seem to be absent, humans still regularly confound classical economic theory by appearing to act much less selfishly than predicted. The most famous experimental example of unexplained economic altruism in this kind of context occurs in the so-called ultimatum game. In the most basic version of this game, two players, strangers to each other, are randomly labeled Player A and Player B. Player A is given $10, and both given the following instructions: Player A may offer anywhere from $0 to $10 to Player B, but if Player B rejects the offer then neither player gets anything. If Player B accepts, then each retains the agreed-upon division.
If we were really purely short-run self-interest machines, the most rational play (that is, the Nash equilibrium\(^9\)) is for Player A to offer $1, since he can predict that a rational Player B would rather have $1 than no dollars and will therefore accept. But of course that’s not what we humans actually do. Instead, we sense that Player B might be insulted if the offer is as low as $1, and may reject it even if it is “irrational” for him to do so. In effect, Player A makes a rational prediction about Player B’s “irrationality.”\(^{10}\) And that’s exactly how the ultimatum games gets played—and researchers have played it millions of times—across almost all cultures and demographics.

In industrial societies, the mean offer is around $4, and offers lower than $3 are frequently rejected.\(^{11}\) In pre-industrial societies, the mean offer is the equivalent of $2.60, and the variation is greater.\(^{12}\) But these results are still stunning. Even in the most primitive pre-industrial societies, people do not act in the ruthlessly “selfish” way Adam Smith predicted. Why not?

Economists now understand “self-interest” to be a complicated calculation from a myriad of variables, including strategic guesses about how competitors and other actors

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\(^9\) The Nash equilibrium is a mathematically rigorous description of the strategy in any sufficiently complex n-person non-zero sum game that is, roughly speaking, immune to changes in the other person’s strategy. See John Nash, Equilibrium Points in N-person Games, 36 PROC. OF THE NAT. ACAD. OF SCIENCES USA 48-49 (1950).

\(^{10}\) I put these in quotes because of course the essential lesson of these games is that our assumptions about what is “rational” and what is “irrational” depend on premises that classical economists have made much too narrow. As one of my students said to me after we played the game in class, and after he rejected the equivalent of a $2 offer (we played for candy), “It was worth more than two lousy pieces of candy to see that bum’s face when I rejected and deprived him of his eight pieces. That will teach him.” See generally Francisco Parisi & Vernon L. Smith (eds.), THE LAW AND ECONOMICS OF IRRATIONAL BEHAVIOR (Stanford 2005).

\(^{11}\) HERBERT GINTIS, GAME THEORY EVOLVING: A PROBLEM-CENTERED INTRODUCTION TO MODELING STRATEGIC BEHAVIOR 252-54 (Princeton 2000).

\(^{12}\) Joseph Henrich et al., In Search of Homo Economicus: Behavioral Experiments in Fifteen Small-Scale Societies, 91 AMER. ECON. REV. 73, 74-75 (2001).
in the social milieu might behave. In the end, it seems that we act as individuals not to maximize our individual economic accumulation but rather to maximize our individual happiness.\textsuperscript{13} And of course happiness itself can be a complex gnarl of selfishness, selflessness, emotion, incomplete information and even imperfect memory about how happy we’ve been in the past. This richer notion of “self-interest” explains the apparently altruistic behaviors classical economists could not explain.\textsuperscript{14}

Post-Darwinian biology took an eerily similar path. Many biologists (and, unfortunately, many non-scientists like Herbert Spencer and Oliver Wendell Holmes, Jr.\textsuperscript{15}) assumed that the ultimate products of the forces of natural selection would be animals “red in tooth and claw” as Tennyson put it, all built like sharks, to do nothing but kill, eat and reproduce. Relentless self-interest machines. Übermenschen.

But of course field biologists knew that the real world is not like that all. Natural selection has produced an unimaginable array of species, with no apparent rule that the newer the species the more aggressive. On the contrary, displays of aggression in some species are much more common than actual aggression. Cooperation is everywhere.\textsuperscript{16} Individual animals regularly sacrifice their immediate interests, and sometimes even their lives, for others, kin and non-kin alike. Early evolutionary theory could no more explain

\textsuperscript{13} See, e.g., Daniel Kahneman, Toward National Well-Being Accounts, 94 AMER. ECON. REV. 2429 (2004).

\textsuperscript{14} Kahneman, a psychologist, won the 2002 Nobel Prize in economics for, among other things, this important paradigmatic shift from thinking about self-interest as maximizing value to maximizing happiness.


\textsuperscript{16} See, e.g., LEE ALAN DUGATIN, COOPERATION AMONG ANIMALS (Oxford 1997).
this kind of altruism than classical economics could explain selfless economic behavior in the ultimatum game.

Then two biologists, W.D. Hamilton and Robert Trivers, did for the puzzle of biological altruism what neo-classical economists did for the puzzle of economic altruism. They demonstrated that under the right conditions, what seems to be “altruism” is in fact a strategic behavior that can maximize individual fitness. Hamilton showed that a set of genes that might give an animal a tendency to sacrifice its own welfare for the welfare of its kin could, depending on its breadth, flourish across generations.\(^\text{17}\)

Trivers showed that “altruism” need not even be directed at kin to be adaptive. In any system of sufficient complexity, behaviors that might in the short run seem to be maladaptive might well have an adaptive advantage when viewed in the long-run.\(^\text{18}\) It might have seemed like a good idea in the short-run for our Pleistocene ancestor to steal that cache of food gathered by the group earlier in the day. But he might get caught, and might be punished so severely (for example, by being ostracized from the group, or killed) that in the long run he’d be better off not stealing it.

Investigators since Hamilton and Trivers have been working out the details of these complex reciprocal systems, using the tools of evolutionary theory, ethnology, primatology, information theory and game theory, to develop a picture of human behavior, and human institutions, resonant with the central idea that social and anti-social behaviors alike have deep evolutionary roots.\(^\text{19}\) And as biologists and their


interdisciplinary partners learn more and more about the way the human animal makes happiness-maximizing decisions in complex social networks, insights about the meta-rules of those networks—law—are gaining traction.

**The Original Sin of Social Defection**

Social animals have evolved rules that determine their group membership, and even rules about which rules, when broken, should mean punishment. Indeed, that’s what it means to be a social animal.

Humans are intensely social. We emerged about 100,000 years ago from predecessor species that were themselves apparently intensely social. We’ve spent almost all of that time in small groups of less than 100, mostly related, individuals.

Tens of thousands of years of evolution under these conditions have attuned our brains to make us highly receptive to cooperation with fellow group members, but always constantly probing for, and defending against, any opening in which short-term selfishness will either go undetected or sufficiently unpunished to be worthwhile. “Free riding” is what both economists and biologists now call this anti-social behavior.

But don’t misunderstand. This isn’t aberrant, sociopathic behavior. This is the profound human struggle—the most original of original sins—built into every one of us by evolution: when do I cooperate with the group and when do I defect? Philosophy, religion, law, moral systems of all kind, are in some sense cultural echoes of this deeply imbedded evolutionary ambivalence.

For the human animal there is a second evolutionary challenge. For thousands of generations we have had only one significant predator: ourselves. This environment has
equipped us with a tendency to be profoundly suspicious of individuals not in our group. This tendency may explain many of the most intractable of human pestilences, including ethnic and racial disharmony, but, as discussed below, may also help explain the puzzles of consciousness and free will.\footnote{See text accompanying notes 58 to 62 infra.}

The Evolutionary Roots of Law and Economics

Both within and between groups, humans are and always have been incessant traders. The evolved brains of \textit{Homo exchangius}, as we might re-label ourselves, have allowed us not only to imagine the future, but also to be able to communicate sufficiently about it with each other to permit time-delayed reciprocity. Exchanges need not be limited to simultaneous barter. Five bushels of wheat could be exchanged for the promise of three skins in the future, or, eventually, for currency. Freed from the constraints of simultaneous barter, division of labor offered \textit{Homo exchangius} the prospect of virtually limitless exchange and the resulting creation of unimaginable wealth.

But what could poor \textit{Homo exchangius} do to increase the reliability of the promises of his generally cooperative but always probingly selfish brethren? Answer: make sure the group has institutions that make defecting more costly, or that are otherwise designed to foster trust. In this way, the law itself is coming to be seen as having emerged not as an arbitrary cultural construct but as an extension of our evolved natures as relentless free traders. Promises must be kept. Exchanges must be voluntary. Violations of these first two rules must be discouraged and serious violations punished.
These insights are driving many exciting legal applications, including new ways of looking at the purposes of the criminal law, the role of apology in both civil and criminal law, the roots of property law, the arguably rootless nature of intellectual property law, privacy and even the foundations of tort and contract.

In addition to these particular applications of evolution to law, many law and biology scholars are exploring even deeper foundational questions. Let me touch on three.

21 See, e.g., Ernst Fehr & E. Fischbacher, Third-Party Punishment and Social Norms, 25 EVOL. HUM. BEHAV. 63 (2004); Stephen J. Morse, New Neuroscience, Old Problems, in NEUROSCIENCE, AND THE LAW: BRAIN, MIND AND THE SCALES OF JUSTICE 157-198 (B. Garland, ed., Dana 2004); Robert A. Sapolsky, The Frontal Cortex and the Criminal Justice System, 359 PHIL. TRANS. ROY. SOC. (B) 1787 (2004); Hoffman & Goldsmith, supra note 7. Notice that an evolutionary perspective does not lead to a set of monolithic conclusions about these difficult issues. Professor Sapolsky argues that neuroscience may well shake the criminal law to its free-will roots, Professor Morse argues it will have no such impact, and Professor Goldsmith and I suggest it will reinforce, not challenge, the criminal law’s retributive roots.


23 See, e.g., Jeffrey E. Stake, The Property Instinct, 359 PHIL. TRANS. ROY. SOC. (B) 1763 (2004).

24 Unlike corporeal property, whose legal roots go back as far as recorded time, the law of intellectual property is relatively recent. Its first iteration—copyright—traces its origins to the 1500s, when the English monarch granted a monopoly to the stationers’ guild. PAUL GOLDSTEIN, COPYRIGHT’S HIGHWAY: FROM GUTENBERG TO THE CELESTIAL JUKEBOX 41-50 (1994). Does this mean we have an “instinct” for real and personal property but not an “instinct” for intellectual property? Perhaps. But another way to look at the difference is that intellectual property is just the application of older, traditional, property norms to a new species of property. See Note, The More Things Change, the More They Stay the Same: Copyright, Digital Technology and Social Norms, 56 STAN. L. REV. 531 (2003). No one would suggest, for example, that an owner of a residential condominium has any less “instinct” for defending that property from an intruder than an owner of a house. The difference in the legal contours of a particular species of property may mask a common, and presumably evolutionarily-based, set of values regarding its use. Others, including Richard Posner, have argued that the real roots of intellectual property law lie in privacy. See RICHARD A. POSNER, THE ECONOMICS OF JUSTICE 148 (Harvard 1981).


The Law of Law’s Leverage, Time-Delayed Rationality and the Universal Sense of Relative Blameworthiness

Owen Jones, who holds a joint appointment in the law school and the department of biology at Vanderbilt, has written extensively on what he has dubbed “the law of law’s leverage.” Early critics of the biological take on law often quite rightly accused law and biology scholars of violating Hume’s naturalistic fallacy—just because a human behavior, like rape, may have evolutionary roots does not mean it is right. Jones addressed the problem by making the simple observation that even if the law is viewed in the typical post-modern way as a cultural check on our basest impulses, it would be quite useful for us to know which of those impulses may have biological roots (and therefore may be more difficult to change) and which don’t. This could have practical, as well as descriptive, benefits, including the corollary that reputational punishment may be more effective in some circumstances than traditional incarceration.

Jones has also written at great length about the following problem: our biologically-driven behaviors evolved 100,000 years ago in an environment that is quite unlike the environment today. As a result, behaviors that may have been “rational” in the late Pleistocene—that is, adaptive—may seem completely irrational and maladaptive today. Jones calls this the problem of “time-shifted rationality.” As he puts it:

[W]e not only should allow for, but should indeed expect, that there will be times when a perfectly functioning brain—functioning precisely as it

27 In Hume’s language, the “is” is not necessarily the “ought.”


was designed to function--will incline us toward behavior that, viewed only in the present tense and measured only by outcomes in current environments, will appear to be substantively irrational. This is simply because the brain was designed to process information in ways tending to yield behaviors that were substantively rational in different environments than the ones in which we now find ourselves.30

For example, stress typically reduces people’s sex drive and ability to digest food, a result that seems to make no adaptive sense in the modern world. Just when we most need our esteem and strength, as the modern world closes in on us with things like divorces, lawsuits and business failures, our bodies seem programmed to desert us. But when one considers that this result was the product of an evolutionary environment in which an existential threat required all systems to focus on fight or flight, this partial shutdown response is perfectly rational.31 As Jones puts it, “most severe and survivable [threats 100,000 years ago] passed more quickly than multi-district litigation, divorce proceedings or corporate takeovers.”32

Like the law of law’s leverage, recognizing time-shifted rationality may help police, legislatures and even sentencing courts recognize that some behaviors, which on their face seem “irrational,” might be less amenable to corrective legal action than others. Is time-shifted rationality an excuse? Of course not. But it might mean, for example, that for some crimes we should reduce our emphasis on rehabilitation, and even on deterrence, and focus on punishment.33 For others, more socially-based forms of opprobrium, like shaming and apology, may be appropriate.

30 Id. at 1173.
31 Id.
32 Id.
33 See Hoffman & Goldsmith, supra note 7.
Finally, one of the most exciting areas of research is being done by criminologists exploring the universality of blameworthiness. Evolutionary insights are leading to a kind of post-Darwinian view of the central role of punishment (and mercy) as an embedded behavior critical to our evolution and, ultimately, our civilization. I was only half-joking when I responded to a questioner at a law and biology conference a few years ago who suggested that sometimes Johnny just can’t “help” himself when he robs a gas station, by saying that as a judge I just can’t “help” myself when I then punish Johnny. The urge to punish free-riders is as real, and as evolutionarily important, as the urge to free-ride. It is, in fact, at the core of what it means to be civilized. The challenge is to design legal institutions that can quantify the proper amount of just desert, and thus avoid the social costs of either under- or over-punishment.

One of the most serious challenges to this re-emergent retributionism is the problem of quantifying just desert. What Judge A thinks is a proper amount of punishment for a certain crime may be completely different from what Judge B thinks, or so goes this relativistic argument against any system grounded on just deserts. This belief that views of blameworthiness are highly variable has not only been an argument made at theoretical heights,\(^{34}\) it is the catechism behind sentencing guidelines.\(^{35}\)

But work being done by three scholars, Paul Robinson and Rob Kurzban at the University of Pennsylvania, and John Darley at Princeton, is challenging this relativistic view of blameworthiness, and is suggesting instead that there is widespread, and finely-

\(^{34}\) See, e.g. Bernard Bosanquet, Some Suggestions in Ethics 188, 203 (Kessenger 2007) [1919] (“There is no estimate which can determine degrees of moral guilt in actual individual cases. Such a thing is wholly inconceivable.”).

\(^{35}\) Stephen Breyer, The Federal Sentencing Guidelines and the Key Compromises upon Which They Rest, 17 Hofstra L. Rev. 1, 15-17 (1988) (“the Commission soon realized that only a crude ranking of behavior in terms of just deserts, based on objective and practical criteria, could be developed”).
tuned, agreement about the relative blameworthiness of different crimes. Robinson et al. wrote 24 crime narratives, and asked participants in the study to order them from least blameworthy to most.\(^{36}\) The results were breathtakingly uniform. Among the 246 participants, the pair-wise agreement was over 90%, and a more sophisticated statistical measure of overall agreement was even more impressive.

An equally astonishing aspect of this study is that this agreement about relative blameworthiness crossed economic, racial, ethnic, gender, political and other demographic lines. It seems all of us, at least those of us who are not sociopaths, have no trouble at all making very fine distinctions between the just deserts for different crimes, and exhibit widespread agreement about those distinctions.

Robinson et al. acknowledge that uniformity in relative blameworthiness does not always translate into uniformity in actual sentences, but they suggest this is largely an artifact of what they call the “problem of end point.” If the worst crime in Judge A’s jurisdiction carries a death sentence, and the worst crime in Judge B’s jurisdiction carries only 40 years, then the scales on which their presumably identical lists of relative blameworthiness are stretched will produce different sentences.

Of course, this is only a partial explanation of sentence disparity. Even if Judges A and B share the same end point, as federal judges have for the better part of a century, there is no doubt that the identical relative scales that Robinson et al. have posited can produce, and have produced, significant sentence variance.

But there is also no doubt that these results, if they hold, demolish the kind of “sentencing-by-tinkering-with-a-thousand-factors” approach of many sentencing guidelines. Judges know what crimes are more serious than other crimes, because all humans know that.

On a grander scale, this work may also go a long way toward rescuing neo-retribution from its relativistic critics. I send Johnny to prison because he deserves it, and because by going to prison he can earn his way back into the moral fold. Whether other judges agree with that theory or not, it looks like we all have a fairly uniform and refined sense of the difference between just and unjust deserts.

Law, Emotion and the Probabilistic Brain

There is a giant elephant in the living room of law and biology, and indeed in the whole New Synthesis of modern biology: brains, not genes, cause behaviors. How, exactly, are behavioral tendencies, let alone behaviors, encoded in brains? Very little is known about this process. The sheer complexity of the brain is the biggest hurdle. The

37 And in the post-Booker world, see United States v. Booker, 543 U.S. 220 (2005) (striking federal sentencing guidelines but leaving them in place as non-mandatory), a Congress considering returning to mandatory guidelines may want to consider that to do so may largely be an exercise in futility, even if the constitutional hurdles of Booker and its predecessors could be overcome.

38 With apologies to Hegel, who said it better:

[P]unishment is regarded as containing the criminal’s right and hence by being punished he is honored as a rational being. He does not receive this due of honor unless the concept and measure of his punishment are derived from his own act. Still less does he receive it if he is treated either as a harmful animal who has to be made harmless, or with a view to deterring and reforming him.

Georg Hegel, PHILOSOPHY OF RIGHT 71 (T.M. Knox trans., Oxford 1942) [1821].

39 Robinson, Kevin McCabe (a neuroeconomist from George Mason), Rene Marois (a neuroscientist from Vanderbilt, Frank Krueger (a neuroscientist from NIH), Owen Jones and I are currently designing experiments to run a version of the Robinson et al. study in an fMRI magnet, in an effort to identify the neural correlates of these shared intuitions of relative blameworthiness.
average human brain has a billion neurons, and each neuron connects on average to between 1,000 and 10,000 other neurons. Compare that level of complexity with the recently-completed full wiring diagram of the nematode, whose nervous system (one cannot call it a “brain”) has only 302 neurons.40

But the brain-to-behavior problem is much more than just a problem of combinatorics. It also packs the philosophical punch of treading near the black hole of free will and determinism. How can behaviors, or even “behavioral tendencies,” be inherited by humans if humans are agents operating with free will? It is no accident that the MacArthur Law and Neuroscience Project includes several prominent philosophers.41

Despite these calculational and philosophical hazards, many of the recent efforts in law and biology have focused on neuroscience. In fact, a whole new interdisciplinary, called neuroeconomics, is emerging to examine the physical processes that occur in the brain when humans face this ubiquitous question of whether to cooperate or defect. Moreover, it seems that every day or two, neuroeconomists and traditional neuroscientists alike announce that they have found neural correlates associated with a particular human behavior or perception, including, among many others, perceiving motion,42 seeing in 3-D,43 hunger,44 memory,45 hearing dissonant music,46 forming intentions,47 exercising self-

41 Judy Illes from the University of British Columbia, Walter Sinott-Armstrong from Dartmouth College, Gary Watson from the University of California Riverside, Phillip Pettit from Princeton University, Susan Wolf from the University of North Carolina, Gideon Yaffe from the University of Southern California, Joshua Greene from Harvard University and Adina Roskies from Dartmouth College.
42 Gene R. Stoner & Thomas D. Albright, Neural Correlates of Perceptual Motion Coherence, 358 NATURE 412 (July 30, 1992).
43 Ken-Ichiro Tsutsui, et al., Neural Correlates for Perception of 3D Surface Orientation from Texture Gradient, 298 SCIENCE 409 (October 11, 2002).
control, accepting or rejecting in the ultimatum game, social rejection, empathy, optimism, moral judgment and even consciousness.

As a very general principle, the brain-imaging work neuroscientists are doing is painting a picture of the brain that is very much unlike the picture we have held since Rene Descartes first posited a fundamental difference between “simple” behaviors and “complex” behaviors, or what we might also label “reflex” and “cognition.” The modern emergent picture is of a brain that recruits many different areas in complex, simultaneous and non-simultaneous cascades, and that involves seamless feedback loops between frontal “controls” and more primitive parts. It seems that the traditional

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46 Or, more accurately, listening to music that violates harmonic expectations. Nikolaus Steinbeis et al., The Role of Harmonic Expectancy in Violations in in Musical Emotions: Evidence from Subjective, Physiological and Neural Responses, 18 J. COGNITIVE NEUROSCIENCE 1380 (August 1, 2006).

47 Peter Nachev, et al., Volition and Conflict in Human Medial Frontal Cortex, 15 CURR. BIOL. 122 (2005).

48 Marcel Brass & Patrick Haggard, To Do or Not to Do: The Neural Signature of Self-Control, 27 J. NEUROSCIENCE 9141 (August 22, 2007);

49 Alan G. Sanfey, et al., The Neural Basis of Economic Decision-making in the Ultimatum Game, 300 SCIENCE 1755 (June 13, 2003).

50 Jaak Panksepp, Feeling the Pain of Social Loss, 302 SCIENCE 237 (October 10, 2003).

51 Tania Singer, et al., Empathy for Pain Involves the Affective But Not Sensory Components of Pain, 303 SCIENCE 1157 (February 20, 2004).

52 Tali Sharot, et al., Neural Mechanisms Mediating Optimism Bias, 450 NATURE 102 (November 1, 2007).


54 Ian Glynn, An Intriguing Door—The Neural Correlates of Consciousness, 413 NATURE 683 (October 18, 2001).

55 Descartes actually called the non-reflex category of behaviors the “soul.” Rene Descartes, L’Homme [Treatise on Man], (T.S. Hall, tr., Harvard 1972) [1649].
counterpoints “simple v. complex,” “reflex v. cognition” and even “emotion v. reasoning” are losing, if they have not already lost, all neurological distinction.

As a by-product of these neurological insights, law and biology scholars are doing lots of work on the role of emotion in law. Of course, it is not difficult to imagine why, as an evolutionary matter, our brains have come to be equipped with a seamless and interlinking way of being able to react without thinking when necessary (to flee that predator) or, perhaps less obviously, why emotion can be a kind of lubricant that prevents us from being hopelessly indecisive when we consciously ponder an important even if not life-threatening decision.

But the elephant’s still in the living room, because none of this work suggests any mechanism by which favored genes convert their behavioral benefits into the architecture of the brains they build. That is the $64,000 question of behavioral neuroscience, and although no gene-to-brain-to-behavior mechanism has yet been discovered, there is tantalizing evidence suggesting a solution, though it is not a solution that will please apostles of traditional free will.

Several neuroscientists have started to suggest that, just as it is becoming apparent that the distinction between “reflex” and “cognition” is artificial, perhaps the distinction between “determinate” and “indeterminate” is also artificial. Perhaps the brain—both in its “simple” and “complex” activities—is a probability machine rather than some contraption that inexplicably switches back and forth between reflexive/determinate outcomes (burn your hand, pull it back) and cognitive/indeterminate outcomes (how much to offer in the ultimatum game). Perhaps
all behaviors are represented in the brain by a set of probability distributions, which are then continuously influenced by the interaction between ultimate causes (the initial probabilities that evolution built into brains) and proximate causes (the particular environmental challenges brains are called upon to solve).

In this model, a “reflex” is just an extreme kind of probability distribution—one with a very high probability bunched near a single action, the response. When you burn your hand, it is extremely likely (but not determinate) that your brain will decide to pull the hand back. The high probability of that particular action masks its inherently indeterminate (and “cognitive”) character. Likewise, when you decide to offer a certain amount in the ultimatum game, you are randomly engaging a distribution of probable behaviors, though the probabilities are more evenly distributed over a wider range, leaving you with the conscious sense that you “decided” what to do. But in both cases, according to the probabilistic model, the particular “decision” is an indeterminate outcome bounded only by the probability distribution of all outcomes.

NYU neuroeconomist Paul Glimcher and his colleagues have performed a series of spectacular neurological experiments that suggest that the brain works exactly in this probabilistic way. Using a variety of neurobiological techniques to study the neural firings in the brains of monkeys and humans as they make decisions during various kinds of games, the experimenters found that when the strength and frequency of those firings are accumulated and plotted over time, they look virtually identical to the probabilistic outcomes in decision-making by individual humans over time—the so-called “utility

function” of modern economics. This is a remarkable result, suggesting an essential unity between the way a single brain makes a single decision, and the patterns that emerge when brains make many decisions over time.

Thus, although we cannot predict whether the brain of any particular person will offer $4 in the ultimatum game, we can surmise that the population-wide average of $4 reflects the fact that the brains in that population have a probability distribution for this behavior that peaks near $4. The genius of the probabilistic model is that it preserves the indeterminacy (free will?) of a particular individual’s behavior, while explaining the perfectly determinate behavior of large groups of individuals, or of a single individual over many trials. It also suggests the real possibility that some behaviors are heritable, because brains have of course been inherited.

**Free Will, Responsibility and Excuse**

But indeterminacy is hardly the same as free will. The model of the probabilistic brain may solve all kinds of difficult neuroscientific problems by treating free will as a kind of exhaust fume of randomness. This kind of stochastic view of “decision” making may not even bother most neuroscientists or modern philosophers. But it should bother the heck out of legal scholars and judges, since the law seems to be premised on notions of free will and responsibility. Here again, however, evolution may offer the glimpse of a way out.

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58 See, e.g., Sapolsky, supra note 21.
Without tumbling too far down the rabbit hole of free will and consciousness, let me just mention that lots of wonderful insights are being knitted together by biologically-informed thinkers who share the central evolutionary idea that, whatever the true nature of these difficult self-referential notions, they most likely are the products of evolution and therefore, at least at one time, had adaptive value.\textsuperscript{59} Blessed with incredible computing power and the ability to imagine that the future may depend on our present actions, human brains would lose much of their effectiveness if they didn’t also come equipped with the belief, illusion or not, that they are free to make decisions and that those decisions will matter. That is, a conscious ancestor, blessed and cursed with the feeling of free will, was much more likely to survive than one without these traits.

Think of a strong, action-oriented hunter, clear-headed and able to use his brain to figure things out, but fairly un-reflective. Now imagine a belly-button watching introvert obsessed with whether anything matters, whether he really has free will, whether it’s just all a dream. Which one do you think survived to pass on his genes to us?

There is also an important theory of mind component to the evolutionary story of consciousness and free will. As I’ve already mentioned, when we emerged as a separate species our principal predator was other humans.\textsuperscript{60} When our ancestor saw that stranger coming over the hill, he’d be much more likely to have survived if he had a strong belief

\textsuperscript{59} See, e.g., FRANCIS CRICK, THE ASTONISHING HYPOTHESIS: THE SCIENTIFIC SEARCH FOR THE SOUL (Scribner 1995); JOHN SEARLE, FREEDOM AND NEUROBIOLOGY: REFLECTIONS ON FREE WILL, LANGUAGE, AND POLITICAL POWER (Columbia 2006); MARY MIDGLEY, THE ETHICAL PRIMATE (Taylor & Francis 2007); Anthony Freeman, Keith Sutherland and Benjamin Libet, eds., THE VOLITIONAL BRAIN: TOWARD A NEUROSCIENCE OF FREE WILL (Imprint 2000).

\textsuperscript{60} See text accompanying note 20 supra.
that the stranger was perfectly capable of forming an intention to kill and acting on that intention.\textsuperscript{61}

Whatever its pedigree, there is no doubt that humans come equipped with a powerful sense of free will. That powerful sense of free will drives a powerful sense of responsibility when an individual breaches the social contract. We have no trouble holding people responsible for breaking the norms that bind us because we have no trouble presuming they were capable of deciding not to break them.\textsuperscript{62}

But as is often the case with evolution, a behavior is most successful when it is flexible enough to retain its value at the margins, when the environment changes and the margins become the norm. Or to put it another way, since the whole function of rules for group membership and group exclusion was to stabilize the group, to the net selective advantage of individual members, an overwrought sense of responsibility, blameworthiness or punishability could itself have destabilized the group.\textsuperscript{63} Punishment is very costly, not just to the person punished but also to the group and its punishment designees.

As a result, our ancestors lived in groups that cared about, and punished, only serious violations of the social contract, and were keenly sensitive to circumstances in which everyone might be better off if some wrongs were forgiven and went unpunished. Contrition is an important part of the decision to forgive, perhaps as a signaling device

\textsuperscript{61} Note that this is an oddly inverted kind of theory of mind. The traditional theory of mind notion is that we know what we are thinking, and we assume that other people’s minds work like ours does. But this evolutionary explanation for consciousness and free will suggests that its adaptive value comes from assuming other people have consciousness and intentionality.

\textsuperscript{62} We are also endowed, as discussed above, with a remarkably universal sense, once an act is deemed blameworthy, of how blameworthy it is with respect to other wrongful acts. See text accompanying notes 35 to 39 supra.
used by the group to measure whether the free rider could return to the fold without significant punishment.

This co-evolved tendency to moderate punishment with mercy and forgiveness may be why, at least in part, we have fairly universal principles of criminal law that generally require mens rea before an actor is punished, and that recognize that even if an act is accompanied by intention, sometimes the act must be excused because the actor suffers from some condition that affects his rationality. In the language of the criminal law, these are the principles of culpability and excuse. No net selective advantage would have devolved to group members by punishing a wrongdoer whose wrong was an accident, or whose mental deficiencies prevented him from complying with the rules of the group.

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63 See Rockenbach & Milinski, supra note 5; Hoffman & Goldsmith, supra note 7.

64 “Mens rea” is Latin for “guilty mind.” The phrase comes from the English legal precept “Actus non facit reum nisi mens rea sit” (“An act is not guilty unless the mind is guilty”), which dates from at least the time of Henry I in the early 1100s, and which was likely based on the writings of St. Augustine. Paul Robinson, Mens Rea, University of Pennsylvania, Scholarship at Penn Law Paper No. 35 (1999), available on line at http://lsr.nellco.org/apenn/wps/papers/35; Francis Bowes Sayre, Mens Rea, 45 HARR. L. REV. 974, 974 (1932). Virtually every civilization that has left a record on the matter—including the Babylonians, Jews, Egyptians, Greeks, and Romans—all recognized the idea that both the act and intention must be judged by the law. See, Max Radin, Intent, Criminal, in 8 ENCYC. SOC. SCI. 126 (Edwin R. A. Seligman & Alvin Johnson eds., 1932). It is true that this general rule had some strict liability exceptions, such as the quite common ancient rule that a man was strictly liable for the acts of his slaves, and even a strict liability view of homicide. See 2 POLLOCK & MAITLAND, THE HISTORY OF ENGLISH LAW 470-73 (2nd ed., 1968). But these exceptions did not displace the rule that even in ancient times—when access to the mind was so limited, at least by modern standards—civilized people cared both about the wrongdoer’s acts and his intentions.

65 Forms of the insanity defense, for example, were well known in antiquity. See DANIEL N. ROBINSON, WILD BEASTS & IDLE HUMOURS: THE INSANITY DEFENSE FROM ANTIQUITY TO THE PRESENT (1996). When even the “modern” M’Naghten formulation of the defense, adopted by the House of Lords in 1843, was a codification of formulations that had long been the common law of England. Anthony Platt & Bernard L. Diamond, The Origins of the “Right and Wrong” Test of Criminal Responsibility and Its Subsequent Development in the United States: An Historical Survey, 54 CAL. L. REV. 1227 (1966). See generally ISAAC RAY, A TREATISE ON THE MEDICAL JURISPRUDENCE OF INSANITY (1838).
Holmes wrote that even a dog knows the difference between being kicked and being stumbled over. Not only do humans (and maybe canines) intuitively recognize the difference between an intentional act and an accident, we likewise know that, with very few exceptions, accidents should not be punished the same as intentional acts.

But this leaves us with a difficult neural tension. We have a deeply embedded sense that we should not punish accidents the same as non-accidents, yet an equally powerful sense that most human actions are intentional, and therefore a corresponding skepticism about protestations by the wrongdoer that the wrong was an accident or that the actor was sufficiently irrational to be excused. This tension is largely responsible for our ambivalent feelings about doctrines of legal excuse, such as insanity, and the sometimes tortured forms those doctrines take.

Natural Law Makes a Comeback

For me, the most exciting fallout from the consilience of law, economics and biology is that the long-discredited idea of natural law may be making a comeback. There may well be segments of the law, maybe nearly all of it, that are neither cultural constructs nor mere market lubricants, but instead rules that reflect our deepest evolved natures as social animals. A core of right and wrong, if the post-modernists would forgive me for saying. That’s a comforting thought to those of us who toil at the altars of individual responsibility we call courtrooms.

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Conclusion

Law and biology has reached the kind of critical intellectual mass that law and economics reached two decades ago. An evolutionary perspective, by its very nature, informs virtually every aspect of inquiry into the human condition, and will therefore touch every human institution, including the law. Will this perspective change the way trial judges sentence embezzlers, or the way appellate courts look at the constitutionality of hate crimes, or the way legislatures define insanity? Probably not. Law and economics didn’t do much of that either.

Instead, this evolutionary perspective is the kind of referential shift that, as two law and biology scholars recently described it, changes everything and changes nothing. It changes nothing because evolved human nature will continue to animate those of us who write, interpret, enforce and break laws. I once described this as the “duh effect.” Most of these insights have a strangely familiar and obvious character, precisely because they are insights shared by all of us as part of our evolved natures as human beings. Is it any surprise to anyone, for example, that stepfathers kill their infant children at rates substantially greater than the rates at which natural fathers kill their infants? Yet that insight is unlikely to animate legal reforms in any obvious way. Few


68 Joshua Greene & Jonathan Cohen, For the Law, Neuroscience Changes Nothing and Everything, 359 PHIL. TRANS R. SOC. LOND. (B) 1775 (2004). Greene and Cohen argue that although neuroscience will likely not cause any significant changes in existing legal doctrines, it could have a transformative effect on the law by changing people’s moral intuitions about free will and responsibility.


70 Jones & Goldsmith, supra note 7, at 433-34.
of us, for example, would support a change that would presume biological fathers innocent but stepfathers guilty of killing their infants.

But the evolutionary perspective also changes everything. It rescues the law from political and philosophical extremists who have been claiming, from the Sophists through the Critical Legal Studies crowd, that law is an arbitrary exercise of raw power. Quite the contrary, the law is an expression of a kind of deep, evolved, social syntax. It describes a core of behaviors that most of us know is wrong, because those behaviors represent a violation of the 100,000-year-old accommodation between self and group that evolution has somehow wired into (almost) all of our brains.

Likewise, an evolutionary view rescues law from the narrow law and economics theorists, who may appreciate that deterrence by punishment is part of the evolved accommodation, but do not appreciate (or at least cannot explain) the moral core of that accommodation. Law is not a simple market lubricant, nor a cumbersome contraption that needs regular efficiency tune-ups. The behaviors that humans engage in to maximize their happiness are bounded (indeed, even defined) by underlying principles that label some behaviors socially acceptable and some socially unacceptable.

It might make you quite happy to steal your neighbor’s cow, and your neighbor might even be willing not to turn you into the police at the right ex post facto price. But freedom of contract and principles of supply and demand are insufficient to explain why most psychiatrically unimpaired people derive no happiness from stealing, or from
allowing others to steal from them, even at the right post-stealing price.\footnote{This is a slightly different, and less gruesome, version of Posner’s famous discussion of torture. In a free society, a few people may want to torture and a few people may be willing to torture, at the right price. There is therefore no reason to outlaw this sort of “voluntary” torture, and indeed the high price of torture will eventually drive the behavior beyond the means of even the wealthiest of torturers. \textit{Posner}, supra note 24. You’ve got to love the libertarian implications of such a world, but of course it is not the real world. In the real world psychiatrically unimpaired people derive no happiness from torturing or being tortured.} The law discourages some behaviors (and occasionally encourages others) not because those behaviors have reached some arbitrary price equilibrium, but because those behaviors are a deeply shared part of our moral intuitions. It is, if the post-modernists will again forgive me, wrong to steal, whether or not the victim later agrees to recompense, because we evolved to engage in \textit{reciprocal} exchanges. Small social groups in which everyone was stealing from one another would hardly have survived to produce \textit{Homo exchangius}.

The law and biology synthesis is far from complete. Very little is known about the actual environment in which humans evolved, and as a result many of the “insights” about the arguably adaptive nature of some human behaviors are little more than guesses. There is even less known about the meta-behaviors of that evolutionary environment, that is, about the rules of group inclusion and exclusion that presumably evolved along with the underlying rules themselves.

As discussed in this essay, the brain-to-behavior problem remains the biggest scientific barrier to a fuller understanding of evolved human nature. The biggest philosophical barrier remains the naturalistic fallacy: although we should never be afraid to use words like “right” and “wrong” in any discussion of law and the evolution of moral intuitions, we should always be aware of Hume’s command never to confuse the is with the ought.
While these and other issues should give us great pause, and keep us skeptical and humble, they are all small potatoes compared to the profoundly powerful referential shift this viewpoint provides. The law will never be the same after these evolutionary insights, because our view of ourselves will never be the same.