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Hardwiring: Innateness in the Age of the Brain

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### Abstract

“Hardwired” is a term commonly used to describe the properties of certain behaviors or brain regions. As its usage has increased exponentially in the past 50 years, both in popular media and the scholarly literature, the concept appears to have gained a cloak of respectability in scientific discourse. However, its specific meaning is difficult to pinpoint. In this paper, I examine how “hardwired” has been used in the psychological and neuroscientific literature. The analysis reveals two major themes: one centers on certain purported characteristics of behaviors or brain regions, such as fixedness; the other places these and other characteristics within an evolutionary framework. Overall, the analysis reveals a degree of overlap between “hardwiring” and the folk biology concept of innateness. Various complications arise from such overlap, casting doubts on the usefulness and legitimacy of “hardwired” in scientific discourse.

## Introduction

“Insofar as “biological bases” have replaced innate knowledge and structure in the vocabularies of many, they have inherited, so to speak, the implications of the earlier terms while legitimating them with the aura of methodological sanctity.” (Oyama, 2000a, p. 6)

It is a common refrain that human beings are “hardwired” for some types of behavior. References to “hardwiring” are found frequently in a variety of contexts and texts, not only magazines or popular books about psychology, but also plays and literary essays, typically within the overarching narrative of “human nature” (e.g., Stoppard, 2015; Wallace, 2005). For example, humans are said to be “hardwired” for prejudice (Wartik, 2004), morality (Tancredi, 2005), ripeness (Herbert, 2010), and relationships (Jap, 2016). The term has enjoyed a wide and enduring popularity in reference to sex differences. In her popular book, *The Female Brain* (2006), Louann Brizendine informs the readers that women and men behave differently because their brains are “hardwired” differently, due to their different hormonal realities. Similarly, Baron-Cohen’s *The Essential Difference* (2003) opens with the claim “The female brain is predominantly hard-wired for empathy. The male brain is predominantly hard-wired for understanding and building systems” (p. 1).

A search with Ngram Viewer, a digital humanities tool whose database includes millions of books published from 1600 to 2008 (Greenfield, 2013), reveals a steady increase in the use of the term over the past 50 years (Figure 1). Perhaps unsurprisingly, this increase characterizes the scholarly literature as well, as shown by a search in PsychInfo and Medline (Figure 2). The frequent use of “hardwired” in the academic literature shows that it has become an acceptable concept in science. However, a few voices have argued against the use of the term. Churchland (2002) remarked on the ambiguity of its meaning:

“If “hardwired” means “a behavior that depends on brain wiring,” then we need to ask, “As opposed to *what*? So far as is known, all behavior depends on brain wiring. If “hardwired” means “caused by genes,” we have already seen unqualified versions of this idea wrecked on the shoals of developmental complexity. Sometimes “hardwired” is used to refer to a circuit that is not modifiable postnatally. Typically, this usage too is

problematic, since virtually all of a brain’s functions are modifiable in one way or another ... Perhaps there exists in some subculture a consistent, useful, and *unambiguous* role for the expression of “hardwired,” but because it is so heavily encrusted with misconception and misdirection, it is preferable to see more precise terminology.” (pp. 327-328; italics in the original).

### INSERT FIGURES 1 AND 2 APPROXIMATELY HERE

More recently, Lilienfeld et al. (2015) too contended that its use should be dismissed, as

“... growing data on neural plasticity suggest that, with the possible exception of inborn reflexes, remarkably few psychological capacities in humans are genuinely hard-wired, that is, inflexible in their behavioral expression (...). Moreover, virtually all psychological capacities, including emotions and language, are modifiable by environmental experiences (...).” (p. 4; citations have been removed).

Churchland (2002) and Lilienfeld and colleagues (2015) provided at least three different meanings of “hardwired”: strictly tied to the wiring of the brain, caused by genes, and fixed. Earlier, Johnston (1987) also associated the term with multiple connotations, in contrast with “softwired”:

“Hard-wired behavior is developmentally inflexible, specialized in its function, and depends on neural structures whose organization is specified by the genes. Soft-wired behavior is readily modifiable in development, more adaptable in function, and depends on experience provided by the environment.” (p. 170).

Dictionary definitions, which capture common intuitions about the meaning and use of words, also suggest a plurality of meanings. “Hardwired” is a metaphor borrowed from engineering. The Oxford English Dictionary (OED; Hardwired, n.d.) defines the term as applied in engineering and computer science as

Of a computer or other electronic device: containing or involving permanently connected circuitry for implementing a specific, unchangeable function. Of a function: implemented by means of such circuitry.

These definitions not only speak of fixed physical connections but also of a fixed structure-function relationship. Electronic devices are built for a specific purpose, that is, to carry out a specific set of tasks: food processors chop, mix, and puree food; calculators perform various arithmetical operations. Each function is carried out by a specific circuit, activated by the pressing of a specific button. Functions in hardwired engineered systems are unchangeable, except in the case of

deterioration or breakup, and intimately tied to, or determined by, the structure of the machine. Changes in functions are attainable only through changes in structure. In this context, “hardwired” devices are contrasted with “programmable” general purpose machines (computers), in which the same fixed structure (hardware) permits the execution of different functions or software programs, and “wireless” mechanisms, which do not rely on the transfer of information through fixed connections.

The OED recently (June 2015) introduced a second meaning to describe the use of “hardwired” in reference to the brain and behavior:

Present as a permanent or inherent quality of the brain or nervous system; (of the nervous system or its parts) having permanent or long-lasting synaptic connections. More generally: (of a pattern of behaviour, ability, principle, etc.) made standard or instinctive, esp. through learning, conditioning, or repetition; (of a person) predisposed *to* do something, esp. through genetic or other biological influences<sup>1</sup>.

The Merriam-Webster’s online dictionary offers parallel definitions in terms of “implemented in the form of permanent electronic circuits; *also*: connected or incorporated by or as if by permanent electrical connections” and “genetically or innately determined: *inborn*” (Hardwired, n.d.). Current synonyms of the term include “built-in, constitutional, essential, immanent, innate, intrinsic, natural.” Clearly, the adoption of “hardwired” in the brain and behavioral sciences has extended and complicated its meaning in terms of origins, that is, it hints at why some behaviors exist and how they might develop.

The plurality of meanings and synonymy between “hardwiring” and innateness raise issues about the usefulness and legitimacy of the term in scientific discourse. First, the OED definition includes connotations seemingly in contrast with each other, such as inherent permanence and permanence gained through practice. Stability reached through practice relies on changes occurring

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<sup>1</sup> Before June 2015, only a transfer entry “in reference to the brain and its function” was present in the OED along with three different quotations, the earliest of which was dated 1971 (Blakemore, 1971). The introduction of the new definition attests to the widespread use of the word in the past few decades.

in a flexible system, which is therefore not “hardwired.” This type of mapping would render the distinction between “hardwired” and “non-hardwired” meaningless and therefore ill-suited for scientific investigation. Furthermore, synonyms as “inherent” and “innate” are semantically opaque (Mameli & Bateson, 2006) and therefore do not help clarify what “hardwired” means. As a consequence, they do not constitute acceptable operational definitions that can be used productively in science. Most importantly, they are not scientific terms but concepts that belong to the folk biology sphere; as such, their association with “hardwired” has the potential of perpetuating misleading views about biological processes, such as the idea that biological organisms are defined by certain basic and constant characteristics (essentialism) and that the information for the development of an organism exists somewhere before the developmental process takes place (preformationism, tied to terms like blueprint, instruction, preprogramming, etc.). These views have long been critiqued as false, unscientific, and problematic from a logical point of view (e.g., Griffiths, 2002; Mayr, 1996; Oyama, 2000a). Therefore, it is likely that these outdated views accompany the use of “hardwired” as well.

Philosophers of science and developmental psychobiologists have analyzed the concept of innateness in depth and documented additional problems and shortcomings. Some recent analyses are briefly summarized here<sup>2</sup>, as they are relevant for the present evaluation of “hardwiring.”

### Analyses of the concept of innateness

Bateson (1991, p. 21) listed the following meanings associated with “innate”: present at birth, a behavioral difference caused by a genetic difference, adapted over the course of evolution, unchanged through development, shared by all members of the species, not learned, a distinctly

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<sup>2</sup> A comprehensive analysis or critique of the concept of innateness is outside the scope of this paper. Earlier analyses of its use and meaning exist, such as Lehrman (1970) and McClintock (1979). Both authors discussed the semantic ambiguity of the term as used in biology and psychology.

organized system of behavior driven from within (see also Scholz, 2002, in reference to this last connotation). Griffiths (2002) added an eighth meaning to this list based on his analysis of the psychological literature: “something that can be taken as given with respect to the set of causal factors currently under investigation” (p. 73). This meaning refers to the trend of explaining psychological phenomena in terms of biological phenomena, especially in relation to purportedly innate traits. These traits are seen as having “biological bases” characterized by the unfolding of physiological processes that proceed blindly in the absence of environmental influences or learning.

Griffiths (2002) summarized three main ideas that are behind the use of “innate”: developmental fixity (“the trait is in some sense hard to change”), species nature (“the innate trait reflects what it is to be an organism *of that kind*”), and intended outcome (“the innate traits are how an organism is *meant* to develop”; p. 71, italics in the original). Each of these ideas in turn embodies a chain of related connotations. For example, developmental fixity conveys the impressions that the development of a trait is not affected by the environment, and that deviation from what appears to be a goal-directed process impairs development or yields abnormal traits. Species nature is associated with ideas of typicality and universality. Intended outcome is related to ideas of normativity, in turn associated to natural selection, preprogramming, design, and genetic determination (pp. 71-72): the lack of a specific adaptive trait is considered abnormal.

More recently, Mamei and Bateson (2006) identified and analyzed 26 different meanings associated with innateness (see their Table 1, p. 177). Their goal was to establish whether this concept could be replaced by a proper scientific candidate based on the premise that

“The innate/non-innate distinction has a legitimate role to play in science only if it relates to a coherent body of evidence and is able to play an important and positive role in the development of scientific theories” (p. 156).

Most candidates were excluded because they were deemed to be inchoate or empty. For example, the adoption of a definition such as innate-as-non-acquired and innate-as-genetically-determined would automatically exclude every phenotype, as all phenotypes appear at a certain time during development and are not present earlier, and no phenotype needs only genes for its development. If “innate” is used with the meaning of “genetically-influenced,” then all phenotypes are included. Similarly, the expression “genetically-encoded,” which requires that the sequence of nucleotides provides specific information about the development of a trait, is scientifically inaccurate, as developmental processes are not coded in the genome. Innate-as-unlearned is problematic for other reasons. Learning is a controversial concept in itself, as it encompasses multiple definitions and mechanisms both at the behavioral and neural level; it can include specific contingencies or broader systemic effects (e.g., food, stress), and it is difficult to draw a clear distinction between the two. It becomes problematic, then, to define what “lack of learning” is. Furthermore, as Bateson and Martin (2000) have discussed, at the practical level it is very difficult to demonstrate that some form of learning has not taken place, because it is arduous, if not impossible, to remove all possibilities for learning. Even isolation experiments, traditionally used to test whether the emergence of a trait requires learning or some sort of sensory experience, cannot completely isolate individuals from an environment, external or internal, and their own behavior. As Lehrman (1953) famously put it, “The important question is not “Is the animal isolated?” but “*From what* is the animal isolated?”” (p. 343). For example, the organism’s behavior can be crucial for the emergence of a trait, as shown by Gottlieb in his studies with eggs incubated in isolation: the vocalizations made by embryo ducklings after perforating the air space inside the egg led to their preference for the maternal mallard call. As this preference is present at birth, it had previously been thought to be unlearned or innate (Gottlieb, 1997). Finally, the necessary experience for the development of a behavior might be provided by a variety of factors, that is, a trait can develop



through a variety of routes. For example, the development of predatory behavior in cats might rely on practice, observation, or playing (Bateson, 2000). Therefore, removing one form of experience might not impact the development of the trait.

After most connotations were rejected on these grounds, Mameli and Bateson (2006) identified eight of the 26 connotations that could potentially constitute scientifically useful candidates to replace the folk concept of innateness. They included connotations such as reliably appearing in a specific stage of the life cycle, species-typical, adaptive, developmentally canalized, etc. However, the authors' pointed out that these definitions are not necessarily compatible with each other, as they refer to biological phenomena that empirically dissociate. That is, the presence of a property can occur independently from the presence of the others. For example, what is adaptive is not necessarily developmentally fixed and might require an extensive period of learning or social experiences (e.g., hunting skills in predatory species); what appears reliably at a given developmental stage is not necessarily species-typical (e.g., the reproductive behavior of queen bees) nor adaptive (e.g., PKU). Similarly, according to Mameli and Bateson, the belief that water is a liquid might be considered species-typical in humans, and it appears at a particular stage during development, to some extent, but it is not developmentally canalized or adaptive, or at least its adaptiveness has not been demonstrated.

As these connotations empirically dissociate, the presence of a characteristic or property cannot be inferred by the presence of others. However, such inferences (termed cross by Oyama, 2000b, and illicit by Griffiths, 2002) are frequently drawn and fostered by the adoption of terms that conflate different concepts and are semantically ambiguous. Mameli and Bateson (2006) discuss how the various connotations or ideas characterizing innateness are indeed often treated as equivalent or at least correlated; as such, they are often used in clusters. As an example, they cite the adaptive thinking logic adopted by many evolutionary psychologists, according to which Darwinian

adaptations develop reliably, emerge at a specific time during development in a “normal” environment, have a genetic basis, are shared across “most or all” members of a species, are produced by the process of natural selection, etc. (e.g., Buss, 2003, pp. 39-40)<sup>3</sup>. However, equivalency or correlation of such properties is typically either contradicted by empirical findings or not demonstrated; they might coexist in some cases, but not in others. Their equivalence or correlation must be established empirically in order to understand the development of a given behavior in a given species. Mameli and Bateson (2006) asserted that empirical investigations on the co-occurrence of such traits not only have not been conducted but that they have also been thwarted by the reliance on concepts such as “innate”<sup>4</sup>:

“A thorough investigation of such questions has been hindered by indiscriminate use of the label ‘innate’. The vernacular concept of innateness seems to be a multifaceted or ‘protean’ concept (Bateson and Martin 1999). Because all finalists capture some aspect of the vernacular distinction between innate and non-innate traits, the use of the label ‘innate’ encourages researchers to think that such proposals are roughly equivalent to each other, to bundle together notions that should be distinguished from each other, and to assume that the questions just mentioned have already been fully answered, when in fact they haven’t.” (p. 179)

For Mameli and Bateson (2006), then, scientists should not use labels such as “innate” until they can demonstrate that the defining properties of the concept are highly correlated. In the absence of such correlation, what is innate according to one connotation might not be innate according to another connotation, and vice versa (see their Table 2, p. 180); therefore, the distinction between innate and not-innate (e.g., acquired or learned) does not rely on a coherent body of empirical evidence (see also Bateson & Mameli, 2007). This lack of coherence raises serious issues regarding the usefulness of “innate” in science.

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<sup>3</sup> Clustering is by no means limited to evolutionary psychologists. For example, according to Chomsky (1980), human beings are innately endowed with a cognitive structure or “mental organ” that explains our ability to learn a language. Such structure is assumed to be unlearned, present at birth, genetically determined, and to develop through an “intrinsically determined process” (p. 2). For further examples, see Oyama (2000b, p. 53).

<sup>4</sup> The use of terms such as “innate” and “instinct” to explain behavior has been criticized as counterproductive in this sense by many authors, such as Lehrman (1953), Beach (1955), Schneirla (1966), and Thelen & Smith (1994). For a more recent exchange, see Griffiths and Machery (2008) and Weinberg and Mallon (2008).

### Goal of the present study

The previous section had two major objectives: first, to outline the various meanings associated with the term “innate” based on previous analyses of the concept, and second, to articulate the problems associated with using the same term to refer to different biological realities or phenomena in a scientific setting. These problems concern the legitimacy of the concept of innateness in the sciences, its productivity in terms of hypothesis generation and testing, and finally its role in advancing our understanding of how organisms develop and behaviors emerge.

The synonymy between innateness and “hardwiring” raises the question of whether the problems described in the previous section might affect the use of “hardwiring” as well. The purpose of this paper is therefore to provide an analysis of how the concept of “hardwiring” has been used in psychology and neuroscience since its appearance in these contexts at the beginning of the 1970s. Although the concept has infiltrated our daily conversations and even attracted the curiosity of linguists and writers (Lieberman, 2009; Safire, 2000), its use has not been evaluated systematically.

The analysis was guided by three main goals:

1. To identify and analyze the connotations associated with “hardwired.” The dictionary definitions and quotations considered above suggest that structural or behavioral fixedness only partially captures the concept. It is therefore of interest to document how the term has been used in the scientific literature in reference to brain and behavior.
2. To explore whether the semantic attributes of “hardwired” overlap with those of “innate.”
3. To establish whether clustering and illicit inferences also characterize the use of “hardwired.”

Johnston (1987) argued that dichotomies such as “hardwired vs. softwired” are variations on the innate-learned theme, and therefore share the same shortcomings in investigating and explaining development. One of the purposes of this paper is to document and evaluate the extent of this rebranding. The existence of a semantic overlap between “innate” and “hardwired” and the presence of clustering and illicit inferences for “hardwired” would cast doubt on the usefulness of “hardwired” in scientific practice and theory.

### **Method**

The analysis provided here is based on text analysis of a variety of sources available in digital format through scholarly databases, such as PsychInfo and Medline, and web search engines such as Google Books, Google Scholar Alerts, and NGram Viewer. As errors have been documented for Google Books, mostly due to its optical recognition system, I have relied on a variety of digital tools to verify the accuracy of a given source and limited my analysis to the texts for which I was able to obtain hardcopies. The earliest reference available through this method was dated 1971 (Blakemore, 1971). Therefore, the present analysis focuses on how “hardwired” has been used in the past 45 years. As it was unfeasible to peruse and document every use of the term, the analysis mostly reflects usage in materials from peer-reviewed publications, academic books, and publications on brain and behavior written for a general audience.

Below are quotations that exemplify the various meanings of “hardwired.” For the sake of concision, and in order not to overwhelm the reader with numerous quotations from disparate texts, I have limited the in-text quotations and included additional quotations in Appendix One (some of these quotations are also cited in the text). I have included passages in which the meaning of “hardwired” was defined by the author/s or could be identified based on the analysis of the immediate context. It was often difficult to reach an unequivocal interpretation, as “hardwired” is

rarely accompanied by a definition, citations, or substantiating evidence. I discuss some of these examples and the pitfalls associated with such lack of precision later in the paper. I have also included quotations in which the authors state that a behavior or a system is not “hardwired.” These quotations help define how the term is used in a given context and therefore its intended connotation. It is important to point out that statements about “hardwiring” in the quotations included in the paper were not necessarily endorsed by the quotations’ authors. In several cases, authors reported other authors’ positions or general views in the field, and later proceeded to refute them. Finally, my main goal in this paper was to unpack the meanings of “hardwired” and reveal some of the assumptions that underlie the use of this concept; therefore, a critique of “hardwired” from an empirical point of view and a discussion of whether “hardwiring” is an adequate metaphor to explain the development of biological organisms are beyond the scope of this paper.

## Results

This analysis found at least 11 meanings for “hardwired.” A brief description and examples are given for each of them.

### 1. Hardwired as fixed, resistant to change

Fixedness, or the inability to change, is one of the earliest and most frequent connotations of “hardwired.” Blakemore (1971) used the term with this connotation when he described Sperry’s work on the regeneration of the optic nerve in amphibians. During regeneration, the nerve synaptic endings reconnect with the original neurons in the optic tectum, even if the eye has been rotated by 180 degrees (Sperry, 1943). The reestablishing of the original connections creates problems of orienting towards prey in these animals, problems that are not ameliorated even after months. As Blakemore (1971) summarized,

“Visual experience has no influence at all on this “hard wiring”: the animals never learn to correct their inappropriate responses” (p. 614).

“Hardwired” neural structures are characterized by fixed axonal projections or synaptic connections. Changes in the strength of synaptic connections started being documented in the 1960s (e.g., Bliss & Lømo, 1973; Kandel & Tauc, 1965); in this context, “hardwired” was employed to indicate lack of change and contrasted with “softwired” or malleable:

“... some inputs to a neuron are far more hard-wired, if you will, than others. If you tried to play games with certain synaptic interconnections, some of them are really, really fixed, but if you play games with others they habituate or show decrements or increments in their response.” (Peterson, 1973, p. 109)<sup>5</sup>

“The factors determining which cell assemblies come into play at any moment in life are thus fourfold: The ongoing activity of neurons carried forward from the immediate past, the incoming sensory excitation arising from both the internal milieu and the external environment, the “hard wired” anatomical structure of the brain, and the “soft wired” relative strengths of synapses ...” (Goddard, 1980, p. 233)

Changes in projections, synaptic strength, or other aspects of the nervous system are taken as evidence that a system is not “hardwired” (these counterexamples abound in the literature on neural plasticity):

“Until recently, the vomeronasal system (VNS) has been commonly described as being specialized in the detection of innate chemosignals. Accordingly, its circuitry has been considered necessarily stable, if not hard-wired, in order to allow stereotyped behavioral responses. However, both first and second order projections of the rodent VNS continuously change their synaptic connectivity due to ongoing postnatal and adult neurogenesis.” (Oboti & Peretto, 2014, 1)

Hardwired-as-fixed is also used to refer to behaviors, as seen earlier in the Lilienfeld et al.’s (2015) quotation in reference to “inborn” reflexes considered “genuinely hard-wired, that is, inflexible in their behavioral expression” (p. 4). Behavioral fixedness is assumed to reflect structural

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<sup>5</sup> This quotation is part of the Q&A discussion following Peterson’s lecture at the “*Behavioral Genetics: Simple Systems*” Symposium held at the University of Colorado, Boulder, on March 4-5, 1971, whose proceedings were published in 1973. Peterson’s lecture, titled “RNA metabolism in response to neural stimulation in *Aplysia*,” focused on his recent work on changes in synaptic strength.

fixedness; for example, the “hardwiring” of inborn reflexes is contrasted, in Liliefeld et al., with neural plasticity.

## 2. Hardwired as reflecting a fixed relationship between stimulus and response (S-R invariance)

As some behaviors are comprised of sequences of motor acts performed in a given order, fixedness is applied to the entire sequence, which is considered to be invariant. “Hardwired” mechanisms thus guarantee a reliable and obligated relationship between stimulus and response, relationship that is not modulated by contextual factors:

“It is not surprising that both situations have been described: that some behavior patterns are “hard-wired” so that some behaviors are performed in an unvarying sequence following the initiation of the sequence by one of a pair of animals, and, alternatively, that some behaviors are performed in sequences with a probability that is dependent on many variables including the preceding behavior.” (Norton, 1977, p. 5-6)

Once again, fixedness of structure is therefore used to explain the fixedness of certain behaviors or responses:

“This response, too, must be reliable and reproducible and hence the nervous system mechanism between input and output must be itself invariant; to use the fashionable term, hard-wired.” (Rose, 1978, p. 32)

## 3. Hardwired as developmentally fixed or constrained

The first two meanings pertain to fixedness of traits once they have come into being. Hardwired-as-fixed has also been used in reference to aspects of development. In these cases, development is portrayed as constrained (in terms of possible outcomes):

“For behavior that is more stereotyped, however, (i.e., behavior that appears to be more “hardwired,” with a much tighter or narrower range of developmental outcomes), the correspondence between experience and the outcome might not be so obvious. This is where the search for ontogenetic mechanisms becomes rather difficult.” (Miller, 1997, p. 463)

“Under normal circumstances, adult stem cells are hardwired to only produce only a subset of cell types.” (Nissar, Martowirogo, & Gilbert, 2016, p. 180)

and insensitive to contextual factors or experiences:

“Mate preferences may also differ in the degree to which they are “hard-wired” in the sense of requiring little or no socialization to develop versus requiring extensive socialization during ontogenesis.” (Buss, 1992, p. 262)

“We did not find any evidence that the development of the sophisticated receptive-field organization of tangential neurons depends on sensory experience. Instead, the input to the tangential neurons seems to be “hardwired” and the specificity of these cells to optic flow induced during self-motions of the animal may have evolved on a phylogenetical time scale” (Karameier, Tabor, Egelhaaf, & Krapp, 2001, p. 1).

What is seemingly shared by these uses of “hardwired” is the view that, somehow, development of certain traits is “driven from within.” In contrast, the sensitivity of developmental processes to contextual variables is taken as evidence against the existence of circuits or behaviors whose development unfold rigidly and inevitably:

“This evidence for plasticity in cerebellar circuitry indicates that phylogenetically stable structures, as well as phylogenetically newer ones, are not “hardwired” and can be modified by environmental experience.” (Floeter & Greenough, 1979, p. 229)

“Behavioral tests with the [fruit fly] mutants have suggested experience-dependent components in behavioral patterns, such as courtship, which had appeared to be hard-wired.” (Quinn & Greenspan, 1984, pp. 77-78)

Hardwired-as-developmentally-fixed has been also used to refer to entire developmental programs:

“A defining property of metazoans is the regulatory program for development that is hardwired in their genomic DNA sequence.” (Arnone & Davidson, 1997, p. 1851)

What is “hardwired” in this example can be thought of as a process, not an outcome, and the process regulating its prolonged coming into existence is considered fixed<sup>6</sup>.

#### 4. Hardwired as automatic, not represented

Fixedness and invariance are often associated with other aspects of “hardwired” circuits or machines, such as their automaticity and their allowing for the execution of behaviors that are not consciously controlled or represented:

“..., a process is hard-wired if, at least roughly, it is (at the relevant time) invariant, automatic, not under conscious or programmable control; if it is a matter of hardware, not software. What goes on in a pocket calculator when the square-root button is pushed is, thus, a good example.” (Stocker, 1982, p. 445)

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<sup>6</sup> I would like to thank an anonymous reviewer for suggesting this distinction.



“Fodor also assumes that the language faculty is “hard-wired.” ... Part of the point of hard-wiring – of saying that something is hard-wired – is that rules (as opposed to input) needn't be represented. We could build a device that represents and executes the rule IF PULLED THEN STRETCH, but a rubber band has it hard-wired: it executes the rule without representing it. When we hard-wire a program what we do is build something that, like the rubber band, executes the rules in question without representing them. I don't know how it is with grammar, but I know it makes a difference.” (Cummins, 1985, pp. 106-107)

Lack of representation is tied to lack of conscious control and automaticity. Here, one of the defining meanings of engineered machines is applied almost literally: behaviors (or rules) are implemented directly in terms of circuitry.

### 5. Hardwired as unlearned, not learned

“Hardwired” behaviors are often contrasted with learned behaviors:

“Here we explore the role of both learned and hard-wired behavior in a predator–prey model of a coevolutionary arms race, namely, predatory larval antlions and one of their prey, sand-dwelling ants.” (Hollis, Harrsch, & Nowbahari, 2015, p. 68)

In this context, the physiological processes that underlie “unlearned” behaviors are also considered to be “hardwired” or “prewired,” especially when they are present early during development or at birth:

“Many recent infancy experiments demonstrate precocious abilities in new-borns (*sic*). One interpretation of these findings is that no real learning has occurred—the ability must be hard-wired ....” (Elman et al., 2001, p. 156)

“Whether or not human brains are genetically pre-wired for language processing with a language acquisition device, they are incontrovertibly not pre-wired with a hard-wired, reading acquisition device. Children *learn* to read, acquiring the requisite reading skills via substantial effort, and most often with explicit instruction. Learning to read thus is accompanied by functional reorganization of brain systems that clearly evolved for other functions.” (Barber & Kutas, 2007, p. 99; italics in the original)

Traits that develop based on learning or some form of experience are deemed to be not “hardwired”:

“These results indicate that invariant object recognition is not a hardwired property of vision, but is learned rapidly when newborns encounter a slowly changing visual world.” (Wood & Wood, 2016, p. 1)

The contrast between hardwired-as-unlearned and learned, and the one between hardwired-as-fixed and changeable, is also present in the context of connectionist models. Based on views of learning as reflecting changes at the synaptic level (e.g., Hebb, 1949; Kandel & Taub, 1965), “learning in connectionist models amounts to changing the strength of connections between the nodes, based on what tends to go with what” (McClelland, 1985, p. 116). Knowledge here is gained through training or “programmable connectionist mechanisms, in which the connections needed to meet the current processing demands can be set up on line, as the processing demands arise” (p. 114). This is in contrast to connectionist networks in which the connection weights between nodes do not change, such as the interactive activation model of word recognition by McClelland and Rumelhart (1981). In such networks, “the knowledge which guides processing is hard-wired into the connections between the processing units in which the processing take place” (McClelland, 1985, p. 116). In a sense, the circuit is the underlying physical implementation of the knowledge, as also suggested by Stoker’ (1982) and Cummins’ (1985) focus on automaticity, cited above.

## 6. Hardwired as structured to perform a given function

A related connotation pertains to the second meaning of “hardwiring” in engineering: a circuit structured to perform a specific function or a function that can be explained by relying on the structural characteristics of the neural systems supporting it:

“... the circuitry of the visuosensory SC [superior colliculus] is hard-wired to give higher priority to more peripheral targets, and this property is conferred by a uniquely structured, dedicated inhibitory circuit” (Bayguinov, Ghitani, Jackson, & Basso, 2015, p. 662).

Similarly, the visual system in humans “... behaves as though hardwired to detect square waves” (Campbell, Howell, & Johnstone, 1978, p. 200) and comprises “... relatively hardwired neural filters that are “tuned” to different retinal image correlates of the three-dimensional structure and motion

of solid objects in the environment” (Regan, 1986, p. 127). The expression “hardwired for X” seems to capture this connotation:

“... humans are relatively hard-wired to preattentively identify repeated auditory feature conjunctions even when such conjunctions occur rarely among other similar ones.” (Ruusuvirta, Huotilainen, Fellman, & Näätänen, 2004, p. 2819)

Humans are seen as born with circuits whose structure specifically allows for (and explains, following Griffiths, 2002) some preference or ability:

“... while our data do not conclusively demonstrate that the motor programs for a great many movement patterns are hardwired into the primate central nervous system at birth, they do increase the probability that this hypothesis is correct.” (Taub, 1976, p. 365)

“...infants are born ‘hard-wired’ to prefer tastes that signal beneficial nutrients ... and to reject tastes that signal harmful compounds” (Ventura & Worobey, 2013, p. R401).

“The person is born with a hardwired emotionally based meaning system as well as the ability to learn and formulate meaning on a cognitive level.” (Pascual-Leone, Andreescu, & Greenberg, 2016, pp. 138).

As a consequence, differences in structure cause differences in function and different behaviors among individuals are explained by differences in brain structure:

“..., a number of studies have reported differences in brain structure and function between male-oriented and female-oriented rams, suggesting that sexual partner preferences are neurologically hard-wired.” (Roselli, Larkin, Schrunk, & Stormshak, 2004, p. 233)

In this context, some behaviors or behavioral effects are assumed to reflect structural or architectural characteristics of the nervous system, while others are not. For example, Hugdahl (1996) stated that some behavioral effects in laterality studies are due to ““hardwired” laterality differences” (p. 218), such as the right ear advantage in dichotic listening experiments, although he pointed out that such effects can be changed by manipulating attentional resources towards the left or right space<sup>7</sup>.

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<sup>7</sup> It is unclear what such distinction entails in terms of structure-function relationship. Even attentional effects reflect the modulation of neural activity in sensory systems achieved thanks to a complex network of neural projections involving several cortical and subcortical brain circuits. Interestingly, “hardwired” is here and elsewhere used in contrast with concepts related to attentional control, as if attention introduced an element of volition and reduced automaticity.

### 7. Hardwired as tied to a specific brain region, localized

Functions are said to be “hardwired” if supported by specific and localized structures; that is, “hardwired” functions are localized in particular structures or circuits<sup>8</sup>:

“What is the information content in the brain? Let us consider two opposite and extreme poles of opinion on brain function. In one view, the brain, or at least its outer layers, the cerebral cortex, is equipotent: any part of it may substitute for any other part, and there is no localization of function. In the other view, the brain is completely hard-wired: specific cognitive functions are localized in particular places in the brain.” (Sagan, 1977, p. 29)

“Is it hardwired (in the sense of being ‘associated with specific, localized, and elaborately structured neural systems) or is it implemented by relatively equipotential neural mechanisms?” (Fodor, 1983, p. 37)

Specificity is tied to the idea that some structural constraints exist on the type of process a brain region can support. In this sense, hardwired-as-localized reveals the underlying assumptions that “hardwired” structures are dedicated to perform a given function and thus develop accordingly. Therefore, “hardwired” has been contrasted with “equipotential” (i.e., amenable to change or assumed to be able to accommodate a variety of functions) and associated with functional independence:

“With respect to the occurrence of the aftereffects themselves, we prefer an explanation involving more hard-wired processes: Psychophysical and physiological evidence suggests that depth information from different regions in perceptual three-dimensional space is processed by functionally independent mechanisms in the brain (...)” (Petersik & Boring, 1984, p. 465; citations have been removed)

### 8. Hardwired as adaptive or evolved

“Hardwired” has also been used to refer to structures or behaviors whose existence has been assumed to be adaptive during the evolutionary past:

“[According to the theory of parental investment proposed by Trivers in 1972] The biological reality in humans is that males can reproduce their genes with the minimal investment of a few minutes and a few sperm, whereas the cost to females is usually years of investment in the form of gestation, lactation, and offspring care. In theory, such asymmetry has resulted in hard-wired sex-specific strategies for achieving reproductive success. Males “naturally” seek out and take advantage of opportunities to copulate with as many different females as possible, especially ones who display the fertility markers of youth and beauty. The female is “by nature” more sexually cautious, preferring one male who has resources and appears willing to share them with her and the

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<sup>8</sup> Localization of functions is itself a complex and controversial concept. An in-depth discussion is beyond the scope of the present study. Interested readers can consult Phillips, Zeki, and Barlow (1984).

offspring she will have to nurture.” (Hazan & Diamond, 2000, pp. 186-187)

“The question of adaption of graviceptor is questioned from an evolutionary point of view. It is possible that graviception is hardwired, because life on Earth has evolved under the constant pressure of gravity.” (Jamon, 2014, p. 1)

The theme of adaptiveness is often accompanied by the concept of “genetic hardwiring,” discussed next.

### 9. Hardwired as “under tight genetic control” (genetic hardwiring)

“Genetic hardwiring” is a recurrent theme in the life sciences literature. It has been applied to behaviors, brain regions, and even development itself:

“[Emotional circuits are] ... genetically hard-wired and designed to respond unconditionally to stimuli arising from major life challenging circumstances. ... They organize behavior by activating or inhibiting classes of related action (and concurrent autonomic/hormonal changes) that have proved adaptive in the face of those types of life-challenging circumstances during the evolutionary history of the species” (Panksepp, 1982, p. 411)

“Why did freezing become a genetically hardwired behavior? ... a reasonable hypothesis is that freezing is a beneficial response when faced with a predator.” (LeDoux, 2002, p. 6)

Its precise meaning is unclear, as it is typically not defined, but its use suggests that the hardwiring of a brain circuit or behavior, or indeed entire developmental processes, is under the tight control of genetic activity (genetically determined) or literally coded in the sequence of DNA nucleotides (as Arnone and Davidson’s quotation on the “regulatory program for development” as “hardwired in [the] genomic DNA sequence” mentioned in the hardwired-as-developmentally-fixed section).

### 10. Hardwired as “connected to”

“Hardwired” was also found to signify a physical connection between two systems, as in “connected to,” although the presence of “hard” hints at more than mere connectivity:

“... the concept of a consistent interaction between the nervous and immune system has some physiological basis. ... The observation that some of the cells of the immune system may be “hard wired” is confirmed by information obtained in careful neuroanatomic and ultrastructural analyses in lymphoid tissues such as thymus, spleen and Peyer’s patches...” (Stead, Bienenstock, & Stanisiz, 1987, p. 352)

“This gut-brain axis consists of “hard-wired” anatomical connections, involving vagal and spinal nerves, and humoral components provided by the microbiota and their products, gut tissues, endocrine and immune systems.” (Forsythe, Kunze, & Bienenstock, 2016, p. 1)

### 11. Hardwired as intuitive

“Hardwired” has also been used with the meaning of “intuitive”:

“...early development of agent representation is only *suggestive* of it being ‘intuitive’ (or ‘hardwired’). What further suggests intuitive status is its incorrigibility in the face of counter-evidence. Consider other intuitive processes, such as those that give rise to visual illusions, such as the Müller-Lyer Illusion. In the Müller-Lyer Illusion, two lines that are actually of the same length, look different lengths. What makes this an intuitive process is that no amount of counter-evidence eliminates the misleading percept. Even if you measure the lengths of the lines, and, on that basis, come to *believe* that they are the same length, they will not cease to be *experienced* as different lengths. The claim that agent representation is intuitive (or hardwired) amounts to claiming that it should be incorrigible in a similar way.” (Wilkinson & Bell, 2016, p.114; italics in the original)

This use of “hardwired” seems to be related to Fodor’s (1983) concept of informational encapsulation, whereby some systems are less permeable to background information, contextual factors, or beliefs than other systems. Indeed, the Müller-Lyer illusion is one of the examples mentioned by Fodor to explain the concept (p. 66). Thus, there seems to exist a degree of overlap between “hardwired” and the concept of Fodorian module, as some characteristics are shared: tied to the workings of specific and localized neural structures, automatic, informationally encapsulated, and “innately specified”, that is, characterized by a structure not formed by “some sort of learning process” (Fodor, 1983, p. 37).

## **Discussion**

The quotations discussed in the previous section exemplify how “hardwired” has been used in the psychology and neuroscience literature in the past 45 years. Here is a summary of the main connotations tied to the use of the term:

- (1) Fixed, resistant to change
- (2) Fixed stimulus-response relationship
- (3) Developmentally fixed, constrained

- (4) Automatic, not represented
- (5) Unlearned, not learned
- (6) Structured to perform a given function (“hardwired” for)
- (7) Tied to a specific region, localized
- (8) Adaptive/evolved
- (9) Genetically programmed/determined (genetic hardwiring)
- (10) Connected to
- (11) Intuitive (informationally encapsulated?)

This list shows that the term has been used with a variety of meanings. Such plurality can be condensed into two major uses of “hardwired.” First, the term is evoked to characterize the features of a particular behavior or neural system, for example in terms of fixedness, automaticity, localization, connectivity, and informational encapsulation (meanings 1, 4, 7, 10, and 11, respectively). Second, “hardwired” is situated within a narrative about origins. In this context, “hardwired” behaviors rely on dedicated neural regions that have evolved to support those specific behaviors (meaning 6); their specialization is determined by biological processes (typically genetic in nature<sup>9</sup>; meaning 9) that are not shaped by experiential or contextual factors (meaning 3) or learning (meaning 5), and are assumed to be adaptive (meaning 8). Once activated, they act automatically and obligatorily, thanks to an invariant relationship between input and output (meaning 2). Structure specifies, and explains, function. Some of these behaviors and brain systems are functional and “ready to go” at birth, although others reliably emerge later in life. These two themes often intersect. Indeed, I argue that the theme of origins is easily evoked when we use “hardwiring” in reference to biological organisms. Fixedness of structure and function in an engineered machine is explained by the intention of creating a device with certain characteristics for the execution of a specific goal, and

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<sup>9</sup> In much of the literature on “hardwired” sex differences, the “hardwiring” is seen as the result of prenatal hormones, such as testosterone, action (e.g., Baron-Cohen, 2003; Brizendine, 2006). While the hypothesized mechanisms drive the attention away from genes, differences in prenatal testosterone levels are typically, although not exclusively, driven by the presence or absence of the Y chromosome in males. It is perhaps for this reason that both Baron-Cohen (2003) and Brizendine (2006) comfortably refer to the “female brain” or “male brain” as being responsible for essential differences in behavior between the sexes, not to brains characterized by high or low levels of prenatal testosterone, regardless of genetic sex.

therefore by design. Claims that such characteristics are present in living organisms beg the question of their origins. Themes of adaptiveness and preparedness therefore become prominent. For example, “hardwired” behaviors or preferences observed at birth are typically considered to reflect the activity of “prewired” circuits whose structure is the result of genetic “programming” and natural selection. If a behavior or preference is present at birth, the assumption is that it must have been selected because advantageous. Questions of origins are obviously important and critical in biological and behavioral sciences. However, they are often quickly addressed by appealing to evolutionary explanations, whether or not substantiating evidence is available. The existence of such behaviors is simply explained by the activation of dedicated neural systems that have evolved to support them or by assuming their existence.

The list of meanings discussed above then reveals a partial overlap between the meanings of “hardwired” and “innate”, as outlined by Bateson (1991), Griffiths (2002), and Mameli and Bateson (2006). For example, in reference to Griffiths’ analysis, they share concepts of developmental fixedness (the development of a trait exhibits a restricted range of outcomes and is not affected by environmental factors) and intended outcome (adaptiveness, genetic determinism). Connotations such as unlearned, are also shared, especially for behaviors present at birth, in addition to having “biological bases” (Bateson, 1991). These connotations, which include themes such as genetic determinism (genetic hardwiring), structural fixedness, and insensitivity to context, are, through the use of the term “hardwiring,” directly applied to aspects of the nervous system, which in turn are used to provide causal explanations of behavior. If one of the meanings of “innate” concerns differences in genotype that are responsible for differences in phenotype, “hardwiring” offers a variant: differences in brain structure or architecture explain differences in behavior.

Interestingly, two of the ideas typically associated with innateness, universality and species typicality, are not used as explicit definitions of “hardwired,” although “hardwired” behaviors and



brain circuits are typically assumed to be species-typical or universal (or at least shared by individuals of the same sex and age, as evidenced by the literature on sex differences in humans):

“If color categories are functional at or near-birth, if they have an identifiable neurological substrate, and if it is “hard wired,” then human infants will be expected to partition the spectrum in uniform ways before they have experience with language or with culture, as indeed seems to occur. Afterwards, development may follow different courses.” (Bornstein, 1987, p. 292)

“... if basic emotions are part of the biological makeup of a species, then one might expect them to be “hardwired,” and so one would expect to find neurophysiological or anatomical evidence of them in all (normal) members of the species.” (Ortony & Turner, 1990, p. 320)

“Further evidence that the dispositions for interpersonal interaction in different nonverbal channels (face, voice, touch, etc.) are relatively hard-wired comes from research on grooming behavior (Suomi, chap. 7, this volume). Grooming is ubiquitous both in animals and humans-including German university students-but may recently have become “repressed” in Western culture (...).” (Segerstråle & Molnár, 1997, pp. 9-10)

“Subcortical circuits are clearly more likely to be hardwired than cortical ones, but we shouldn’t reject outright the possibility that some cortical circuits may also be hardwired. (For example, it has been proposed that the perception of facial expressions of emotion is performed by a species-specific face perception module in the primate, including human, cortex.)” (LeDoux, 2002, p. 89)

The link between “hardwiring” and species typicality is evident in all these quotations.

However, “hardwired” appears to have a different, although not clearly defined, connotation, vaguely tied to the concept of “having biological bases.” Here, the two concepts are inferred from each other. In some examples (e.g., Bornstein, 1987; Ortony & Turner, 1990), if behaviors are “hardwired,” they are assumed to be species-typical. Conversely, in Segerstråle & Molnár (1997), if they are “ubiquitous,” they are assumed to be “hardwired.” Such relationship can be easily explained within an evolutionary framework, according to which, what is “hardwired” is “hardwired by evolution” (a frequent expression in the literature): brain circuits responsible for certain behaviors are assumed to be shaped via genetic programs that organize their development because purportedly adaptive. As a consequence, such structures and behaviors are seen as heritable, developing reliably, and species-typical (and characterizing “human nature”). Universality or species typicality for “hardwired” traits seem also implicit in expressions such as “humans are hardwired for X.” Therefore, although not used as explicit definitions, these meanings are part and parcel of the concept of “hardwired.”

In this narrative, “hardwired” is often a synonym of “innate” and indeed the two terms often co-occur within the same text. Their equivalence is also demonstrated by the fact that they are used interchangeably or as a translation of sorts. For example, Elman et al. (2001) discussed Spelke’s (1994) interpretation of behaviors observed in newborns as reflecting “hard-wired” abilities, as “no real learning has occurred” (p. 156). Spelke (1994) did not use the label “hardwired” in the cited work, but instead stated that such precocious behaviors reflect “innate” knowledge. More recently, in his critique of Goldin-Meadow’s (2015) position on the nature of language acquisition mechanisms, Everett (2015) argued that homesigns, gestural communication systems developed by deaf children who are not exposed to a conventional sign language, do not “... provide arguments for either the universality of hierarchy in human languages nor the nativist hypothesis that such knowledge is hard-wired” (p. 919). However, Goldin-Meadow (2015) never uses the term “hardwired,” but argues that resilience in language acquisition relies on “innate structures that guide the process of language learning” (p. 908).

Furthermore, as for “innate,” the various connotations of “hardwired” are often presented as equivalent or correlated. Sagan (1977) used “prewired” as a synonym of “hardwired” and tied information already present in the system (e.g., present at birth) with constraints on change:

“Prewired: Computer jargon for information already in place. Also called hard-wired. The more prewiring, the less plasticity.” (p. 265)

Purportedly automatic behaviors present at birth are considered unlearned and genetically-hardwired (Wilson, 1978, pp. 62-63). The “hardwired” emotional circuits described by Panksepp (1982) are tied to the functioning of specific brain regions (p. 408), genetically hardwired, and designed the way they are because they proved adaptive in our evolutionary past (p. 411). Similarly, the perceived attractiveness of a female face is deemed to be “hardwired” as it is present early in life

(and therefore assumed to require minimal or no socialization to emerge), shows little variability across infants, and is similar to preferences in adults (Buss, 1992, p. 262). Fodor (1983) conceptualized “hardwired” modules as clusters of features (automaticity, high speed, domain-specificity, informational encapsulation, reliable development, etc.)<sup>10</sup>. Karmeier et al. (2001) tied the “hardwired” receptive field organization of neurons in the fly, which, according to the authors, does not require sensory experience to develop, to evolution. Rowland and Motofei (2006) characterized “hardwired” biological domains as reflexive, programmed, genetically set, and less variable in terms of individual differences; in contrast, they view “softwired” domains as programmable, experienced-based, and varying depending on the context (see their Figure 2, p. 79). Wilson and Fox (2007) associate the term “hardwired” with evolution, genetic determinism, dedicated neural regions, and lack of “ontogenetic development” (p. 470). Other examples of clustering are offered in Appendix Two.

Because of the semantic overlap with “innate,” the same problems described by Griffiths (2002) and Mameli and Bateson (2006) apply to “hardwired.” Specifically, some of the connotations (e.g., acquired, unlearned, genetically determined, etc.) are unclear, inchoate, or controversial. The same problems that characterize “unlearned” (e.g., difficulty in establishing that a trait is not learned) characterize hardwired-as-developmentally fixed, as insensitivity to one context does not preclude other contexts from affecting the development of a trait. Furthermore, the various connotations do not necessarily refer to equivalent or correlated biological phenomena. Preferences observed in newborns are shaped by experiences occurring in utero or before hatching (e.g., DeCasper & Spence, 1986; Gottlieb, 1997; Mampe, Friederici, Cristophe, & Wermke, 2009). Aspects of the nervous system that are present and functional at birth can change during development (e.g.,

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<sup>10</sup> Fodor proposed that modules do not need to share all of these characteristics, prompting some authors to remark that such flexibility weakens the concept’s theoretical power (e.g., Karmiloff-Smith, 2006).

Blakemore & Cooper, 1970; Wiesel & Hubel, 1963). Adaptive behaviors might require some sort of experience in order to develop (e.g., imprinting), and what appears to be unlearned needs not being tied to genetic hardwiring (e.g., Gottlieb, 1997). Automaticity characterizes learned behaviors that are defined in opposition to hardwired-as-unlearned behaviors, for example word recognition during reading (e.g., Stroop effect). Reflexes present at birth, the quintessential “hardwired” behavior for many writers, are not performed obligatorily but are sensitive to the context (Adolph & Bergen, 2011). Brain regions purportedly devoted to process a given type of information, such as the face fusiform area, are activated by other objects of expertise such as birds and cars (e.g., Gauthier et al., 2000); therefore, their processing can change. Finally, what may be adaptive need not necessarily be characterized by structural fixedness, as demonstrated by neurogenesis and connectivity changes in the olfactory bulb (Oboti & Peretto, 2014).

The risk of cross or illicit inferences is exacerbated by the fact that “hardwired” is often not defined or not followed by pertinent citations. Semantic vagueness makes it difficult to evaluate the empirical evidence for claims of “hardwiring”. Consider the following quotation:

“Attraction and sex are hard-wired, universal, behaviors programmed in single cell organisms as well as in complex nervous systems important for sociality, competition, and reproductive success.” (Gobrogge & Wang, 2016, p. 80)

Because universality and behavioral programming (whose exact meaning is also unclear) are explicitly stated, alternatives might include: having specific neural systems supporting these behaviors, developmentally fixed, genetically determined, unlearned, or automatic. Or consider the expression “Humans are hardwired for X”. The expression often refers to extremely complex behaviors, such in “Human beings are hardwired to nurture, protect, and promote the welfare of others...” (Collins, Ford, Guichard, Kane, & Feeney 2010, p. 367). As I suggested, “hardwired” here might indicate having structures that support specific behaviors. Other candidates might include: having structures that have evolved to support such behaviors or

characterized by developmentally fixed traits. Because the various terms describe characteristics that are not equivalent or can dissociate, one form of evidence cannot substitute another.

Fixedness itself can be interpreted in a variety of ways if the nature of what is fixed is not clarified. Consider the following example:

“... the ability of the visual system to abstract invariant relations from the kind of patterns I have been describing is the product of “hard-wired”, or fixed, visual pathways originating at the retina and terminating in the cortex” (Johansson, 1975, p. 87)

“Fixed” here could refer to the stability of connections, once in place (meaning 1), to the developmental process during which such connections become established (meaning 3), or even to the regularity of the pattern of connections across individuals of the same species. Unless a precise meaning is provided, the type of evidence required to establish whether such pathways are “fixed” remains unspecified.

Fluctuations of meanings appear even within the same text. In reviewing work in the then-emergent field of neural plasticity, Blakemore (1971) used “hardwired” with at least two different meanings: not amenable to change based on learning (p. 614) and structured at birth for a given function (p. 615). The two connotations refer to different biological phenomena, as their occurrence can dissociate: structures or behaviors that are present and functional at birth can change and those that are difficult to change can develop and be observed throughout life. Similarly, in their chapter on nonverbal communication, Segerstråle and Molnár (1997) used “hardwired” with the meaning of having a biological basis (pp. 8 and 15) and adaptive or “phylogenetically rooted” (pp. 9-10, as revealed by the analysis of the cited works by Suomi and Schiefenvölen on grooming in the same volume). LeDoux (2002) also uses “hardwired” with a variety of connotations, such as genetically determined and adaptive (p. 6), innate (as unlearned; p. 63), and species-specific circuit dedicated to

a specific function (p. 89). Once again, using the same term to refer to different traits might lead to the incorrect assumption that these traits are equivalent or interchangeable.

Finally, what is “hardwired” for one definition is not necessarily “hardwired” for another. For example, hardwired-as-fixed and hardwired-as-invariant in terms of stimulus-response relationship have been used to describe behaviors characterized by stereotyped sequences of motor acts and triggered by the presentation of a specific stimulus, such as reflexes present at birth. These definitions do not necessarily include behaviors that are considered “hardwired” based on different definitions, such as localized in specific neural circuits (e.g., speaking or signing a language). Similarly, what is considered hardwired-as-localized has been used to characterize functions supported by specific brain regions, such as parts of the visual systems and the motor cortex. However, most of these areas change with experience<sup>11</sup>, and therefore are not “hardwired” for hardwired-as-fixed. Finally, behaviors deemed to be adaptive do not necessarily exhibit automaticity, lack of representation, encapsulation, or localization of functions (e.g., hunting in in predatory species).

### Conclusions

The main goals of this paper were to characterize the meaning of “hardwiring” in brain and behavioral sciences, to examine the degree of overlap with the concept of innateness and the degree to which different connotations are treated as equivalent and clustered. The present analysis showed that “hardwired” assumes a variety of meanings in the scientific literature. The term is applied in reference to the characteristics of certain behaviors, such as their fixedness, their association to the workings of specific and identifiable neural system, and automaticity. However, these connotations are typically situated within a narrative about origins. As such, “hardwired” is used to identify

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<sup>11</sup> Obviously, all aspects of the nervous system change during development. Therefore, the concept of hardwired-as-fixed is intrinsically problematic when applied to biological organisms.

behaviors that are species-typical and supported by the functioning of dedicated neural regions that have evolved to specifically support them, because these behaviors are considered adaptive. The development of these behaviors and systems is reliable across individuals and guaranteed by the unfolding of biological processes orchestrated by internal (typically genetic in nature) mechanisms. Some of these behaviors are observed at birth, and therefore considered unlearned, “preprogrammed” or “prewired,” supported by neural systems in place before their use. Others reliably emerge later in life. Some of these behaviors, generally those tied to perception, movement, and emotion, are described as automatic and invariant in terms of behavioral expression. Once these neural systems are activated, for instance by the presence of an environmental stimulus, the behavioral response is triggered automatically, mandatorily, and without conscious control. This narrative is familiar; indeed, not only it characterizes “innate” behaviors, but also instinctive behaviors:

“The debate has been confused because the term “instinct” means remarkably different things to different people. To some, “instinct” means a distinctly organized system of behavioral patterns, such as that involved in searching for and consuming food. The different modules of behavior have been likened to the various tools found on a Swiss Army knife. For others, an instinct is simply behavior that is not learned. Instinct has also been used as a label for behavior that is present at birth (the strict meaning of “innate”) or, like sexual behavior, patterns that develop in full form at a particular stage in the life cycle. Another connotation of instinct is that once such behavior has developed it does not change. Instinct has also been portrayed as behavior that develops before it serves any biological function, like some aspects of sexual behavior. Instinct is often seen as the product of Darwinian evolution, so that, over many generations, the behavior was adapted for its present use. Instinctive behavior is supposedly shared by all members of the species (or at least by members of the same sex and age). Confusingly, it has also been used to refer to a behavioral difference between individuals caused by a genetic difference—so instincts are both universal and part of individual differences.” (Bateson & Martin, 2000, p. 87; see also Table 1 on p. 198 in Bateson, 2000)

Not only do “hardwired” behaviors share many of the characteristics of so-called innate behaviors: the two terms are considered, and used as, synonyms. This similarity extends to authors’ tendency to cluster the various connotations together, as if they refer to equivalent or co-occurring traits. However, the traits describe different biological phenomena and often dissociate; therefore, we cannot assume that behaviors or neural systems characterized by the presence of one trait will also exhibit features typically associated with other traits. Such an assumption, which increases the

risk of lumping together behaviors defined by different characteristics, is fostered by the adoption of the same term to refer to different phenomena and exacerbated by the practice of not defining what “hardwiring” means in a given context. In the absence of unambiguous and operational definitions, leeway is given for the type of empirical evidence required to substantiate claims of “hardwiring.” Furthermore, what is “hardwired” for one definition is not necessarily “hardwired” for another. Therefore, the use of the concept does not rely on a coherent body of empirical evidence. This lack of coherence raises doubts regarding the usefulness of “hardwired” in science.

Similarly to “innate,” “hardwired” is used in contrast to features such as learned, acquired, influenced by the context or environmental factors, controlled (vs. automatic), and non-adaptive. Such labeling conveys the impression that at least some of the characteristics of a trait have been elucidated because they have been contrasted with their opposite. However, these dichotomies do not hold for many behaviors (e.g., traits present at birth can be learned) or are based on concepts that are scientifically controversial, such as genetically determined and unlearned. Ironically, the use of “hardwired” seems to transcend such dichotomies: the label has been used to refer to behaviors present at birth and to behaviors that develop later in life; to behaviors deemed to be unlearned and to behaviors that require learning or some type of experience; to neural structures that are deemed to be fixed and to structures that are known to change; to behaviors shown to rely on the workings of specific neural systems and to behaviors whose neurophysiological underpinnings or correlates are unknown; to behaviors characterized by a certain degree of automaticity and to behaviors whose automaticity has never been tested. However, such transcendence stems from the indiscriminate use of the term, not from the adoption of a theoretical approach that views these and related dichotomies as obsolete and ill-conceived (e.g., Johnston, 1987; Oyama, 2000a; Thelen & Smith, 1994). Indeed, the “hardwiring” of a system is typically assumed, not tested. The concept is commonly invoked to explain (or explain away) intricate trees of complex behaviors that appear to



lack direct experiences to seed them. As a result, “hardwired” functions as an endpoint, not as a productive scientific hypothesis.

As mentioned, some authors have indeed argued that the use of labels and metaphors such as “innate,” “instinct,” “hardwired” and “preprogramming” might hinder the investigation of outstanding questions about the development of behavior. For instance, showing that the development of a behavior is insensitive to a given experimental manipulation does not entail insensitivity to any contextual factors (Griffiths & Machery, 2008<sup>12</sup>). The literature provides many examples on the role of non-obvious factors on development of traits. In one of these cases, a preference for visual stimuli that resemble jungle fowls is present in chicks that were raised in darkness. One might conclude, as no visual experience is necessary for its emergence, that such preference is “hardwired.” But its development is still dependent on some form of experience. Research by Bolhuis and colleagues showed that non-visual experiences such as running on a wheel or being exposed to the taped sound of the maternal call are able to induce the predisposition in chicks reared in darkness (Bolhuis & Honey, 1998). If these experiences are absent, the predisposition to follow the jungle fowl does not emerge in these chicks. Therefore, a visual preference can emerge thanks to non-visual experiences. As all behaviors, even the so-called instinctive ones, develop, efforts should go into elucidating their developmental precursors. We must move beyond the illusory reassurance of labeling them as “hardwired” or “innate” to foster such curiosity and investigation.

It is therefore tempting to view “hardwired” as a powerful metaphor that has allowed us to reframe our intuitions and assumptions regarding certain types of behaviors by seemingly grounding them in the reality of neural circuits and mechanisms. In this view, “hardwired” can be

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<sup>12</sup> In their critique of innateness, Griffiths & Machery (2008) argued that the concept functions as an “anti-heuristic,” as “... [it] encourages researchers to check the obvious sources of environmental input, and then to stop looking”; p. 405).

conceptualized as the reframing of innateness in the age of the brain: so-called innate preferences, skills, and behaviors are now explained by appealing to the existence of dedicated neural circuits. These circuits are “wired” in a “hard” fashion by evolution and therefore seen as fixed within, and across, individuals and generations. Fixedness is explained by appealing to the special role of genes in organizing these circuits, which are organized specifically to perform certain functions. Their characteristics, organization, and functioning differ from those supporting behaviors that are not considered “hardwired” (e.g., reading). In line with concepts of cognitive science developed in the 1970s and 1980s, circuits are described as sharing the characteristics of Fodorian modules (e.g., automaticity, functional specificity, localization, etc.). The direct and explicit appeal to brain mechanisms is perhaps the novel element in the concept of “hardwired” with respect to “innate,” although reliance on hypothetical dedicated (and genetically determined) circuits implicitly pervades the innateness literature and was a critical element of theories on instincts (such as von Uexküll’s and Lorenz’ concept of “innate releasing mechanisms” to explain the triggering of fixed action patterns upon the presentation of a sign stimulus; Tinbergen, 1951, p. 42). Technological advances in neuroscience are allowing researchers to map circuits and start defining the relationship between architectural aspects of the brain and function. However, such relationship remains a complex one; defining and establishing causal structure-function relations is not a trivial matter (e.g., Wallisch & Movshon, 2008). Explanations of behavior based on the workings of specific circuits must be established empirically and causally, not by assuming the existence of dedicated networks or describing neural correlates. Unfortunately, a casual approach is adopted in addressing these issues, especially when human behavior is concerned. As a consequence, expressions such as “humans are hardwired for X” abound, even for complex behaviors whose physiological correlates, let alone their underpinnings, are unknown.

The present analysis shows that the meanings of “hardwired” and “innate” do not overlap completely. The analyses provided by Bateson (1991), Griffiths (2002), and Mameli and Bateson (2006), do not explicitly mention features such as fixedness (once a trait has developed), automaticity, lack of representation, encapsulation, and localization, although some of these concepts have been invoked to characterize “innate” neural circuits assumed to support “innate” behaviors. As mentioned, some of these connotations overlap with those of modular systems proposed by Fodor (1983), which were also deemed to be “innate” and “hardwired.” These concepts seem to resonate with each other and are invoked to explain the existence of certain types of behaviors. Indeed, Griffiths (2002) points out that the idea that one of the meanings of “innate” as proposed by Bateson (1991), “a distinctly organized system of behavior driven from within” (p. 73) concerns a “conception of unit of mental evolution from classical ethology which resonates strongly with the idea of a ‘mental module’ found in contemporary evolutionary psychology (...)” (p. 82). The concept of module is also evoked by Bateson and Martin (2000, p. 87) in their discussion of instincts (see quotation above, p. 30) and by Bateson & Mameli (2007) in their analysis of innateness. It is therefore possible that the concept of “hardwired” offered a shift from the implementational vagueness of “innate” towards a more detailed way to conceptualize certain types of neural circuits and behaviors, especially during a time in which scientific investigation of the neurophysiological bases of behavior expanded considerably and a range of new concepts was made available by cognitive scientists<sup>13</sup>. Future work should unpack and explore these relationships more in detail.

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<sup>13</sup> The reference to how functions are physically implemented might explain why the use of “hardwired” has spilled over to other contexts, revealing a flexibility that does not seem to characterize “innate.” For example, in his book *Living Originalism*, Balkin (2011) distinguishes between “hardwired” rules of the Constitution, interpreted in determined and obligate fashion (e.g., each state is represented by two senators in the Senate), and standards or principles whose interpretation and implementation are left open to allow the political process to take place, for example through practice or precedents (e.g., Section 1 of the Fourteenth Amendment). In the context of medical research, selection bias in randomized controlled clinical trials has been considered a form of “hardwired” bias, as it introduces limitations that cannot be removed or corrected with statistical methods (Prasad & Berger, 2015). Such limitations are now intrinsic to the research process. These examples do not adopt the “hardwired” metaphor to explain how constraints are

The partial overlap between “hardwired” and “innate” raises the question of whether any of the non-shared meanings constitute useful candidates for “hardwired.” As concepts and definitions proposed to characterize the nature of some cognitive processes, these meanings have helped scientists outline concrete steps to test hypotheses on how mechanisms and circuits might be organized and function. As a result, research in the past few decades has provided a much more nuanced view of how the brain is organized in terms of the ability of neural circuits to change through life (e.g., Roeder & Roesler, 2002), sensitivity to contextual influences (from other circuits or internal systems) and experiences (e.g., Fontanini & Katz, 2008; Ghazanfar & Schroeder, 2006), and lack of one-to-one mapping between brain regions and cognitive skills or behaviors (e.g., Price & Friston, 2005). If these characteristics (automaticity, lack of representation, encapsulation, etc.) vary as a matter of degree, it might be possible to adopt “hardwired” to refer to behaviors or neural systems that are on one side of the spectrum. However, these features do not characterize the complex behaviors that are typically associated with the concept of “hardwiring,” as some of these behaviors have been found to exhibit flexibility and carried out in a controlled or deliberate fashion. Furthermore, these traits might not necessarily co-occur. For example, linguistic skills are considered “hardwired” in the human brain because they are tied to the work of specific neural circuits (Broca and Wernicke’s areas; Konner, 2002, p. 151). However, some of the functions to which these regions contribute (e.g., aspects of speech production and perception) cannot be described in terms automaticity, lack of representation, or encapsulation (e.g., Bruderer, Danielson, Kandhadai, & Werker, 2015; Devlin & Watkins, 2007).

The overlap between “hardwired” and “innate” reveals that familiar dichotomies and narratives, albeit outdated, still enjoy broad popularity in psychology. Indeed, the concept of “hardwired” might

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implemented at the physical level; however, the level at which such constraints are implemented is clear, even in terms of origins (human intentions and human error, respectively).

contribute to perpetuating them<sup>14</sup>. As Oyama (2000a) and Johnston (1987) argued, the terminology used to describe and explain certain behaviors has changed, in the sense that has become more technical, and seemingly more scientific; however, the underlying assumptions have remained the same. These assumptions, which pertain to thinking about developmental processes in dichotomous terms (e.g., biological vs. acquired, unlearned vs. learned, fixed vs. changeable, hard- vs. soft-wired, nature vs. nurture), have proven to be irresistible even in the presence of complications (like the ones discussed in this paper), empirical data that challenge them, and sophisticated views on development that address their shortcomings (e.g., developmental and dynamic system theories; Oyama, 2000a; Thelen & Smith, 1994). Perhaps abandoning these terms will not prevent us from engaging in dichotomous thinking, as Johnston has argued (p. 179); a drastic change in narrative will require a reconceptualization and redefinition of the very concepts that have made this narrative so pervasive and persistent, such as nature and nurture (for a proposal, see Oyama, 2000a). However, replacing “hardwired” with more precise, operational definitions might lead scientists and writers to acknowledge the specificity and limits of their investigations and claims, therefore reducing the confusion created by conflating different theoretical concepts, scientific questions, and phenomena.

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<sup>14</sup> Perpetuation appears to survive the limits of linguistic translation. For example, “hardwired” in Baron-Cohen’s (2003) famous claim “The female brain is predominantly hard-wired for empathy. The male brain is predominantly hard-wired for understanding and building systems” (p. 1) is translated as “programmed” in the Italian version (“Il cervello femminile e’ “programmato” per l’empatia. Il cervello maschile e’ “programmato” per la comprensione e l’elaborazione di sistemi” (2004, p. 3; interestingly, the adverb “predominantly” has not been included in the Italian translation). The idea of programming ties together ideas of design, evolution, developmental fixedness, and inevitability (innateness, in other words).

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## Appendix One

Additional examples of how “hardwired” and “hardwiring” have been used throughout the scientific literature, organized by the connotations discussed in the text. Quotations within each section follow a chronological order.

Fixed, resistant to change

“Although multisensory neurons are found in many areas of the brain, those in the midbrain (i.e., superior colliculus, SC) have been studied most extensively and have served as a model for understanding some of the neural operating principles of multisensory integration ... However, this capability is not hard-wired at birth. Very young SC neurons are responsive only to unimodal inputs; it is not until many days later that some of them begin to respond to inputs from more than a single sensory modality, and even then they are not yet capable of integrating these inputs to produce the synthesized multisensory signals that characterize the normal adult.” (Stein, Wallace, & Stanford, 1999, p. 72)

“It was long believed that the synaptic networks and functional organization of the brain were hard wired from birth and could not change during adult life” (Lundborg, 2003, p. 213)

“..., myelin and myelin-associated inhibitors are also implicated in reduced developmental plasticity (...), with high myelin content being related to more hard-wired and less plastic regions in the cortex (...).” (Walhovd et al., 2016, p. 51)

Fixed as reflecting an invariant relationship between stimulus and response

“Deese (1985) has pointed out that in the early history of neurophysiology an important distinction was drawn between involuntary reflexes and voluntary behavior, the former implying fixed or hardwired, input-output systems, the latter implying volitional behavior and choice.” (Lazarus, 1991, p. 87)

“We argue, however, that context-specificity is not equivalent to flexibility in mapping of sound and referent (here: different predator or food types). In fact, one could conceive a completely hard-wired system where specific releasers invariably give rise to highly specific responses, such as the responses of female bush crickets to male song of the species...” (Fischer & Price, 2016, p. 5)

Developmentally fixed

“Cowbirds ... are brood parasites, which means that the young ones are raised by a foster species and have no reliable early contact with their parents (...). Thus, the young cowbird faces a chance of learning the “wrong” species typical behaviors leading to lower reproductive fitness. Evolutionary theorists have argued that cowbirds must be a hard-wired species immune to postnatal experience to avoid mis-mating. Even strong proponents of nurture have suggested that the cowbird would need an innate safety net to prevent mating errors (...).” (West & King, 2008, p. 384; citations have been removed)

“We found that astrocytes depend on cues from mature neurons to control their complex molecular profile in vivo. This challenges the concept that astrocytes contain hardwired molecular and physiological programs that are fully determined during development and indicates that neurons communicate with astrocytes to actively regulate their local environment in the brain.” (Farmer et al., 2016, pp. 851-852)

Automatic, not represented

“If dogs that were in the attack posture had to willfully summon all the details of that posture in order to get ready to do battle, it would just take too long. They would be defeated by dogs that had a hard-wired link between the relevant muscle groups and the emotionally aroused condition of the brain. Therefore, according to Darwin, the only

surviving dogs were those for which there were automatic links between emotional arousal in the brain and the relevant muscular positions in the body.” (Frank, 1997, pp. 288-289).

“PPI [prepulse inhibition] has been hypothesized to be automatic, or “hard wired,” because it is unlearned ...” (Schell et al., 2000, p. 409).

“Psychologists, neuroscientists, and economists often conceptualize decisions as arising from processes that lie along a continuum from automatic (i.e., “hardwired” or overlearned, but relatively inflexible) to controlled (less efficient and effortful, but more flexible).” (Rand et al., 2017, p. 1)

#### Not learned/unlearned

“Tools such as levers have a logic to them: One must apply force to the beam, not the fulcrum, for the contraption to function as a lever. In like manner, stimuli must respect the logic of the nervous system, be that hard-wired or learned.” (Killeen, 1992, p. 433)

“Why might it pay for the child to learn parts of a language rather than having the whole system hard-wired?” (Pinker, 1994, p. 242)

“A second group of alternative explanations could propose that any connection between expression and physiological change is learned and not hard-wired. The extreme version of this viewpoint sees emotions as totally socially constructed...” (Ekman & Keltner, 1997, p. 37)

“Insect neural circuits perform both hard-wired and learned sensorimotor transformations.” (Huston & Jayaraman, 2011, p. 527)

#### Structured to perform a specific function; “hardwired for X”

“According to Hubel and Wiesel these cells are hard-wired and ready for action as soon as the kitten open its eyes, at about 10 days old. They found that cells in the kitten cortex are not so easily excitable but are still basically orientation-selective even if not so specific” (Blakemore, 1971, p. 615)

“Although each emotive circuit may be nonspecific in the sense that it can provoke several distinct emotive actions, they may all be specific (hard-wired), in the sense that each generates a single, homogeneous psycho-behavioral tendency...” (Panksepp, 1982, p. 413)

“The overriding issue of interpretation, however, is the question of association *versus* causality. In very simple terms, the following three possible correlations between brain structure and sexual orientation can be envisaged. (1) Homosexual behaviour is indeed hard-wired and is caused directly by the differences in brain structure. Men are destined to be homosexual because, for whatever aetiological reason, the processes of neurodevelopment result in a nucleus or tract of abnormal size or neuronal constitution, and the effect of this difference is to produce a homosexual orientation.” (Harrison et al., 1994, p. 814; italics in the original)

“... the emotional brain’s hardwired responses serve to inform a person of internal experiences and external surroundings. During the healthy lifespan of a person, these emotional responses further develop via learning experiences and cultural influences.” (Pascual-Leone et al., 2016, p. 139)

#### Tied to specificity of brain regions (localized)

“Distinct emotional processes reflect activity in specific hard-wired brain circuits” (Panksepp, 1982, p. 408)

“... consistent with all we know about the way the brain works, we can modify the Broca-Wernicke notion of functional centers in favor of a more complex notion of circuits. But none of these refinements make Broca and Wernicke wrong, nor do they undermine the idea that language is somehow hardwired in the brain.” (Konner, 2002, p. 151)

“The ability to follow another individual's gaze direction is affected in individuals with autism and other psychopathological disorders, and after particular localized brain lesions. The hypothesis that gaze following is “hard-wired” in the brain, and may be localized within a circuit linking the superior temporal sulcus, amygdala, and orbitofrontal cortex is discussed.” (Emery, 2000, p. 581)

#### Adaptive /evolved

“... it is helpful to distinguish between behavioral ecologists and those who implicitly or explicitly postulate that specific behavior patterns are hard-wired as a result of selection.... Arguments framed in terms of this [second] orientation lead to specious claims that male abandonment or child abuse, say, are “natural.” (Lamb, 1987, p. 79)

“On both the sending (behavioral) side and the receiving (judgment) side of nonverbal communication, some patterns seem to be hardwired, that is, the product of natural selection.” (Patterson, 2009, p. 131)

“Our moral values have evolved over the course of millions of years and are based on universal values of which we're unconscious. Moral behavior manifests itself at a very early stage of development. Since such behavior is also displayed by animals, it would seem to be hardwired.” (Swaab, 2014, p. 249)

“This experiment provided incontrovertible evidence that when it comes to “being ourselves,” we humans like to have our cake and eat it, too. We revel in the idea of being our own person, but our brain is hardwired for group living. So natural selection came up with a nifty little app that affords us the illusion of being just like everyone else. It tells us that our behavioral choices are rational and appropriate while offering us the sociocognitive autonomy we crave.” (Dutton & Abrams, 2016, p. 46)

#### Genetically programmed/determined (genetic hardwiring)

“The simplest and most automatic of such behaviors may well be genetically hard-wired into cellular units of the human brain and facial nerves, such that the pattern of contraction of the facial muscles develops during early postnatal development by a chain of physiological events requiring a minimum of learning.” (Wilson, 1978, pp. 62-63).

“What are the necessary conditions for the development of an articulatory loop? Is the articulatory loop necessarily tied to language? Does it require lifelong practice with a complex input–output system? Or can any motorically enacted stimulus lend itself to the use of an articulatory loop? If the latter is true, it would suggest that the articulatory loop observed for language is not a “mechanism” at all (either genetically hard-wired or ontogenetically developed), but is, rather, the strategic recruitment of sensory and motor resources.” (Wilson & Fox, 2007, p. 470)

“Separate from the question of analysis is the source of the knowledge of the language the speaker possesses. Was it learned or was it somehow hard-wired into the speaker's genome?” (Everett, 2015, p. 919)

“[Drosophila] Males display an innate ability to engage in aggression, suggesting that the development and function of the circuits underlying aggression are genetically hardwired.” (Hooper, 2016, p. 109)

#### Connected to

“Innate emotional reactions occur when the amygdala is turned on (by innate or learned triggers) because the response is hardwired to the amygdala” (LeDoux, 1998, p. 261)

“Bidirectional communication between the spleen and brain occurs via the immune system and the central nervous system (CNS). The peripheral lymphoid organs, including the spleen, are hardwired to the autonomous nervous system...” (Zhao, 2016, p. 191; citations have been removed)

## Appendix Two

## Additional examples of clustering

“It is generally assumed that sequences of species-specific postures and movements are the expression of the activity of brain mechanisms involved in specific motivational states. In ethology it is often implied that such mechanisms have a direct genetic basis and are somehow hardwired in the brain. If that is true, then one should be able to find differences in the responses to manipulations of brain mechanisms involved in species-specific responses between genetically different strains.” (Kruk et al., 1990, pp. 177-178)

“Much of the study of emotion in psychology has proceeded from the assumption that there are certain “basic” emotions which are in some way “hard-wired” physiologically into the human brain and nervous system (...). This group of scholars sees emotions as part of human physiology, properties of a precultural social human body and existing separate from and prior to cultural encrustations. Emotions are understood as primarily genetic, based on evolutionary adaptation, and functional in the production of “behavioural homeostasis” (...). These “basic emotions” may be culturally glossed and combined to form other, complex emotions.” (Tarlow, 2000, p. 715; citations have been removed)

“After 13 to 23 h of training we still saw no improvement in performance, and thus concluded that the precedence effect is not easily unlearned and must therefore have some hardwired mechanisms that are rapid, automatic, and not cognitively mediated.” (Litovsky et al., 2000, p. 2350)

“This might be taken to suggest that the human evolutionary history with spoken language has hard-wired into the brain a dedicated mechanism, which uses speech-based representations for working memory.” (Wilson & Fox, 2007, p. 470)

“Because the processing of auditory stimuli in the environment has biological relevance, it became preattentive, automatic, adaptive (...), and disrupts the ongoing processing of other stimuli (...). Though this hard wired reaction to sound changes evolved in humans’ ancestors to insure survival, it is observed for background sound changes of all types, threatening or not.” (Fraser & Bradford, 2013, p. 63; citations have been removed)

“However, tuning is mature at birth (...) and thus, may be more immune to the neuroplasticity apparent at all higher stages of the auditory brain. This has bolstered the long-held view that early sensory processing is largely hard-wired and resistant to neuroplastic change resulting from auditory experience or learning.” (Bidelman et al., 2016, p. 40; citations have been removed)

## Figure legend

Figure 1. Frequency of “hardwired” is here quantified on the  $y$  axis as a percentage calculated by “dividing the number of instances of the word in a particular year by the total number of words in that year.” (Greenfield, 2013, p. 1724). An increase in frequency often signals a broadening of the meaning that a certain word assumes in time.

Figure 2. Frequency of use from 1966 to 2015. The search in both databases (for “hardwired” OR “hard-wired”) was performed through the entire publication (“all text”). Note that the two databases are not independent but share some journals. Furthermore, in a few cases, the two terms are also used with their original meaning of a hardwired device, especially in Medline. Also note the different scale, as the two terms are used more frequently in Medline than PsychInfo.

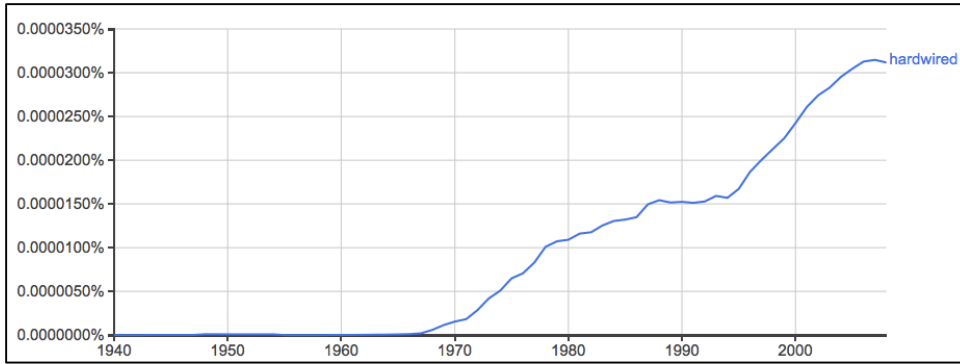


Figure 1

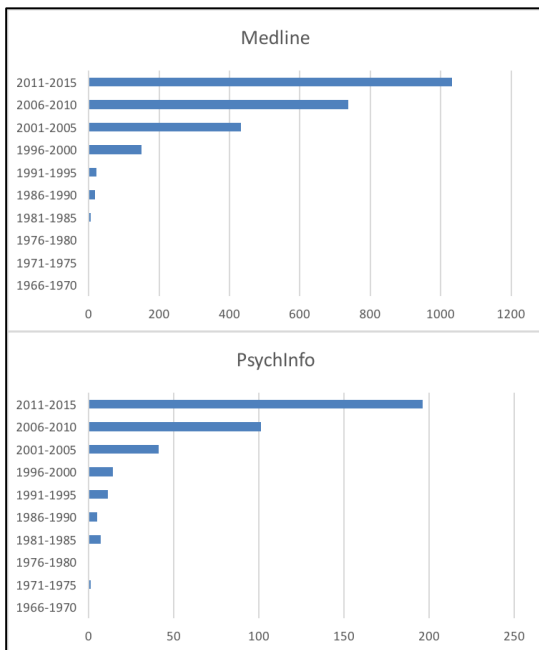


Figure 2