Conclusion

During my time in graduate school, a "crisis" emerged in my field. One of the watershed moments included Daryl Bem publishing statistical evidence for Extrasensory Perception (ESP; Bem, 2011) using research practices and statistical methods that many felt were routine in psychology and certainly not objectionable enough to warrant a rejection from the field's flagship journal. A year later, Daniel Kahneman wrote an email to colleagues calling for more attempts to replicate priming studies and warning of a "train wreck looming". The email was republished in *Nature News* (Yong, 2012). Such concerns have been simmering for a while[1], but with events such as these, the pot overflowed. The field responded with clearer identification (and disapproval) of researcher degrees of freedom ("p-hacking"; Simmons, Nelson, & Simonsohn, 2011), new methods to detect such violations (Simonsohn, 2013; Simonsohn, Nelson, & Simmons, 2014), routine reporting of effect sizes and confidence intervals (Cumming, 2013), large-scale replication attempts (Yong, 2013), pre-registration of studies similar to practices in pharmaceutical research (Nosek & Lakens, 2014), and badges for good practices (Eich, 2014). The discussion continues as I write this dissertation and at least one major journal (Psychological Science) has changed its rules with respect to statistical practices and reporting research practices.

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[1] Examples include criticisms of null hypothesis testing and discussions of Bayesian vs frequentist approaches, including Jacob Cohen's classic "The earth is round, $p<.05$" (Cohen, 1994) and the edited volume "What if there were no significance test" (Harlow, Mulaik, & Steiger, 1997); discussions about the practice of HARKing – Hypothesizing After the Results are Known (Kerr, 1998) and what Charles Peirce called "abductive" reasoning as an alternative to the hypothetico-deductive approach to science (e.g. Rozeboom, 1997); Walter Mischel describing what he called "The Toothbrush Problem" (Mischel, 2009) where researchers avoiding using other researcher's theories as they would avoid using other people's toothbrushes and discussions on common methods and how to make psychology a cumulative science (e.g. Psychological Methods released a special issue titled "Multi-Study Methods for Building a Cumulative Psychological Science" in June, 2009).

The approach taken in this dissertation offers a different perspective to the common consensus. There are statistical issues in the field, mainly centered around researcher degrees of freedom and the abuse and misuse of statistical methods, which some of the suggestions listed above may help resolve, but at its core, our field's problem is one of theory.

1.1 A Theory of Human Behavior

The advantage of a good theory is that it not only makes predictions about what to expect, but also exclusions about what not to expect. As Karl Popper (1962) puts it, "the more a theory forbids, the better it is." (p. 36). With our scientific intuitions tuned by theory rather than life experience, we're better able to identify when something seems "off". When neutrinos appeared to be travelling faster than the speed of light (Agafonova et al., 2012), physicists knew something was wrong, because it violated the Theory of Special Relativity. If vinegar (acetic acid) and baking soda (sodium bicarbonate) combined in your child's model volcano doesn't produce carbon dioxide and hot ice (sodium acetate) solution, chemists know something is wrong, because it violates the Periodic Table and Collision Theory. If fossil rabbits were found in the Precambrian era, biologists would know something was wrong, because it violates the Theory of Evolution. But if humans seem to prefer less choice to more (Schwartz & Kliban, 2004), does this violate our Theory of Human Behavior? What if humans prefer more choice to less or show no preference at all (Scheibehenne, Greifeneder, & Todd, 2010)? If humans appear to walk slower when they're reminded of old people (Bargh, Chen, & Burrows, 1996) does this violate our Theory of Human Behavior? What if they walk faster or ambulate unperturbed by memories (Doyen, Klein, Pichon, & Cleeremans, 2012)? Without an overarching scientific Theory of Human Behavior from which to draw hypotheses and tune our intuitions, it can be difficult to distinguish results that are unusual and interesting from results that are unusual and likely wrong.

There are explanations for the two examples I offered – the choice overload and elderly behavioral primes – and these explanations do come from a Theory of Human Behavior. But that Theory emerges from each researcher's own life experience and perhaps past experimental data. We might call these explanations theories or hypotheses, but as theories they lack generality in predictive power and as hypotheses they flow from each researcher's culturally specific intuitions (Henrich, Heine, & Norenzayan, 2010) rather than an overarching theory.

Mini-theories and hypotheses based on intuitions or past data are not necessarily a problem. In an applied context, such as pharmaceutical trials, testing a drug and showing its efficacy works regardless of the drug's origins[2]. In the applied science of declaring drugs effective for human use, the pharmaceutical sciences have established useful best practices such as multiple studies and pre-registration of methods, sample sizes, and analyses. These practices help establish the presence and size of an effect and prevent changing hypotheses after seeing results (Kerr, 1998). In a basic science context, in principle these hypotheses or mini-theories could coalesce into a larger overarching theory, but in practice avoidance of others mini-theories (Mischel, 2009) and a lack of common methods can slow down or prevent the cumulative process. Moreover mini-theories, especially if they are not formally specified, lend themselves to confirmation rather than falsification and as Popper (1962) points out, "It is easy to obtain confirmations… for nearly every theory—if we look for confirmations" (p.36)[3]. One key advantage to a Theory of Human Behavior in the quest for a

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[2] Examples of such origins include traditional knowledge (St John's wort), past side effects (Viagra), similar chemical compounds (Captopril was the first ACE inhibitor heart medication developed, but others such as perindopril and ramipril soon followed).

[3] Karl Popper (1962) (p.36) lists 7 criteria for a scientific theory, quoted below.

1. It is easy to obtain confirmations, or verifications, for nearly every theory—if we look for confirmations.
2. Confirmations should count only if they are the result of *risky predictions*; that is to say, if, unenlightened by the theory in question, we should have expected an event which was incompatible with the theory—an event which would have refuted the theory.

cumulative science is that it allows us to interpret past findings in the way that the Periodic Table and Collision Theory allow you interpret pre-Mendeleev chemical experiments.

Psychology has decades of data gathered using clever methods and manipulations, but with that data now under suspicion[4], a Theory of Human Behavior would be a useful way to parse which results are most suspicious and thereby move forward as a cumulative science. But the mere fact that such an overarching theory would be useful, does not imply that one exists or that any will suffice. There are many candidate theories. A popular Theory of Human Behavior in economics is that of economic man or Homo Economicus, a theory borne out of 19th century philosophy (Persky, 1995). Homo Economicus conforms to the requirements of a scientific theory and is going through a process of improvement after some of its predictions have been challenged (Gintis, 2000; Henrich et al., 2001; Kahneman & Tversky, 1979; Thaler, 2000). I suspect that the most predictive Theory of Human Behavior will flow from the Theory of Evolution, connect with the growing body of knowledge in neuroscience and genetics, and explain both cross-species differences and cross-

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3. Every 'good' scientific theory is a prohibition: it forbids certain things to happen. The more a theory forbids, the better it is.
4. A theory which is not refutable by any conceivable event is nonscientific. Irrefutability is not a virtue of a theory (as people often think) but a vice.
5. Every genuine *test* of a theory is an attempt to falsify it, or to refute it. Testability is falsifiability; but there are degrees of testabilty: some theories are more testable, more exposed to refutation, than others; they take, as it were, greater risks.
6. Confirming evidence should not count *except when it is the result of a genuine test of the theory*; and this means that it can be presented as a serious but unsuccessful attempt to falsify the theory. …
7. Some genuinely testable theories, when found to be false, are still upheld by their admirers—for example by introducing *ad hoc* some auxiliary assumption, or by re-interpreting the theory *ad hoc* in such a way that it escapes refutation. Such a procedure is always possible, but it rescues the theory from refutation only at the price of destroying, or at least lowering, its scientific status.

One can sum up all this by saying that *the criterion of the scientific status of a theory is its falsifiability, or refutability, or testability*.

[4] The latest draft of the Open Science Framework's Many Labs replication effort found that only 3 of the 10 effects tested replicated: https://osf.io/s59bg/

cultural variation. It is such a theory that is extended (Chapter 2), tested (Chapters 3 and 4) and challenged with suggested improvements (Chapter 5) in this dissertation.

Humans are an evolved species and Dobzhansky's (1973) famous phrase applies as much to our psychology as to our biology – "Nothing makes sense except in the light of evolution". Like all other species on the planet, all aspects of our behavior must flow from the evolutionary processes that led to our present state. My dissertation builds on and tests one candidate evolutionary Theory of Human Behavior – Dual Inheritance Theory (or Gene-Culture Coevolution) – the idea that the same evolutionary processes that led to every species on the planet led humans down a unique pathway. Selective forces, some of which are described in Chapter 2, led to the development of a suite of psychological abilities and tendencies that allowed our species to learn from each other with high fidelity. This high fidelity learning led to a second-line of inheritance – culture. Genes adapted to this new selection environment, which now included culture and those genes in turn enabled new cultural information in a co-evolutionary process.

From a Dual Inheritance Theory perspective, the research enterprise involves understanding how evolution shaped our brains and bodies in ways that allowed us to acquire culture (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981), identifying what psychology is required for culture and how culture emerges from that psychology (e.g. Henrich & McElreath, 2003; Schaller & Crandall, 2003), how culture mutually shapes our brains and bodies (e.g. Laland, Odling-Smee, & Myles, 2010), and how culture itself evolves and leads to cross-cultural differences and societal-level phenomena (e.g. Heine & Norenzayan, 2006; Henrich & Boyd, 2008; Henrich, Boyd, & Richerson, 2008; Norenzayan & Heine, 2005; Schaller & Murray, 2008). Dual Inheritance Theory and Cultural Evolution offer several predictions and exclusions for the psychology of our species. The chapters of this dissertation contribute to this enterprise, both in theory and in tests of theory.

1.1.1 Building Theory

The best scientific theories make general predictions and exclusions about what to expect and not expect and are more parsimonious than alternatives. These theories can be expressed in many ways. Natural Selection as a Theory of Evolution was first expressed as a verbal argument (Darwin, 1859). Evolutionary theory has come a long way in the century and a half since Darwin published his classic[5]. For example, we now know about genetics and have a much better understanding of the many processes through which species diversify and evolve. Since the Modern Synthesis, evolutionary biology has expressed its theories using mathematical and computational models. There are good reasons for why this is a useful tool for theory building.

Researchers use formal mathematical and computational models in all kinds of ways – high fidelity simulations of reality (MSC Software, 2004), precise quantitative predictions of systems like the stock market (Chan, 2009), probabilistic models for tasks like facial recognition (Liu & Wechsler, 2002) and so on. Unlike in these cases, biologists, anthropologists, and psychologists often use formal models as aids to thinking through the logic of an argument in order to make testable *qualitative* predictions about phenomena (e.g. Aoki & Feldman, 2014; Boyd & Richerson, 1985; Hastie & Kameda, 2005; Kendal, Giraldeau, & Laland, 2009; MacCoun, 2012; Nowak, Szamrej, & Latané, 1990; Tanford & Penrod, 1983, 1984). By formally defining assumptions, logic, and predictions, anyone can challenge the theory by either testing the predictions or by modifying the assumptions or logic. By deciding on the minimal set of assumptions required to explain a phenomena and formally expressing these assumptions, the logic that follows, and the predictions and then modifying assumptions, logic, and predictions in the face of empirical evidence, we can

[5] Although perhaps because our tendency to rely on prestigious figures (Chudek, Heller, Birch, & Henrich, 2012; Henrich & Gil-White, 2001), researchers still tend to use Darwin's words to bolster their case.

start to build a cumulative science. And expressing these in the language of mathematics has some advantages in the quest for a cumulative science.

Why not rely on verbal arguments? Well, for simple if-then causal relationships, you can get away with words. For example, when the sun is out people eat more ice cream. And perhaps this is mediated by temperature. But our minds are limited in memory and processing (Gigerenzer & Selten, 2002; Kahneman, 2011; Miller, 1956) so arguing with words or just thinking through a theory – effectively simulating in our minds – gets fuzzy fast. In their now classic 1985 book, Robert Boyd and Peter J Richerson express the choices of how to express a theory as, "the real choice is between an intuitive, perhaps covert, general theory and an explicit, often mathematical one… Many aspects of a scientist's mental model are likely to be vague and never expressed" (p.27). Thankfully, we have a couple of cultural technologies that allow us to overcome these mental limitations: analytic models – solvable systems of equations – and when it gets more complicated, computational models. By building formal testable theories to explain the world, we can test competing theories, and bring the theories of the biological, psychological, anthropological, and human evolutionary sciences into a broader scientific framework.

Since *Homo habilis* (or perhaps *Australopithecus*; Harmand et al., 2015)first banged two rocks together to make a chopping tool, specialized tools have allowed us to overcome the limitations of our bodies. Hammers let you hit harder; trains let you travel further. In modern societies, many tools are instrumental in overcoming the limitations of our mental faculties. The simple pen and paper let you remember more, computers let you calculate faster. Most hypotheses in the psychological sciences are generated without the need for any such specialized tools, because the typical objects of inquiry (unidirectional causal relations operating at a single level of analysis) are amenable to informal logical deduction. Although, as I have argued, there are advantages to a Theory of Human

Behavior, especially in a basic science context. But even without a broader Theory of Human Behavior, when addressing questions about phenomena defined by more complex causal relations that play out dynamically over time and produce emergent consequences that must be measured at a different level of analysis entirely, specialized tools *are* needed. Mathematical and computational models can be thought of as aids to thinking, allowing us to work through the logic and assumptions of systems more complex than our minds can fully represent. Models need to be abstract enough to be more tractable than reality, but realistic enough to sufficiently capture the problem and inform our understanding of it. They allow us to make formal, precise predictions that go beyond the imprecision of words. But models are only useful insofar as their logic and assumptions are informed by empirical research, and in turn they make predictions that can be tested empirically.

1.1.2 Testing Theory

General unifying theoretical frameworks like Dual Inheritance Theory are not monolithic or complete. The details are worked out by generating "sub-theories" and testing them. These formal theories make specific predictions; different theories make competing predictions. To distinguish between competing theories, we must turn to empirical data.

There are many ways we can test theoretical predictions. Each method has its pros and cons. Laboratory experiments, used in both Chapters 3 and 4, give you control at the expense of true ecological validity. In field experiments, you lose some of that control, but gain ecological validity. Finally, there are existing data-based methods, such as those used in Chapter 2 and suggested in Chapter 5. However, without randomized controlled trials, causality is more difficult to infer and at best we can say that they do not falsify the theory. Together these methods are best deployed not to confirm a theory, but in a good Popperian manner test competing theories and hopefully falsify one[6].

1.1.3 Present Research Enterprise

The approach I have discussed thus far is the approach used throughout this dissertation. In Chapter 2, I challenged the most popular explanation for the evolution of large brains – The Social Brain Hypothesis (Dunbar, 1998). I presented a formal model and argue that the Social Brain Hypothesis is actually part of a larger more general process, which I call the Cultural Brain Hypothesis. The Cultural Brain Hypothesis model makes several predictions, which I test using existing data. These results reveal that the Cultural Brain Hypothesis can explain the same evidence as the Social Brain Hypothesis, but also additional evidence that has yet to be explained by a single theory. I therefore argue that the Cultural Brain Hypothesis is a more general and parsimonious explanation to alternative theories. Further, under some conditions the same mechanisms underlying the Cultural Brain Hypothesis also lead to a separate evolutionary pathway where culture accumulates and exerts further selection pressures on large brains, which in turn allow for more culture. The conditions that lead to this autocatalytic coevolution are the predictions of the Cumulative Cultural Brain Hypothesis. The predictions are consistent with other more specific models and with empirical data, including the data presented in Chapters 3 and 4.

Different formal theories may make the same predictions, but have different assumptions and logic underlying those predictions. Thus they may both be consistent with existing correlational

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[6] Of course, one falsification is not enough to overturn a theory. And theories can and should be modified until they can stand no more against the weight of contrary evidence. Even so, scientists are humans and scientific revolutions rarely proceed in this ideal manner. Instead scientific revolutions may go through Kuhn's 5 phases and perhaps require a generational shift. As Max Planck is reported to have said: "A new scientific truth does not triumph by convincing its opponents and making them see the light, but rather because its opponents eventually die, and a new generation grows up that is familiar with it" (Kuhn, 1962).

data and only separable by an experiment. This is the case for the relationship between sociality and cultural complexity, tested in Chapter 3. Take the case of cultural loss following population loss. Cultural drift style models predict that this loss is caused by a process analogous to genetic drift, whereby there are fewer people to remember the culture. On the other hand, "treadmill" style models predict that this loss is due to a loss in sociality – the size and interconnectedness of populations – which is required to compensate for imperfect transmission fidelity. Our results were consistent with a treadmill style model.

Theories also shape the way in which experiments are designed and can help explain why they fail to show results. Muthukrishna, Shulman, Vasilescu, and Henrich (2013), reported in Chapter 3, was not the first experiment to test these competing theories. Caldwell and Millen (2010) previously showed no effect of number of models on mean skill level in a paper airplane task. The impetus for the studies reported in Chapter 3 was that their study failed to capture some necessary aspects of the theory. Specifically, the theoretical models Caldwell and Millen (2010) tested predicted that if some skill or other cultural trait is sufficiently easy to learn or cognitively transparent, then increasing the number of models available to learners will have little impact (Henrich, 2004). That is, making a simple paper airplane is too easy to learn and their experiment was therefore not a test of the competing theories. When we used tasks that were difficult for an individual to learn in one lab generation (image editing and tying a system of rock climbing knots), the results supported a treadmill model over a drift model.

In Section 1.1, I used choice overload as an example of a finding that does not seem to emerge from a well-specified Theory of Human Behavior. I deliberately chose this example, because of its relevance to the experiments reported in Chapter 4. In two experiments, I tested several social learning predictions that emerge from Dual Inheritance Theory and Cultural Evolutionary models.

These included predictions about the relationship between number of options and social learning. Without a well specified theory, the question asked is "whether more choice is better" where "better" can be operationalized in a variety of perfectly acceptable ways (Schwartz & Kliban, 2004). These are fine applied questions of particular relevance to marketers. But from a basic science perspective, in the enterprise of building an edifice of knowledge about the psychology of our species, starting from the bottom up in trying to understand these phenomena can be difficult, because the question might be unanswerable. Is walking or running better? Even if we specify what better means (the easy part) – let's say, for travelling from home to work – the question may still be unanswerable. It depends on so many other factors. How might we narrow down the large or infinite set of possible predictive factors to build a theory – individual differences like fitness, external factors, like how quickly one needs to get to work, alternative options like driving? This is the essence of abductive reasoning. Even if we were to show that on average people prefer running to walking to work, it can be difficult to determine what factors matter when results don't replicate. Indeed, in the case of choice overload, a meta-analysis suggested no effect of choice overall, but admitted that there may be unspecified moderators driving the effect, if it exists (Scheibehenne et al., 2010). In contrast, a Theory of Human Behavior, especially one derived from larger established theories (such as the Theory of Evolution) not only shapes how to test predictions, but also the question that is asked. From a Dual Inheritance Theory perspective, Scheibehenne et al. (2010) are right in that there are many factors beyond number of choices that determine if "more choice is better". A more appropriate starting point is that humans have faced more and less choice over their evolution. They have a suite of psychological tools to deal with that choice depending on the importance (payoffs) and immediacy (time constraints) of the decision, and what information they have available (individual learning, social information, environmental information, choices themselves, and so on). A more appropriate question is how humans behave with more and less choice under different conditions. Which conditions are important and which are not, can be derived via formal evolutionary theory. Nakahashi, Wakano, and Henrich (2012) model how people react to different sized majorities depending on the number of choices available. Their theory and our empirical results suggest that people are more biased towards majorities as the number of options increases. Our empirical results also suggest that they are more likely to defer to use social information to make that decision. Nakahashi, Wakano, and Henrich's (2012) model is a first attempt to formally model decision-making with multiple choices and there are of course many other important theoretical predictions to be made in this area. A formal Theory of Human Behavior shapes the relevant question and narrows down the search space of important factors.

Chapter 4 is also a good example of experiments finding results that go beyond theory. We started with theory and designed an experiment that captured different aspects of the problem, such as the effect of number of options in Experiment 1. Our results reveal a pattern of conformist biased social learning that closely matches theoretical predictions. But our results also reveal the effect of asocial priors based on individual learning, the effect of number of options on the rate of social learning overall, and the effect of individual differences, and in the case of transmission fidelity (Experiment 2); results contrary or not captured by the theory. All of these point to ways in which the theory needs to be reconciled.

Finally, Chapter 5 is also an example of empirical data challenging theoretical models, but in this case based on assumptions rather than predictions. One simplifying assumption made in many Dual Inheritance Theory models, including the model reported in Chapter 2 is a uniform social structure – i.e. all individuals have roughly the same number of connections. While it may be that network structure is irrelevant to the predictions of these theories, the real world shows some consistent network structures across societies at different scales. These structures may affect human behavior and population-level outcomes and have been shown to affect the efficiency of information transmission (Pasquaretta et al., 2014). One barrier to incorporating these structures into formal theory is a lack of theory to explain how these structures emerge from individual decision-making. In Chapter 5, we introduce a potential theoretical explanation for these network structures and show ways in which they affect population-level outcomes – the consolidation of majorities and the spread of innovations. The effect of these network structures on these outcomes indicates that they may also affect other outcomes of relevance to psychologists, anthropologists, and biologists. Chapter 5 is a first step in this direction.

The Theory of Human Behavior that this dissertation relies on is based on the idea that our basic psychology flows from our capacity for culture. Many aspects of this theory are modeled in Chapter 2. There remain several central questions underlying the evolution and psychology of our species. Some of these have answers in theory, others supported by data, and still others that are poorly understood. In the next section, I lay these out and in doing so, situate the present dissertation.

1.2 Central Questions and Answers

Thus far, I have described one potential answer to why humans are so different to other animals: Humans have a second line of inheritance – cultural inheritance – that has accumulated over generations and shaped our psychology and physiology. This answer opens up further central questions and answers.

1.2.1 Why Now?

Life first appeared on this planet approximately 3.7 billion years ago (Ohtomo, Kakegawa, Ishida, Nagase, & Rosing, 2014). Humans and chimpanzees went their separate ways approximately

4-5 million years ago, the earliest stone tools have been dated at approximately 2.6 million years ago (Semaw et al., 2003) and the particular branch of humans that replaced all others (ours) emerged around 200-300 thousand years ago (Scally & Durbin, 2012). If a second line of inheritance is the key to the human success story, why did it only appear in less than the last 0.1% of the history of life[7]? Like with most of these central questions, research is ongoing, but Dual Inheritance Theory predicts that part of the answer lies in temporal and environmental variation (Aoki & Feldman, 2014; Boyd & Richerson, 1985; Nakahashi et al., 2012). If the environment is stable over space and time, slowly evolving genes can adapt to the environment without the need (and cost) of high cognition. If on the other hand, the environment is highly unstable, the information possessed by previous generations or settled groups is less useful and individual learning is needed to adapt to the changed environment. But between these two extremes is a Goldilocks zone where some amount of social learning is beneficial. With a moderately stable/unstable environment, genes are too slow to adapt, and individual learning is more expensive than simply learning from the adapted previous generation (temporal variability) or others already in the environment (migrants facing spatial variation). It is here that the second line of inheritance can evolve.

Testing these theoretical predictions can be difficult, but in recent years ice cores have provided us with high resolution climate data. Martrat et al. (2007) data reveals that at least in the last 420,000 years, climatic variability has increased, consistent with Boyd and Richerson's (1985) model. Exactly the kind of climate variation one would expect for a cultural species to emerge. So the climatic variability was perfect for social learning and culture to be favored, but humans weren't the

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[7] Speculated sapient dinosaurs aside (Russell & Séguin, 1982).

only species affected by that climatic variability, so the next central question is why did cumulative culture evolve in our species and not others?

1.2.2 Why Us?

The first answer to this question is that our species is not alone in the evolution of social learning. Social learning is widespread in the animal kingdom (Hoppitt & Laland, 2013; Laland, 2008; Whiten & Van Schaik, 2007). Moreover, social learning is positively correlated with brain size (Reader & Laland, 2002) and brain size has been increasing across many taxa (Shultz & Dunbar, 2010). Chapter 2 presented the Cultural Brain Hypothesis, a theoretical explanation for this encephalization and other associated patterns. But of course, while other species may have had similar selection pressures for larger brains and even culture, humans are unique in possessing *cumulative* culture. The answer to why humans are alone in our domination of the planet via the capacity for culture likely lies in proto-human physiology, psychology, and sociality. The complete and precise physiological pre-requisites for a cultural species have yet to be theoretically or empirically expressed. In the meantime, we may speculate. For example, primates have an advantage over intelligent birds (Emery, 2006) and dolphins (Whitehead & Rendell, 2014) in having hands, which are useful for manipulating objects and eventually making and carrying tools. Thus hands, a necessity for arboreal life, may have been exapted once humans began on the path to a cultural species. Hands may have also been useful (though not necessary) for gestural communication, which eventually led to language (Gentilucci & Corballis, 2006). But hands can't be the only pre-requisite – we share them in common with other primates. Bipedalism is another candidate pre-requisite. Bipedalism may have evolved as early as 4.4 million years ago (White, Suwa, & Asfaw, 1994) and together with hands, may have allowed our ancestors to freely communicate with gestures and to make and carry tools over large distances. These and other physiological pre-requisites may have been useful or even necessary for making the transition to a fully cultural species. Most of the later changes were psychological and social and it is here that my dissertation makes its contributions.

1.2.3 What Psychology Do We Need For Culture?

What are the psychological and social foundations of culture? The Cumulative Cultural Brain Hypothesis (Chapter 2) captures some of the psychological and social requirements for the leap from a cultural to a cumulative cultural species. Specifically, it makes 4 predictions: (1) high transmission fidelity, (2) low reproductive skew and/or cooperative breeding, (3) smart individual learning ancestors, and (4) an ecology that can be exploited by more knowledge. There are many psychological and social factors underlying each of these predictions.

The Cumulative Cultural Brain Hypothesis is not alone in highlighting the importance of high fidelity cultural transmission (Claidière & Sperber, 2010; Lewis & Laland, 2012). Several experiments in the psychological sciences have demonstrated that humans have a tendency to *overimitate* – copy with high fidelity (Nielsen, Subiaul, Galef, Zentall, & Whiten, 2012; Over & Carpenter, 2013; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). High fidelity transmission has at least 3 requirements: an ability, a proclivity, and social infrastructure.

The ability to copy information with high fidelity is likely supported by other cognitive mechanisms like theory of mind. Theory of mind may have evolved for non-cultural reasons, such as for dealing with the complexities of life in larger groups. Chimpanzees, for example, do seem to have some components of theory of mind, although they lack full-blown human theory of mind (for a review, see Call & Tomasello, 2008). Despite missing some components of human theory of mind (which may be irrelevant in a chimp world), chimpanzees have shown some ability to imitate (Whiten et al., 2009). Imitation ability is a necessary, but not sufficient requirement for cumulative cultural transmission. A species also needs a proclivity to do so.

Horner and Whiten (2005) first showed that children have a tendency to imitate even causally irrelevant actions. This result has been replicated under different circumstances (Lyons, Young, & Keil, 2007; McGuigan, Whiten, Flynn, & Horner, 2007) and with adults (Flynn & Smith, 2012; McGuigan, Makinson, & Whiten, 2011). Humans, at least human children, are also often selective in when, who, and what they imitate, and understand the difference between goal-driven or conventional actions (Herrmann, Legare, Harris, & Whitehouse, 2013). The human proclivity for high fidelity transmission is supported by various other characteristics of our species.

Humans are social (Boyd & Richerson, 2009) and prosocial (Bell, Richerson, & McElreath, 2009; Chudek & Henrich, 2011), giving learners exposure to several potential models. For more difficult tasks, these models go as far to slow down their actions or even teach (Fogarty, Strimling, & Laland, 2011; Kline, 2014). And children expect this, inferring that more knowledgeable models are also more prosocial (Brosseau-Liard & Birch, 2010)!

Human life history also supports the transmission process. First via an extended juvenile period in which additional learning may take place (Gurven, Kaplan, & Gutierrez, 2006; Henrich, forthcoming; Joffe, 1997). If adolescence is defined as the period between sexual maturity and reproduction, there is some evidence that this period is extending even further (Mathews, Hamilton, & National Center for Health Statistics, 2009), perhaps through cultural evolutionary processes. Second, the transmission process is supported by a long lifespan and post-menopausal period, where females (and perhaps males) serve as repositories of accessible knowledge – an Information Grandmother Hypothesis. There is some evidence of this in orca, another highly cultured species. Orca grandmothers lead hunting groups, particularly when resources are scarce (Brent et al., 2015) and their presence increases the survival of their sons (Foster et al., 2012). In humans, Henrich and Henrich (2010) have suggested this hypothesis in the Supplemental Materials of their paper, which showed evidence that Fijian women acquire their adaptive food taboos from their grandmothers. For additional discussion, see Chapter 8 of Henrich (forthcoming).

1.2.4 What Sociality Do We Need For Culture?

Access to multiple models, and perhaps multiple generations, is necessary for the third aspect of an evolutionary system – variation reduction. "One cultural parent makes no culture" (Enquist, Strimling, Eriksson, Laland, & Sjostrand, 2010). The Cumulative Cultural Brain Hypothesis predicts that lower reproductive skew is more conducive to the entering the realm of cumulative cultural evolution, allowing for more genetic variability. One social structure that may have served both low reproductive skew and easier access to multiple models is cooperative breeding. Several researchers have posited the existence of ancient cooperative breeding human societies (Emlen, 1995; Hrdy, 2009; Kaplan, Gurven, Hill, & Hurtado, 2005; Kaplan, Hill, Lancaster, & Hurtado, 2000; Mace & Sear, 2005; Wiessner, 2002) with some evidence of cooperative breeding among modern hunter-gatherers (Hill & Hurtado, 2009). The suggestion (which to my knowledge, has not been formalized) is that a young proto-human primate may have initially learned from mom as many chimpanzees do today (Boesch, 1991; Lind & Lindenfors, 2010; Taglialatela, Reamer, Schapiro, & Hopkins, 2012). Mom may be the primary model simply because her children spend more time with her. Cooperative breeding may have provided a young proto-human access to more moms (and perhaps dads); a gateway to biased social learning, where a young learner could focus on characteristics of the models rather than how much access they had to them. In the model presented in Chapter 2, once social learning evolves, there is a selection pressure for oblique learning to take advantage of other models in the group and learning biases to select from these. The experiments in Chapter 3 also highlight the importance of sociality – the size and interconnectedness of populations

– in the evolution and accumulation of culture. Individuals with access to more models appeared to learn from the best model and then integrate further information from the next two best models.

1.2.5 How Does This Connect With Our Broader Psychology?

The psychological sciences have a wealth of data on the ways in which information is transmitted between individuals; i.e. cultural transmission. These data are often tests of Dual Inheritance Theory and Cultural Evolution predictions and in other cases can inform these theories (Mesoudi, 2009). Some areas of research within social psychology that are of particular relevance to cultural transmission include conditioning (operant conditioning, classical conditioning), social learning (Bandura, 1977), social influence, including norm psychology (Bond & Smith, 1996; Cialdini & Goldstein, 2004; Moscovici, 1980), persuasion, including attitude change (Albarracín & Vargas, 2010; Kumkale & Albarracín, 2004; Petty & Briñol, 2011), and social cognition more generally (Fiske & Taylor, 2013). Other relevant areas include research on the psychology of leadership (Van Vugt & Ahuja, 2011) and group dynamics (Hogg, 2013). Within cognitive psychology, two particular areas of interest are the psychology of language (Traxler & Gernsbacher, 2011), mental models and schemas, and cognitive biases (Kahneman, 2011). The developmental trajectory of these psychologies are also studied within developmental psychology (e.g. mental models; Legare & Clegg, 2015; language; Werker & Hensch, 2015). Cultural psychology (Kitayama & Cohen, 2010) reveals some of the variability in human psychology and the predictors of these differences. Finally, evolutionary psychology has identified potential genetically evolved biases (e.g. detecting cheaters (Cosmides & Tooby, 1992), parental care motivations (Buckels et al., 2015), sex differences in mating choices (Miller, 2011)). In some cases, these offer a competing Theory of Human Behavior (for other examples, see Laland & Brown, 2011). Recent efforts have sought to unify this line of research with evolutionary theory more broadly, including Dual Inheritance Theory and Cultural Evolution (Barrett, 2014).

There is much work to be done in systematically connecting these areas of research with Dual Inheritance Theory and Cultural Evolution. The present dissertation is an attempt in this direction. A useful starting point is the various biases and learning strategies that have been theoretically and empirically identified (Rendell et al., 2011 offer a catalogue based on their social learning tournament.). These include individual-difference biases like the success bias shown in Chapter 3, frequency dependent biases, like those tested in Chapter 4, individual differences in the application of these biases (IQ was identified as one such individual difference in Chapter 4).

Finally, the Cumulative Cultural Brain Hypothesis predicts innovative ancestors that create knowledge worth exploiting via social learning and an environment where that knowledge translates to survival. We see such innovativeness in our closest cousins (Hopper et al., 2014; Manrique, Völter, & Call, 2013). The ecological prediction is more difficult to predict, but bipedal humans may have had large home ranges from which to forage and animal social learning does seem to focus on food locations and exploitation.

1.2.6 What Are The Other Central Questions?

There are of course many central questions that flow from many of these issues, but whose discussion would lead to a book length discussion section. Here are examples of such central questions:

1. How have human social networks evolved and what role do they play in cultural evolution? Recent research reveals that human social networks are more efficient for information transmission than other primates (Pasquaretta et al., 2014). Chapter 5 is a

first attempt to theoretically understand the origins of these networks and their implications for culture.

2. How do innovations emerge in cultural evolution? Both Charles Darwin and Alfred Wallace arrived upon natural selection at around the same time. Both Isaac Newton and Gottfried Leibniz arrived upon calculus at around the same time. In both these cases, innovation might be seen as cultural recombination of the culture being transmitted at the time. But, it was only Darwin and Wallace who arrived upon natural selection; only Newton and Leibniz who arrived upon calculus. Individual differences matter. In other cases, innovations were entirely serendipitous (e.g. penicillin, vulcanized rubber, microwave heating, Velcro, and Teflon).
3. How do characteristics of the learner, content, and model interact? For example, are individuals more likely to learn some kinds of content from ingroup members than outgroup members?
4. What role has cultural group selection played in the evolution of our species (for review see Chudek, Muthukrishna, & Henrich, 2015; Richerson et al., 2015)?
5. How has cultural evolution changed our biology (both genetically and developmentally)? Some possible examples in recent times include lactase persistence (Laland et al., 2010), intelligence (Cochran, Hardy, & Harpending, 2006), reading ability (McCandliss, Cohen, & Dehaene, 2003), individualism and collectivism (Chiao & Blizinsky, 2009), and ability to use tonal language (Dediu & Ladd, 2007). What are the processes through which this gene-culture coevolution takes place? For example, the line between developmental and genetic changes are blurred if an adaptive trait is acquired via learning, reaches fixation, allowing selection to exert pressures on genes that allow the trait to be acquired more

quickly – i.e. a Baldwin effect (Burman, 2013). Reading ability is a good candidate for a cultural trait going through such selection. Chapter 2 is a Dual Inheritance Theory model about the relationship between genes (for brains and social learning) and culture.

6. What role have founder effects and bottlenecks played in the evolution of our species and in cultural differences between populations? An extreme example can be found in the Pingelap atoll in the Pacific Ocean. In most places in the world complete colorblindness (achromatopsia) is present in 1 in 30,000. The Pingelapese rate is 1 in 12 (Sacks, 1997). The disease is unlikely to be an adaptation or mistake, but can be traced to a population bottleneck caused by a 1775 typhoon, in which most of the population died (Sundin et al., 2000). In a similar fashion, some of what we consider uniquely human may be accidental characteristics (both detrimental and beneficial) caused by population bottlenecks, at least in the distant past (Hawks, Hunley, Lee, & Wolpoff, 2000). In recent times, population differences may also be a result of small migrant founding populations. Karmin et al. (2015) find a drop in Y-chromosome diversity coinciding with the rise of culture. Such founder effects have been measured both genetically and culturally (at least for language; Atkinson, 2011) As one might predict, there is more genetic and linguistic diversity in Africa than anywhere else and both of these decrease with distance from Africa.
7. How does cultural content shape other cultural content? How does one innovation open new "thought spaces" and affect the genesis of other innovations? An example of work in this area is Henrich, Boyd, and Richerson's (2012) research on the evolution of monogamous marriage. In Section 1.3 of the Conclusion, I speculate about the possible role of technology in shaping our theories. Ultimately, this becomes the science of

history and is probably the most neglected area of research in Cultural Evolution, because of how difficult it is to build and test formal models. However, it is also the area that may have the most to say about progress, including scientific progress.

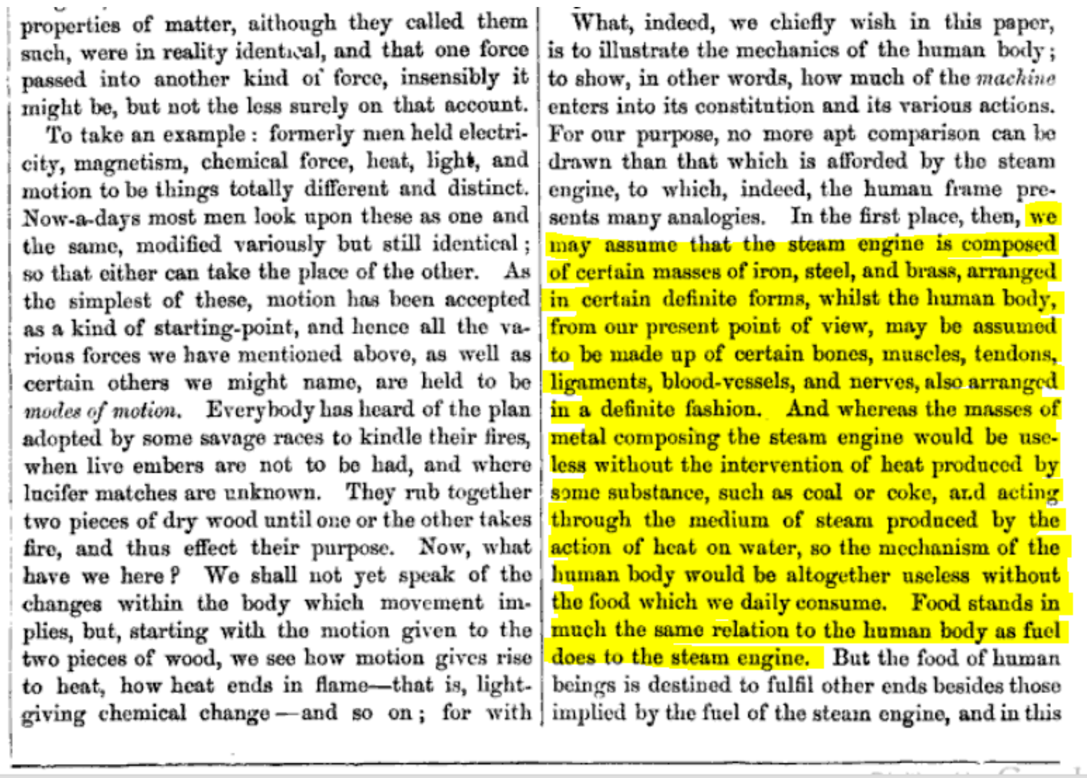
1.3 Technology Shapes Our Theories

I have used the analogy of hardware and software to describe our brains and culture, respectively. As a software engineer, I'm particularly drawn to these analogies, but such analogies are part of a more challenging and perhaps neglected aspect of cultural evolution; the way cultural content affects cultural content. The way ideas affect other ideas; in this case the way technology can affect our theories and open up new "thought spaces". In the next section, I'll briefly go over the way in which technology shapes our theories, particular those related to our own species. I'll then discuss the process of theory building and testing that I've taken in this dissertation. I will end with a future directions on how technology shapes our theories.

Humans have a tendency to use the latest technology as an analogy for what we consider the greatest technology created by nature – ourselves. The 17th century was the era of sophisticated mechanical devices. In 1600 Galileo published *Le Meccaniche* ("On Mechanics") and by 1642 Blaise Pascal had created the first mechanical calculator. It should come as no surprise that it was between 1641 and 1649 that Descartes wrote several works arguing that the human body is like a machine (controlled by a non-material mind or soul), including *Meditationes de Prima Philosophia* ("Meditations on First Philosophy") in 1641 and *La description du corps humain* ("The Description of the Human Body") in 1647. "And as a clock composed of wheels and counter-weights no less exactly observes the laws of nature when it is badly made, and does not show the time properly, than when it entirely satisfies the wishes of its maker, and as, if I consider the body of a man as being a sort of machine so built up and composed of nerves, muscles, veins, blood and skin…" (Descartes, 1641). Descartes wasn't alone. Hobbes (1651) goes further "For what is the 'heart' but a 'spring'; and the 'nerves' but so many 'strings'; and the 'joints' but so many 'wheels,' giving motion to the whole body, such as was intended by the artificer?". A century later, James Watts invented an improved steam engine, a key innovation helping to launch the Industrial Revolution. By the 19th century, even in the popular press, the body was likened to a steam engine, as the excerpt from an 1869 People's Magazine article illustrates (Figure 0.1). We see vestiges of this analogy in early 19th century idioms like "blowing off some steam"[8]. Up until the 20th century technology shaped the analogies for the human body, but Descartes non-material mind or soul still controlled the thoughts of the day. But by the mid 20th century, the computing revolution begins and we now have a metaphor for the mind. Even today, psychology is rife with computing metaphors, focused on permanent and temporary storage, input and output. The computational model of the mind is slowly changing as the field updates to more modern forms of computing. Today, some evolutionary psychologists who take a modular perspective on the mind use the analogy of an iPhone with apps (Kurzban, 2012). With the advent of quantum computing (my current home Vancouver, is home to one of the first commercial

[8] blow off steam. Source: The American Heritage Dictionary of Idioms by Christine Ammer. (2003, 1997).

quantum computing companies, D-wave), I expect to see more "quantum" analogies of the mind[9].


properties of matter, although they called them such, were in reality identical, and that one force passed into another kind of force, insensibly it might be, but not the less surely on that account.

To take an example: formerly men held electricity, magnetism, chemical force, heat, light, and motion to be things totally different and distinct. Now-a-days most men look upon these as one and the same, modified variously but still identical; so that either can take the place of the other. As the simplest of these, motion has been accepted as a kind of starting-point, and hence all the various forces we have mentioned above, as well as certain others we might name, are held to be *modes of motion*. Everybody has heard of the plan adopted by some savage races to kindle their fires, when live embers are not to be had, and where lucifer matches are unknown. They rub together two pieces of dry wood until one or the other takes fire, and thus effect their purpose. Now, what have we here? We shall not yet speak of the changes within the body which movement implies, but, starting with the motion given to the two pieces of wood, we see how motion gives rise to heat, how heat ends in flame—that is, light-giving chemical change—and so on; for with

What, indeed, we chiefly wish in this paper, is to illustrate the mechanics of the human body; to show, in other words, how much of the *machine* enters into its constitution and its various actions. For our purpose, no more apt comparison can be drawn than that which is afforded by the steam engine, to which, indeed, the human frame presents many analogies. In the first place, then, we may assume that the steam engine is composed of certain masses of iron, steel, and brass, arranged in certain definite forms, whilst the human body, from our present point of view, may be assumed to be made up of certain bones, muscles, tendons, ligaments, blood-vessels, and nerves, also arranged in a definite fashion. And whereas the masses of metal composing the steam engine would be useless without the intervention of heat produced by some substance, such as coal or coke, and acting through the medium of steam produced by the action of heat on water, so the mechanism of the human body would be altogether useless without the food which we daily consume. Food stands in much the same relation to the human body as fuel does to the steam engine. But the food of human beings is destined to fulfil other ends besides those implied by the fuel of the steam engine, and in this

Figure 0.1. Excerpt from 1869 People's Magazine article on Muscular Motion.

Technology shapes our metaphors, analogies and theories (Gigerenzer and Goldstein (1996) call this a tools-to-theories heuristic). I suspect a new generation of "digital natives" more familiar with the interaction between software and hardware, Turing completeness (where the computer can fully represent the computer itself), virtualization and abstraction (with software able to replicate hardware, albeit slower) will find Dual Inheritance Theory far more intuitive. However, recognizing the human tendency to use technology as metaphors should also help us identify the limitations of those metaphors. In the case of Dual Inheritance Theory, a useful metaphor is quickly updating software running on more slowly upgraded hardware, but a key difference is that here, the software

[9] Some researchers have already speculated that the mind may in fact be a quantum computer (Koch & Hepp, 2006).

changes the hardware, enabling better software – this is the essence of the model presented in Chapter 2. Nevertheless, I am hopeful that with newer analogies, particularly those emerging from the spectacular advancements in machine learning (e.g. Hinton et al., 2012) we will grow closer to a better description of our species. In the meantime, Dual Inheritance Theory and in particular Cultural Evolution helps us explain how it is that we can even use cultural knowledge to open new "thought spaces" and develop better theories.

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