

SOCIETY, ORGANIZATIONS AND THE BRAIN: BUILDING TOWARDS A UNIFIED COGNITIVE NEUROSCIENCE PERSPECTIVE

EDITED BY : Carl Senior, Nick Lee and Sven Braeutigam
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SOCIETY, ORGANIZATIONS AND THE BRAIN: BUILDING TOWARDS A UNIFIED COGNITIVE NEUROSCIENCE PERSPECTIVE

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This e-book brings together scholars in both the neurosciences and organizational sciences who have adopted various approaches to study the cognitive mechanisms mediating the social behavior that we see within organizations. Such an approach has been termed by ourselves, and others, as ‘organisational cognitive neuroscience’. In recent years there has been a veritable increase in studies that have explored the cognitive mechanisms driving such behaviours, and much progress has been made in understanding the neural underpinnings of processes such as financial exchange, risk awareness and even leadership. However, while these studies are informative and add to our understanding of human cognition they fall short of providing evidence-based recommendations for practice. Specifically, we address the broader issue of how the neuroscientific study of such core social behaviors can be used to improve the very way that we work. To address these gaps in our understanding the chapters in this book serve as a platform that allows scholars in both the neurosciences and the organizational sciences to highlight the work that spans across these two fields.

The consolidation of these two fields also serves to highlight the utility of a unified and singular organizational cognitive neuroscience. This is a fundamentally important outcome of the book as the application of neuroscience to address economically relevant behaviours has seen a variety of fields evolve in their own right, such as neuromarketing, neuroeconomics and so forth. The use of neuro-scientific technologies, in particular fMRI, has indeed led to a bewildering and somewhat suffocating proliferation of new approaches, however, the speed of such developments demands that we must proceed carefully with such ventures or risk some fundamental mistakes. The book that you now hold will consolidate these new neuroscience based approaches and in doing so highlight the importance of this approach in helping us to understand human social behaviour in general. Taken together the chapters provide a framework for scholars within the neurosciences who wish to explore the further the opportunities that the study of organisational behaviour may provide.

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Society, organizations and the brain: building toward a unified cognitive neuroscience perspective

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The Oxford English Dictionary contains the following entry for the word “postal” as:

- adjective relating to or carried out by post.
 - PHRASES go postal US informal go mad, especially from stress. With reference to cases in which postal employees have run amok and shot colleagues.

Even a superficial knowledge of recent events may lead to the conclusion that the contemporary organization is perhaps not an easy thing to manage in a way that guarantees both economic and social prosperity. As such, it seems to be part of the modern human condition to be at least somewhat unhappy, stressed, or otherwise negatively impacted by either organizational life itself, or the impact of organizations on today’s society. Fortunately, however, worst-case scenarios—as implied by the OED above—are very rare.

It does not come as a surprise then, that researchers have expended considerable efforts on exploring and understanding the formation, management, and ethical sustenance of organizations of all kinds and sizes, from bleeding-edge venture enterprises operating in break-neck markets to perhaps non-competitive, non-profit charities. Drawing from an interest in the negative effects workplaces can have on individuals, some of us published a clarion call, raising questions about how a better understanding of our biological systems could inform an understanding of the social behavior that we manifest within organizations (Butler and Senior, 2007a,b). The critical question here is how the organization and the individual interact and influence each other, given that it that organizations are designed as they are by the very same species which will work in them, and equally important how cognitive neuroscience in particular can help to unravel such mechanisms.

Scholars have indeed begun to explore the neuroscience of organizational behavior. These efforts go under the names of Organizational Neuroscience and Organizational Cognitive Neuroscience, terms that refer to cross-disciplinary perspectives on organizational research, which take as their foci of study the cognitive mechanisms that drive human behaviors in response to organizational manifestations (Senior et al., 2008, 2011; Becker et al., 2011; Lee et al., 2012a). Such approaches seem to have some merit in the study of the effects of organizational life on human beings, and also on how one can mitigate the more deleterious effects that appear inherent to such contexts. However, even with such rich empirical intercourse there remains an opportunity to examine further the current state of the art research endeavors that span the biological and organizational domains to inform our understanding of the type of social behavior that most of us will carry out most days for most of our lives.

The articles contained within this research topic do just that, and go beyond merely explicating further the possible mechanisms that drive “social behavior that occurs within organizational manifestations” (Senior et al., 2011, p. 2) but ensure that such an understanding actually informs

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our knowledge of a socially relevant and species specific social behavior. In the call for papers we chose not to restrict the nature of articles, but to ensure that all submissions could inform our wider understanding social behavior in this applied context (Waldman, 2013). The resulting submissions can be loosely grouped into four main clusters—(a) general management, (b) leadership, (c) neuromarketing science, and (d) papers that have made specific recommendations for subsequent work.

To fully realize the potential for the impact of these articles, it is important to first reflect upon the industrial revolution and how it showed that complex products could most profitably be made by breaking them up into small specialized, repetitive tasks. As far back as the early 20th Century, with the emergence of “scientific management” (e.g., Taylor, 1911), and the principles of Fordism, the place of humans in this workflow was also treated as a mechanistic process, to be designed in such a way as to maximize efficiency and minimize defects. In such a context, one could be forgiven for wondering whether working in such organizations was what humans were ideally suited to. Even so, it is undeniable that humans are the only species to have organized itself into abstract organizations (i.e., not solely related to survival or socialization), suggesting that perhaps something about this ability does confer a collective advantage, if not an individual one. In such a context, one would be forgiven for fearing that the application of cognitive neuroscientific technology to helping us understand more about our behaviors within the workplace may drive the onset of what might become a neo-scientific management; one that sees the data from workers as merely a mechanism to maximize efficiency and minimize defects. Yet the articles contained in this research topic show that this is far from the case and, rather than driving biological reductionism, the articles collectively demonstrate the significant impact that such approaches can bring to helping us understand human behavior.

In a novel approach to addressing a significant question, Block et al. (2014) carried out a large-scale interrogation of an existing database on media behavior and found a significant relationship between media usage e.g., Internet, television and other social media, and self-reports of depression. Christoff (2014) takes exploration of the relationship between organizational settings and mental-health a stage further, and argues that a discourse exploring the role emotions play in organizational decision-making is needed. In light of the fact that in modern organizations, so many of us place such heavy emphasis on such media outlets when enacting our working roles, considering the possible effect that they may have on mental health ensures that we consider the welfare of the individual workers of paramount importance (see also Senior and Lee, 2013 for further discussion here).

Taken together, the work by Spain and Harms (2014) and Verbeke et al. (2014), converges on a greater understanding of individual behavior within an organization at a genetic level. This socio-economic approach is then examined further with the submission by Foxall (2014a), who suggests a model for effective managerial behavior; that is, the function of competitive neural systems. The notion of dual systems operating in competition to drive effective managerial behavior was examined further with work by Boyatzis et al. (2014) who carried out an fMRI study

identifying antagonistic neural systems responsible for different types of leadership behaviors.

Such work continues to inform our understanding of how social cognitive neuroscience (Ochsner and Lieberman, 2001) can advance organizational research—a project essentially started by our earlier work (e.g., Lee et al., 2012a). In particular, and possibly as the result of serendipitous collaboration, neuroscientific measuring tools such as functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) have been applied to a number of organizational research questions (e.g., McClure et al., 2004; Braeutigam, 2005; Deppe et al., 2005). Such approaches have given the world terms as “neuroeconomics” (Braeutigam, 2005) and “neuromarketing” (Breiter et al., 2015b), and have inspired some considerable controversy in the scientific press (e.g., *Nature Neuroscience* July 2004). Such debate is healthy and as is shown by Butler (2014), Lindebaum (2014), and Waldman (2013) helps to drive consolidation of theory and clarification of approaches.

This, then, is the foundation of Organizational Cognitive Neuroscience (OCN), which as an approach brings together diversity in research approaches that use neuroscientific theories and methods to examine organizational research issues (Senior et al., 2011; Lee et al., 2012a). Indeed, the benefits of an OCN approach are exemplified by Foxall (2014b), Walla et al. (2014) and Breiter et al. (2015a), who each describe how the study of exchanges within a market scenario can provide insights more general human behavior, which in turn would lead to a more “integrated science of influence” (Breiter et al., 2015b p. 1). These scholars highlight both theoretical and methodological advances within mainstream cognitive neurosciences and the implications for a greater understanding of human behavior when market exchanges are specifically investigated. Such methodological advances are explored further with work by Kopton and Kenning (2014) and Burgess (2013) who, among other things, develop novel statistical approaches for the analysis of hyper scanning data—which looks likely to be a crucial technique in exploring the sort of interactions so central to organizational life.

That said, such work clearly shows that theoretical advancement is not dependent on simply grafting advanced measurement tools (such as fMRI) on to existing theories, as implied by many early uses terms such as “neuromarketing” (and here we recognize that Breiter et al. (2015b) clearly define a more scientifically-rigorous usage of neuromarketing). Instead, the OCN approach explicitly recognizes that it is the interaction between cognitive neuroscience and organizational research as distinct fields of research which is critical—incorporating not just new methods, but also new theoretical explanations. In such a way, the field can lead to advances in both its parent disciplines (Lee et al., 2012b).

We have previously conceptualized OCN as an approach that considers human behavior made in response to organizational manifestations (e.g., products, advertisements) as a set of theoretical layers, each building upon the last to add more context-specific theory (Lee et al., 2012b). At the most abstract level, the behavior of individuals and groups at the intersection between the organization and the human is considered. Yet such behavior is a subset of human social behavior in general.

Therefore it is an additional layer of theory that can be added upon social psychology. In turn, social psychology is founded on theories of cognitive psychology, which also impact directly on many of our responses to organizational manifestations such as advertisements and products. At an even more basic level, are the lower-level brain systems and structures that drive such cognitions, analysis here could be termed the neural level of analysis. To facilitate investigations across the various layers of analysis that are diagnostic of the organizational cognitive neuroscience approach, Rippon et al. (2014) provide a set of recommendations that could be adopted when studying the effects of gender on particular task.

The organizational, social, and neural levels that are described above have been the focus of existing OCN theory (e.g., Lee and Chamberlain, 2007). Yet, at a more fundamental level one can also describe the adaptive forces that have shaped our brain physiology in an evolutionary advantageous manner (Saad and Greengross, 2014). Knowledge of the evolutionary adaptations that may mediate our behavior at the social and ultimately organizational level is essential to complete the explanation of why we behave in the way we do, and also critical in understanding the potential negative (and positive) influence of organizational life on human beings.

To move back to the example of “scientific management” previously alluded to; an understanding of whether the ability to focus on repetitive small tasks may have conferred an evolutionary advantage in the past (which therefore would have led to a predilection for this ability in humans) may then lead to greater understanding of whether scientific management principles are likely to be beneficial to employees. Importantly, this is quite apart from the logical principles of the approach, which may indeed suggest that it may be the most efficient manner with which to produce a complex product with minimum defects. Indeed, the key social processes (within organizations) that humans have a predilection toward are discussed subsequently.

Such an idea has been developed further with the work by Saad and Greengross (2014), who go so far as to say that an understanding of evolutionary theory is of paramount importance when using cognitive neuroscientific technology to explore organizationally-relevant behaviors. However, it is with

the work by Spisak et al. (2014) and Price and Van Vugt (2014) where the importance of studying adaptive behaviors and the role that they may play in facilitating effective organizational is made crystal clear (See also von Rueden, 2014). Developing this further, Susac and Braeutigam (2014) describe how an understanding of the neural substrates underpinning mathematical cognition may in fact facilitate the ability for mathematical reasoning—which itself has implications for the subsequent design of effective education.

Here it is clear that it is not possible to fully understand a given organizationally-relevant behavior by ignoring the various interweaved layers of theory introduced above, Focusing on the neural level—without taking into account the more fundamental evolutionary level, or even the more abstract organizational and social levels—is likely to result in important explanatory contextual factors being overlooked. OCN explicitly recognizes the symbiotic relationship between the layers of theory and in doing so develops more rigorous testable hypotheses, and ties this to advances in research methods that can more accurately test these hypotheses. The studies noted above develop existing OCN theory (e.g., Butler and Senior, 2007a) to show in more depth the evolutionary processes that may impact on our organizationally-relevant actions. The focus here is on how the neural and evolutionary levels interact, and the question of whether such adaptations actually can influence our behavior within, and our response to, organizations and their manifestations.

As noted above, organizations that are designed around the social processes that humans have a predilection for are likely to operate more efficiently. Yet we should not consider the application of neuroscience to understanding organizational behavior as a means merely to make such organizations more efficient. In spite of the working environment being constantly in flux, the central concept of organizational behavior has and will always remain the same. Most of us are likely to spend a major proportion of our lives in a work-related environment. One may argue thus that organizational cognitive neuroscience is an approach by which to understand the cognitive signature of our own species-specific social behavior.

We would like to dedicate this research topic to the many reviewers who considered the submitted papers in such a timely fashion—without them this collection would not have happened.

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The relationship between self-report of depression and media usage

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Depression is a debilitating condition that adversely affects many aspects of a person's life and general health. Earlier work has supported the idea that there may be a relationship between the use of certain media and depression. In this study, we tested if self-report of depression (SRD), which is not a clinically based diagnosis, was associated with increased internet, television, and social media usage by using data collected in the Media Behavior and Influence Study (MBIS) database ($N = 19,776$ subjects). We further assessed the relationship of demographic variables to this association. These analyses found that SRD rates were in the range of published rates of clinically diagnosed major depression. It found that those who tended to use more media also tended to be more depressed, and that segmentation of SRD subjects was weighted toward internet and television usage, which was not the case with non-SRD subjects, who were segmented along social media use. This study found that those who have suffered either economic or physical life setbacks are orders of magnitude more likely to be depressed, even without disproportionately high levels of media use. However, among those that have suffered major life setbacks, high media users—particularly television watchers—were even more likely to report experiencing depression, which suggests that these effects were not just due to individuals having more time for media consumption. These findings provide an example of how Big Data can be used for medical and mental health research, helping to elucidate issues not traditionally tested in the fields of psychiatry or experimental psychology.

Keywords: depression, big data, marketing communications, media use

INTRODUCTION

Depression is known to affect many kinds of human behavior, and is quite common. As of 2005, the lifetime prevalence of major depressive disorder in the US population was reported to be 16.5% (Kessler et al., 2005a), with 6.7% prevalence in a 12-month period, 30.4% of which were severe (or 2.0% of the U.S. population) (Kessler et al., 2005b). Given the prevalence of depression, there is interest from a neuromarketing perspective in how it may be related to patterns of media consumption. Such issues are of fundamental concern for mechanisms of behavior change research and psychology (e.g., Morgenstern et al., 2013).

There is a developing literature evaluating the relationship between various types of media use and psychiatric conditions. For instance, one study found a high positive correlation between internet addiction and depression among university students (Orsal et al., 2012). Another study found that adults with major depressive disorder spent excessive amounts of leisure time on

the computer, while those with dysthymia, panic disorder, and agoraphobia spent more time watching television than the control group or those with other disorders (de Wit et al., 2011). However, results have not always been consistent, particularly in the domain of social media use. A recent paper failed to find any association between social network use and depression in older adolescents (Jelenchick et al., 2013), while other studies have found positive associations between Facebook use and depression in high school students (Pantic et al., 2012), and Facebook use and a lack of subjective well-being in young adults (Kross et al., 2013). Given the heterogeneity across previous studies, and the rapid evolution of media formats over the past decade, we used a large consumer database ($>19,000$ subjects) to assess the relationship between self-reported depression (SRD) and media usage, taking into account demographic information which may impact the incidence of SRD such as employment status and disability. We used SRD since major depression cannot be diagnosed with

big data surveys, and compared the rate of SRD to published incidence data on the diagnosis of major depression.

This study differed from previous studies in the following ways. (1) The sample size of the dataset was substantially larger than any previous study evaluating the relationship between media use and depression. (2) We evaluated the link between depression and multiple domains of media use, whereas most previous studies have focused primarily on single domains. For example, recent work with a smaller database has suggested there is an increase in digital media usage in “depressed” adolescents (Primack et al., 2009), but this study did not investigate its relationship to different subcomponents of media, such as social media, internet, and television.

Our analysis started with descriptive and bivariate statistical analyses. These were followed by omnibus approaches to assess general effects given the number of variables describing media usage: (a) Chi-squared Automatic Interaction Detection or CHAID tree analysis (Kass, 1980; Biggs et al., 1991) (a form of recursive partitioning; Zhang and Singer, 1999) and (b) discriminant analysis.

MATERIALS AND METHODS

DATA ACQUISITION

The dataset was derived from the Media Behavior and Influence Study (MBIS), a syndicated online study of American adult (i.e., ≥ 18 years of age) consumers, conducted twice yearly since 2002 by BIGinsight of Columbus, Ohio. The current wave of 19,776 participants was completed in December, 2012. Using a double opt-in methodology, each MBIS study was balanced to meet demographic criteria established by the US census. MBIS data has been used by a variety of well-known, commercial marketing organizations. Variables of interest included depression by gender, age, employment status, marital status, race and ethnicity, income, education, measures of isolation, and internet, TV and social media use. These variables were selected because they have been variables of interest in previous depression studies, and have been shown to have predictive value (e.g., Catalano and Dooley, 1977; Wilkowska-Chmielewska et al., 2013). Media usage for internet, television, and social media are based on yes/no responses to several day-parts of variable hour durations for a typical weekday (see Supplementary Materials). These blocks of time were shorter for typical waking hours and longer for overnight and weekend periods. Block length was used to weight media usage probability during the calculation of total hours of consumption (i.e., divided by the number of hours in each block of time). Average hour exposure probabilities were calculated for a 24 h period, and minutes per day were estimated by multiplying the result by 1440. Internet, TV, and social media usage were hence composite variables created as probabilities of number of minutes daily usage, derived from data indicating whether or not subjects used the respective services in seven discrete variable-hour blocks.

DATA ANALYSIS

Three types of analysis were performed with this data. First, we performed a descriptive statistical analysis, inclusive of correlations between depression and media consumption variables

to facilitate interpretation of the subsequent analyses. Second, we used the results to inform a type of recursive partitioning (Morgan and Sonquist, 1963; Friedman, 1977; Breiman et al., 1984; Gordon and Olshen, 1984; Quinlan, 1986; Mingers, 1989), namely CHAID tree analysis (Kass, 1980; Biggs et al., 1991). Third, we performed a multivariate discriminate analysis. Given the descriptive statistical analyses were standard, these are not further discussed herein. In all analyses below excepting the CHAID analysis, fewer than 50 total comparisons were made; to correct for multiple comparisons we used a Bonferroni correction for 50 comparisons, requiring a $p < 0.001$ to be considered a significant result.

CHAID tree analysis

We performed two recursive partitioning analyses, one focused on SRD and the second on a variable not of interest, namely non-SRD, to act as a control for SRD results. Our working hypothesis was that the control analysis of non-SRD subjects would not replicate or provide an opponent (i.e., completely non-overlapping) set of nodes to the analysis of SRD subjects.

Construction of statistical CHAID trees (SPSS tree) evaluated the interaction among a number of predictor variables of SRD, and separately non-SRD. Typically, such schemes are defined in terms of demographic variables such as age and gender; however we have also included occupation, education, marital status and media use. Splitting criteria included minimum parent node size of 100 and child node size of 50, and a p -value threshold of 0.05. These splitting criteria were used for both CHAID analyses.

Discriminant analyses

Discriminant analysis was used to conduct a multivariate analysis of variance for the hypothesis that people who self-reported having depression would differ significantly from non-SRD subjects on a linear combination of eleven variables: income, internet usage, TV usage, social media usage, education, age, living in top 10 metropolitan area (MSA), gender, having children, employment status, and disability. The discriminant analysis was run using SPSS defaults, resulting in the canonical linear discriminant analysis. Depression was the binary dependent variable entered in the “group” dialog. The discriminating variables were entered together (i.e., not stepwise) in the variables subcommand. The discriminating variables income, internet usage, TV usage, social media usage, and education, all took on continuous values in the range from 0 to 1. “Living in top 10 MSA,” gender, employment status and disability were binary categorical variables while having children was ordinal. Overall, the data were complete with no missing values (i.e., every subject had every data point).

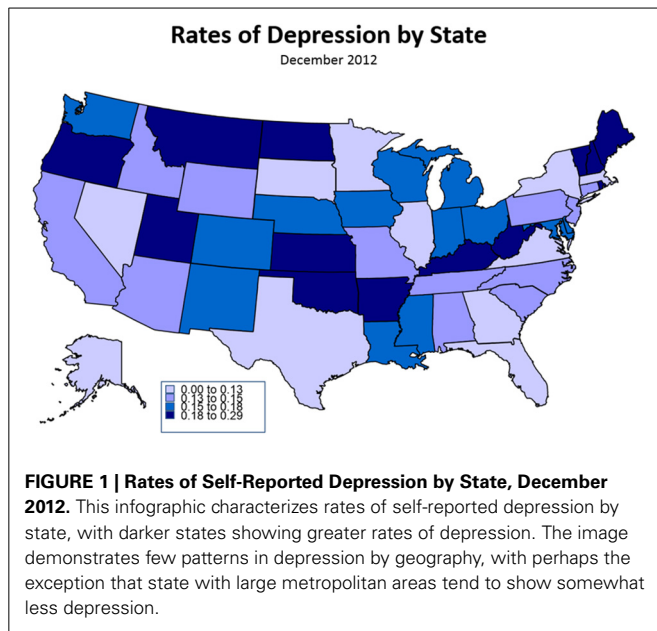
RESULTS

DESCRIPTIVE AND CORRELATION ANALYSES

Geographic and temporal patterns

The MBIS study shows little to no geographic pattern for SRD (Figure 1).

The data does show that SRD among all adults in the USA (18 and over) has grown from 11.2% in 2009 to 12.1% in December, 2012, with a linear trend ($r^2 = 0.246$) (Figure 2). It is interesting that the rate rises to 15.2% in June 2012 (similar to rates in



the 2005 MBIS data where the depressive rate was reported to be 14.9%), then drops to 12.1% in December 2012, which is consistent with a previous study that used the emotive content of tweets to show a similar annual pattern of decreased depression over Christmas (Dodds et al., 2011).

Depression demographics

Gender. Rates of SRD in the current study wave were nearly identical by gender as shown in **Table 1**, with males slightly lower at 11.8%, compared to females at 12.3%.

Age and marital status. Bivariate analysis suggested an inverse linear association of SRD with age, which is consistent with previously reported studies (Henderson et al., 1998). Individuals who were married were also different than those who were unmarried as shown in **Table 1**, with married respondents representing a large portion of the sample (42.5%), and reporting a lower SRD rate of 9.5%. The highest rate of SRD was from those in same sex unions, at 22.2%. Those living with an unmarried partner, divorced or separated, or single (never married) reported rates between 14.1% and 15.5%, while those that were widowed reported rates (12.4%) nearly the same as the overall average.

Race and ethnicity. **Table 1** showed lower rates among Hispanics (10.9%), and lower yet among African-Americans (8.7%) and Asians (7.9%) as compared to Multi-ethnic individuals and Caucasians. SRD was highest among Caucasians (13.6%), who represented more than half (58.4%) of the sample studied.

Income and education. Both income and education (**Table 1**), also demonstrated a strong inverse linear association with SRD, similar to age (statistics not provided given omnibus analyses to follow). Non-high school graduates self-reported a 21.7% depression rate compared to those with post college study or degree at 8.8%. The overall average income was \$62,800, with those reporting depression indicating an average of \$49,000. Occupation

levels showed similar effects, as shown in **Table 1**, with those disabled (unable to work) reporting a 42.7% depression rate. Other high reporting categories included the unemployed at 18.8%, and students at 13.0%. The lowest category was professional and management at 8.2%.

Health and lifestyle characteristics. SRD was also related to the reporting of other health conditions as shown in **Table 1**. Generally, those reporting depression were likely to say they had other health-related conditions, such as anxiety (54.8%). Other conditions more prevalent in SRC subjects included: back pain (42.7%), overweight (37.6%), acid reflux (30.5%), headaches/migraines (29.6%), insomnia/difficulty sleeping (27.5%) (**Table 1**).

Isolation. Residents of states with large urban areas and those living in the top 10 metropolitan statistical areas (MSAs), have lower rates of SRD. The top 10 MSAs include Los Angeles, New York, Chicago, San Francisco, Philadelphia, Washington, Boston, Detroit, Phoenix and Houston. This suggests that residents of rural areas tend to report higher rates of depression.

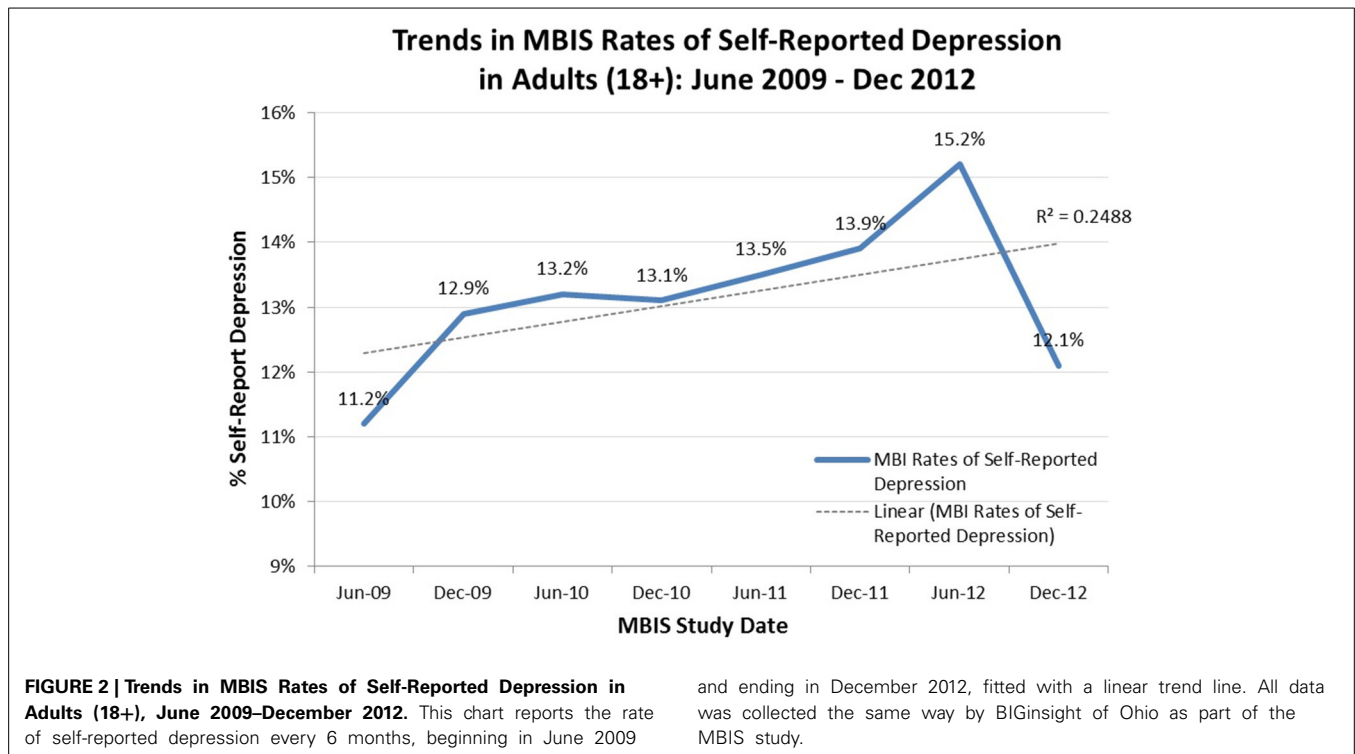
Media use. Overall there were low but significant positive linear correlations between SRD and media consumption. In these descriptive analyses, the three most consumed media were television, on average 129 min per day per adult (18+), the internet, on average 143 min per day, and social media, on average 83 min per day. The bivariate association (r) between SRD and television consumption was 0.089, surfing the internet was 0.089 and social media was 0.063 (all $p < 0.001$).

Media usage quintiles, a method commonly used in the media industry, were created using the composite media usage variables described above, and showed higher rates of depression among the most active users of media. **Figure 3** shows that for the highest 20% of television users (quintile 5, 289 min per day) the SRD rate was 16.9%. The SRD rate among the highest internet users (327 min per day) was also 16.9%. SRD was slightly lower among the highest social media users (279 min per day) at 15.4%. The patterns among all three media categories were the same: higher consumption of any form of media was associated with higher rates of reported depression.

It should be noted that there was some co-linearity between the three media categories. The correlation of television and internet consumption was moderate at 0.495, slightly higher for internet and social media at 0.510, but lower for television and social media at 0.247. All of these correlations were significant ($p < 0.001$), raising the possibility of simultaneous consumption.

CHAID TREE ANALYSIS

The analyses reported above were limited to bivariate correlations. To better understand how multiple variables for media consumption and other demographics/activities related to SRD, a multivariate segmentation scheme was employed based on recursive partitioning (Morgan and Sonquist, 1963; Friedman, 1977; Breiman et al., 1984; Gordon and Olshen, 1984; Quinlan, 1986; Mingers, 1989). The first CHAID tree (Kass, 1980; Biggs et al., 1991) (**Figure 4**) shows the interaction among the predictor



variables on the rate of SRD (the target variable). The second CHAID tree (**Figure 5**) shows the interaction among the predictor variables and those who did not self-report being depressed. The first analysis on depressed individuals generated 22 terminal nodes, while the second on non-depressed subjects generated 21. The trees (**Figures 4, 5**) were pruned to include only 8 and 10 terminal nodes where the depression rate was 15% or more and the non-depression rate was 87% or higher, respectively. The tree nodes showed the variable used to create the node, the depression rate, and the percent of all adults that the node represented. In **Figure 4**, those that were unemployed, for example, were 6.0% of the sample and reported a depression rate of 18.8%. Note that media-related nodes were shown in white and other variables shown in blue/gray.

In the analysis of SRD subjects, the CHAID tree segments (**Figure 4**) that were the basis for understanding the relationship of depression to media and other variables were as follows. In general, factors such as disability, unemployment and lower incomes were associated with higher rates of SRD. Media consumption tended to significantly leverage the rate attributable to these characteristics. Six nodes of interest are briefly described. The node with the highest depression rate (47.3%) was being disabled (1) and in the top two TV consumption quintiles. This was compared to being disabled and in the bottom three TV quintiles with a somewhat lower depression rate (35.2%). The next highest depression node (30.7%) consisted of (2) those who were unemployed, in the top internet quintile, and had less than a college education. Those in a professional or managerial occupation that made \$30,000 or less, and were in the highest TV quintile (3), reported a depression rate of 26.9%. (4) Female students or homemakers older than 34, reported a 20.0% depression rate.

(5) Those in other occupations, including workers, sales, military and retired, that make less than \$42,500 and were in the highest social media quintile, reported a depression rate of 19.1%. (6) Male students or homemakers in the highest two internet quintiles reported a depression rate of 17.4%.

In the analysis of non-depressed individuals (non-SRD), the CHAID tree segments (**Figure 5**) that best explained the relationships between media use, demographic variables, and non-SRD, described ten nodes. The node with the highest non-depression rate (96.2%) was being professional (1) with a salary of \$150,000 and more in the lowest social media quintiles. This was compared to being professional (2) with a salary of \$150,000 and more in the highest social media quintile (89.1%). The next highest non-depression node (3) consisted of those in other occupations, including workers, sales, military and retired, making \$100,000 and more (94.3%). This was contrasted with (4) those in other occupations making \$50,000 to \$100,000 and in the lowest social media quintiles (91.4%), and (5) those in other occupations making \$50,000 to \$100,000 and in the highest social media quintiles (87.7%). Those who were professional making \$75,000 to \$100,000 and in the lowest social media quintile had a non-depression rate of 94.2% (6), whereas those who were professional making \$75,000 to \$100,000 and in the highest social media quintile had a non-depression rate of 89.1% (7). Professionals making \$35,000 to \$75,000 and male gender (8) were higher (91.9%) than those professionals making \$35,000 to \$75,000 and female gender (9). Lastly, students who were male in the lowest web-radio quintile (10) had a non-depression rate of 90.8%. In general, being a student or employed with a high income were most closely associated with not being depressed, particularly when combined with varying levels of social media use.

Table 1 | Depression by demographics, December 2012.

	% All adults	Adults with depression	Index
Age (average years)*	45.4	43.8	96.3
Male	48.3	11.8	97.5
Female	51.7	12.3	101.7
Income (000)*	62.8	49.0	78.0
Have children	29.1	30.2	103.9
Live in top 10 MSA	24.7	10.0	82.6
Married	42.5	9.5	78.5
Living with unmarried partner	7.2	15.5	128.1
Divorced or separated	10.2	15.4	128.3
Widowed	3.0	12.4	102.5
Single, never married	25.7	14.1	116.5
Same sex union	0.5	22.2	183.5
Have not graduated high school	1.5	21.7	179.3
Graduated high school	16.8	13.1	108.3
Technical school or vocational training	5.7	13.8	114.0
1–3 years of college (did not graduate)	20.2	15.1	124.8
Associates or professional degree	8.9	13.2	109.1
Bachelor's degree	22.5	9.4	77.7
Post college study or degree	13.5	8.8	72.7
Business Owner	4.2	11.7	96.7
Professional/managerial	25.5	8.2	67.8
Salesperson	3.6	11.5	95.0
Factory worker/laborer/driver	3.3	9.6	79.3
Clerical or service worker	9.5	11.9	98.3
Homemaker	3.6	14.7	121.5
Student, high school or college	8.4	13.0	107.4
Military	0.7	11.6	95.9
Retired	13.7	10.8	89.3
Unemployed	5.5	18.8	155.4
Disabled (unable to work)	2.0	42.7	352.9
Obsessive-compulsive disorder (OCD)	2.1	9.8	458.1
Anxiety	12.9	54.8	425.8
Dyslexia	0.8	2.6	334.5
Fibromyalgia	2.3	7.4	327.5
Insomnia/difficulty sleeping	8.4	27.5	325.8
Restless leg syndrome(RLS)	4.1	11.6	279.8
Irritable Bowel Syndrome (IBS)/crohn's disease	2.4	6.3	262.6
Chronic bronchitis/COPD	2.9	7.3	252.5
Sleep apnea	6.6	16.4	248.2
Heartburn/indigestion	9.9	22.7	230.3
Headaches/migraines	14.0	29.6	211.5
Back pain	21.5	42.7	198.4
Acid reflux	15.8	30.5	192.9
Heart disease	3.2	5.9	185.9
Hearing impairment	4.3	8.0	184.6

(Continued)

Table 1 | Continued

	% All adults	Adults with depression	Index
Overweight	21.2	37.6	177.1
Arthritis	15.5	27.3	176.4
Asthma	9.7	17.0	174.8
Vision impairment	15.0	24.8	165.2
Enlarged prostate/Benign Prostatic Hyperplasia (BPH)	2.2	3.6	162.6
Diabetes	9.3	15.0	162.1
Osteoporosis	2.5	4.1	161.6
High cholesterol	18.8	29.3	155.9
Black	18.0	8.7	71.9
Asian	3.0	7.9	65.3
Multi	0.8	16.9	139.7
Native	0.4	15.5	128.1
White	58.4	13.6	112.4
Other	0.5	9.9	81.8
Hispanic	18.9	10.9	90.1

The three columns of numeric values represent (i) the percentage of all adults in the survey with the given attribute (excepting income and age, which lists the survey mean), (ii) the percentage of subjects having the given attribute that self-reported depression, and (iii) the index of the given attribute as it relates to depression, which is calculated as the percentage of those depressed, divided by the total number depressed multiplied by 100. Rows on the left of the table are clustered around demographics, relationship status, education, and work identification. Rows on the right are clustered by illnesses separate from depression, and with race/ethnicity (Note: These do not follow NIH definitions of race and ethnicity).

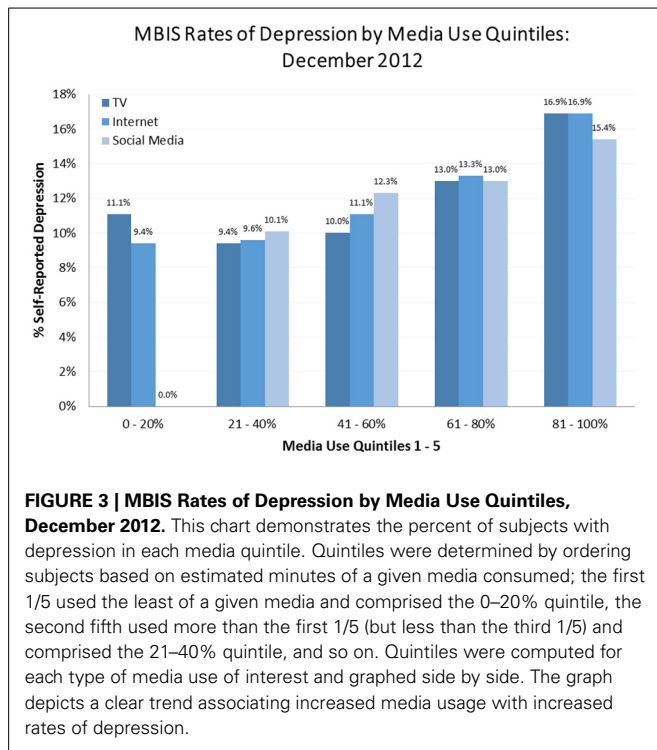
It is important to note that the CHAID analysis with non-SRD did not replicate the analysis with SRD. Furthermore, there was a segmentation observed between these analyses which was distinct, in that the types of media use that segmented the SRD subjects was not the same as that which segmented the non-SRD subjects. The terminal nodes of the two analyses were different along dimensions of occupation, income, and media use.

DISCRIMINANT ANALYSIS

The results of the discriminant analysis revealed that, other than disability and income, the three single best predictors of depression in this model were increased use of television, the internet, and social media (Table 2). The overall Chi-squared test of the discriminant model was significant (Wilk's $\lambda = 0.945$, Chi-square = 922.117, $df = 9$, Canonical correlation = 0.235, $p < 0.001$). The structure matrix demonstrated the weights of the discriminating variables, an indication of their importance for predicting depression: being disabled (0.760), income (−0.519), internet consumption (0.399), television consumption (0.368), social media use (0.278), level of education (−0.255), being unemployed (0.223), age (−0.170), top 10 MSA (−0.142), female gender (0.062), and having children (0.010).

DISCUSSION

The primary finding of this study is that those who tend to use more media in general, also tend to have more self-reports



of depression. We found a current incidence of SRD at 12.1% which is slightly less than reports of lifetime clinical depression and more than the 12 month incidence of diagnoses of major depression. However, the picture is far more nuanced than simple description of descriptive statistics and bivariate correlations between media use and depression. For instance, the CHAID tree analysis with SRD subjects (along with the discriminant analysis) shows that those who have suffered either economic or physical life setbacks are orders of magnitude more likely to be depressed, even without disproportionately high levels of media use (37.2%). However, among those that have suffered major life setbacks, high media users—particularly television watchers—were even more likely to report experiencing depression (47.3% in the highest two quintiles, as compared with 35.2% in the lower three quintiles), which suggests that these effects were not just due to individuals having more time for media consumption. These effects were not observed with the control analysis in non-SRD subjects. That the economically disadvantaged are significantly more likely to experience depression is well supported by research in social psychology, which suggests that lower-income groups feel a sense of disempowerment (Henry, 2005; Stephens et al., 2007). The lack of financial and temporal resources they experience can lead to feelings of a lack of control over one's life and an inability to act efficaciously in the world, which is thought to be a basic human need. Supporting this interpretation, the CHAID analysis of the non-SRD subjects showed that high earners that use less social media tend to be significantly less depressed.

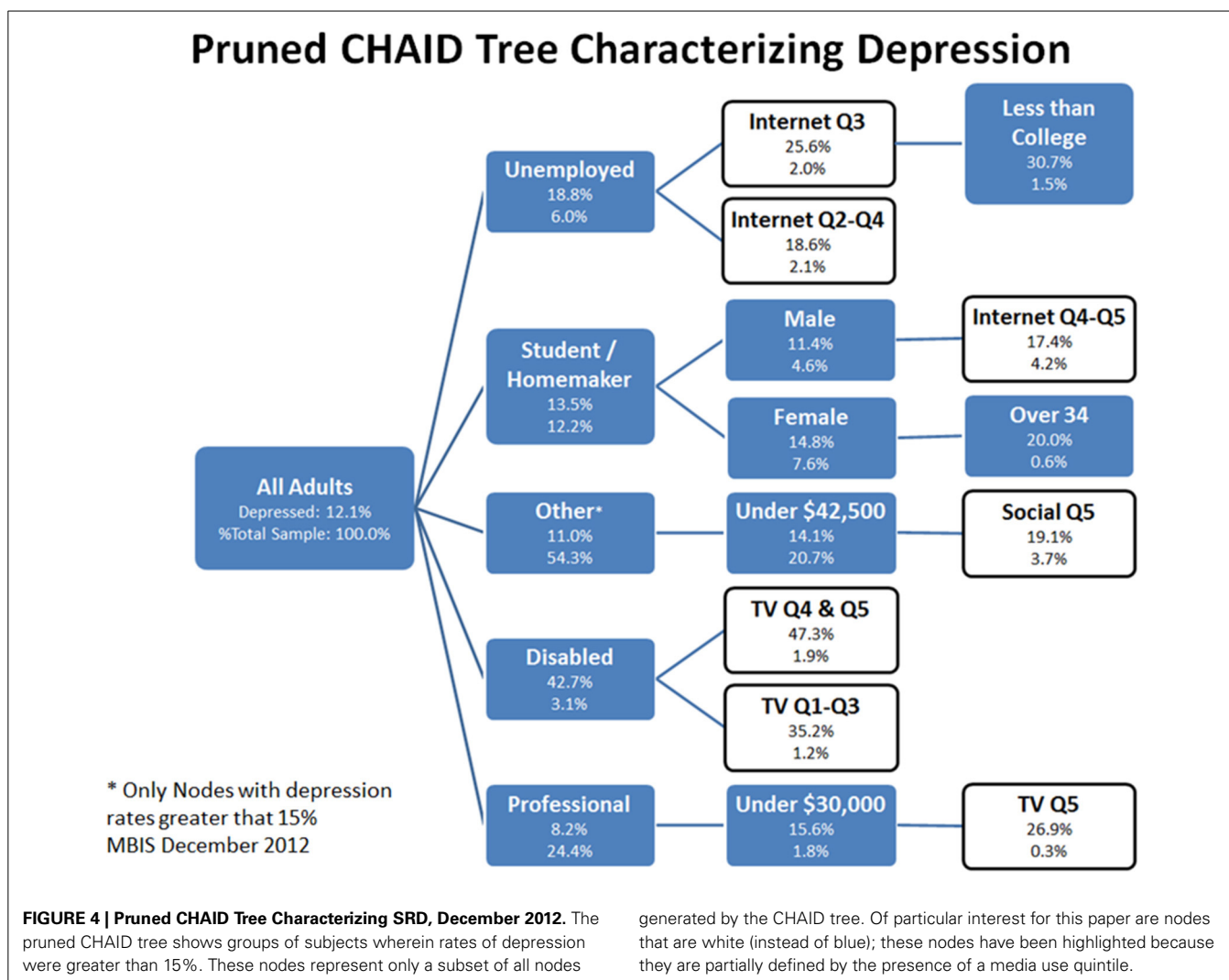
Life challenges may not be the only experiences related to depression. As noted with our descriptive statistical analysis, persistent environmental factors such as isolation can also contribute

to the prevalence of a psychological experience. Generally, isolation is a known correlate of depression symptomology, and our data suggest that residents of rural areas tend to report higher rates of depression. Within the context of isolation, one can distinguish between physical and non-physical isolation; and within non-physical isolation one can look at social and emotional isolation. These various subclasses of isolation find ample support in the literature. Weiss (1973) first distinguished the two types of non-physical isolation—social and emotional—which have subsequently been empirically shown as distinct (DiTommaso and Spinner, 1997). Although conceptually distinct, the various types of isolation interact. Physical isolation has been shown to affect social and emotional isolation, especially for the elderly (Dugan and Kivett, 1994) and adolescents (Brage et al., 1993). We measured social isolation through the proxy of living alone and physical isolation through the proxy of place of residence, finding that both correlate to rates of self-reported depression. For instance, those living in more populated cities (top 10 MSAs) tend to report lower rates of depression.

In addition to the current state of depression, the data we analyzed reveals that SRD has been in a state of flux over the past decade. At the beginning of this time frame, the rates we observed were low compared to 2005 MBIS data where the depressive rate was reported to be 14.9%; a figure consistent with a co-occurring 2005 study wherein a lifetime prevalence rate of 16.5% for major depressive disorder was reported (Kessler et al., 2005a,b). Interestingly, the 2005 MBIS data and the Kessler et al. (2005a,b) data show remarkable concordance despite differences in inclusion criteria (exclusion of non-English speakers in the Kessler et al., 2005a,b studies), the use of a structured clinical interview vs. self-report data, and overall subject demographics. This flux in reported incidence of depression over the past decade is further supported by the MBIS data showing self-reported depression has been on the rise in adults (18+) over the last 4 years in the United States.

It is worth considering the demographics of individuals (e.g., gender) reporting SRD in the context of a flux in depression rates over time. As recently as 5 years ago, females were more likely to report being depressed (i.e., SRD). However, in the most recent MBIS study, the data shows SRD to be similarly associated with both genders, with males reporting only a slightly lower rate of depression. This is different than the rates reported by Primack et al. (2009) where females were shown to be significantly more likely to be depressed, as was also observed in the December 2005 MBIS data. In comparison to prior big data reports, there appears to be a narrowing in the gap of reported depression in females and males, which could potentially reflect a change in the likelihood of genders to self-report. One factor that has remained constant was that depression is inversely related to age, with those younger than 24 reporting the highest rate, and older married persons reporting the lowest.

There are several important limitations to this study that are worth mentioning. First, the data used was self-reported depression, which does not necessarily reflect whether the subject has ever received a clinical diagnosis of depression. The subjective phenotypes of those who have a clinical diagnosis of major depression versus those that self-report depression could skew



the data in a number of different ways. For instance, it has been observed that those who have been diagnosed with depression are sometimes reticent to share their diagnosis. Alternatively, there is a multiplicity of reasons to think that subjects without depression may report being depressed. The balance of these considerations leaves uncertainty in the true sample parameters, although the percentage of subjects with SRD in this study was quite similar to rates of depression found in previous studies.

Second, the variables computed for amount of television, internet, and social media use are not direct measures. These variables are composite variables computed from self-reports of whether or not subjects used those various media during discrete variable-hour-length blocks. This can introduce inter-subject variability along a number of dimensions. For instance, some subjects may report “yes” for one of the intervals based on an hour’s worth of use, while others may respond the same based on several hours’ worth of use. The probabilities computed represent just that, a probability of time spent using a given media relative to other subjects.

Third, the analyses done cannot speak to a causal relationship between media consumption and depression, or to any directionality between the observed associations. We think the likeliest explanation is that these two variables form a complex bi-directional relationship with autocatalytic properties. An alternative explanation is that depression and increased media use are a byproduct of a third confounding factor. It should also be noted that the direction of causality between depression and media use could also vary across individuals (i.e., whether media usage helps to ameliorate depression or whether it contributes to it). Whatever the exact relationship between depression and increased media use, it is clear that the two are closely associated.

Fourth, it is important to acknowledge the potential confounds of concurrent medical illness on assessing associations with SRD. In the literature on major depression, hypotheses have been raised that depression in association with a medical illness does not necessarily reflect the same structural and functional circuitry alterations seen in depression with strong familial heritability (e.g., see Cloninger, 2002; Breiter

Pruned CHAID Tree Characterizing Non-Depression

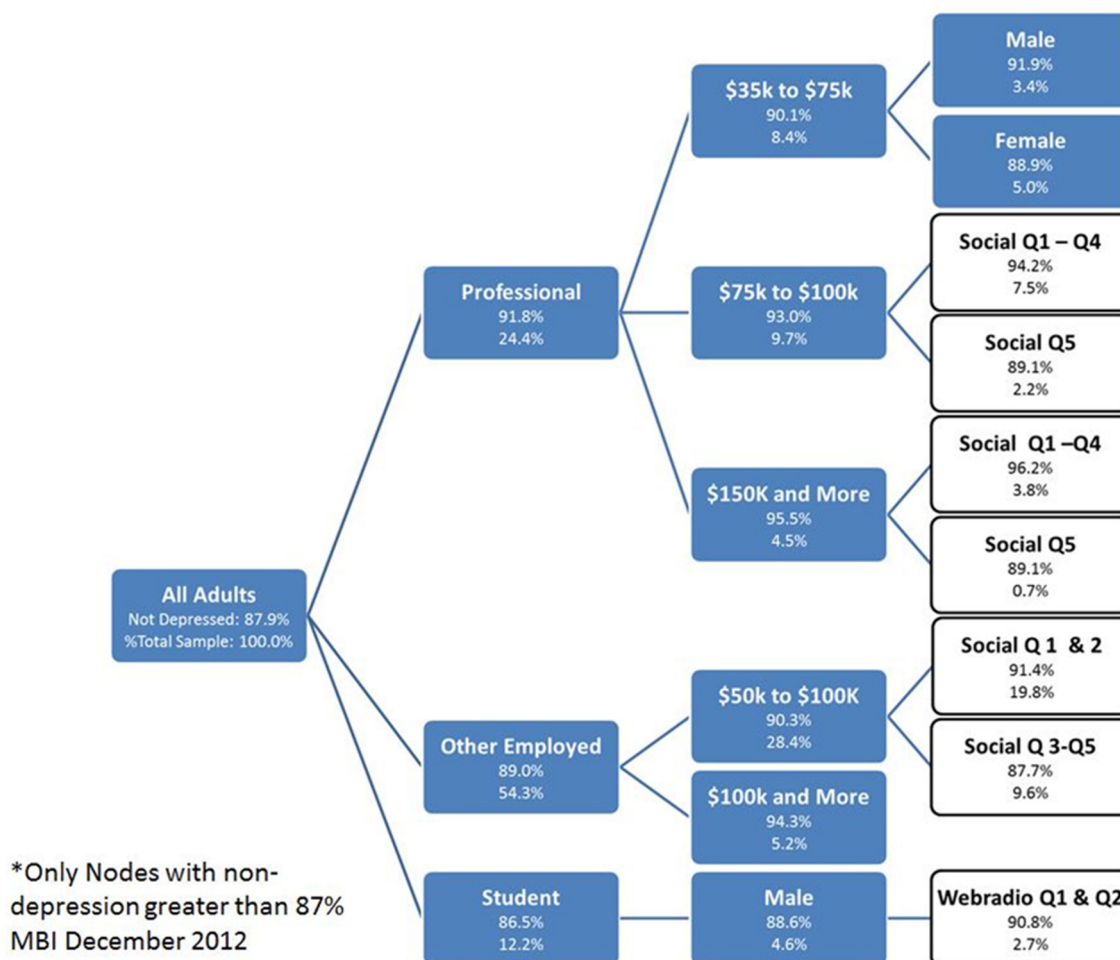


FIGURE 5 | Pruned CHAID Tree Characterizing Non-SRD, December 2012.

The pruned CHAID tree shows groups of subjects wherein rates of non-depression were greater than 87%. These nodes represent only a subset

of all nodes generated by the CHAID tree. Of particular interest for this paper are nodes that are white (instead of blue); these nodes have been highlighted because they are partially defined by the presence of a media use quintile.

and Gasic, 2004; Breiter et al., 2006). There is a strong possibility of biological subtypes in depression (e.g., see Blood et al., 2010), meaning depression comorbid with other illnesses may reflect a directionality with media that is distinct from other putative depressive subtypes. Depression in association with another medical (e.g., severe coronary artery disease) or psychiatric condition (e.g., OCD, generalized anxiety, or body image disorders) may have a complex directional relationship with these other conditions, and there is published evidence that TV viewing itself is associated with anxiety and body image issues (e.g., see Thompson and Heinberg, 2002; de Wit et al., 2011), potentially leading to the self-reported depression. These issues also relate to the potential for drug and alcohol to confound effects with SRD; this data set did not contain such information, so future work is needed to assess the relationship of drug and alcohol effects on SRD and media use.

This information can help to form hypotheses to test in future studies of relevance to psychology. One such hypothesis could relate to the directionality of the relationship between SRD and media, to determine if any media use acts as feedback to exacerbate symptoms. Another hypothesis might attempt to relate the relationship to existing social psychological constructs such as the “empty self” hypothesis. Cushman (1990) developed the “empty self” hypothesis to describe those who feel depressed and may be likely to engage in impulsive or excessive consumption behavior in order to “fill up” a perceived deficiency in the self (see also Ahuvia, 2005). In the context of media usage, the “empty self” might be expected to show increased consumption of media associated with increased SRD; such behavior might be indicative of a subtype of major depression. A third possibility, is a hypothesis that increased media use by SRD subjects acts as indicator of the illness, much like a biomarker. Such hypotheses point to further opportunities for use of big data with psychological research.

Table 2 | Structure matrix of discriminant analysis predicting depression, December 2012.

Canonical correlation 0.235 Wilk's lambda 0.945	Chi-square 922.117 significance <0.001
Disabled	0.760
Income	−0.519
Internet usage	0.399
TV usage	0.368
Social media usage	0.278
Education	−0.255
Unemployed	0.223
Age	−0.170
Living in top 10 MSA	−0.142
Female	0.062
Having children	0.010

This table reports the structure matrix of the discriminant analysis. The nine predictive variables used in the discriminant analysis are reported in the left column, while a measure of that variable's predictive importance in the discriminant function is listed on the right. A variable's importance is determined by its magnitude, while its relationship to depression is determined by its valence. Negative numbers describe an inverse relationship: for example, higher income is predictive of less depression.

In summary, the data reveal that there is a consistent pattern of results that link self-reported depression with increased media use, even when taking into account other variables, such as disability and unemployment. This media use was focused more on internet use and TV exposure, for those making self-reports of depression. The rate of SRD was between two standard indices used in published reports of clinically diagnosed major depression, namely the lifetime prevalence, and recent 12 month incidence of major depression. These observations suggest the current findings with big data may have relevance to the literature focused on the clinical diagnosis of depression.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://www.frontiersin.org/HumanNeuroscience/10.3389/fnhum.2014.00712/abstract>

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Antagonistic neural networks underlying differentiated leadership roles

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The emergence of two distinct leadership roles, the task leader and the socio-emotional leader, has been documented in the leadership literature since the 1950s. Recent research in neuroscience suggests that the division between task-oriented and socio-emotional-oriented roles derives from a fundamental feature of our neurobiology: an antagonistic relationship between two large-scale cortical networks – the task-positive network (TPN) and the default mode network (DMN). Neural activity in TPN tends to inhibit activity in the DMN, and vice versa. The TPN is important for problem solving, focusing of attention, making decisions, and control of action. The DMN plays a central role in emotional self-awareness, social cognition, and ethical decision making. It is also strongly linked to creativity and openness to new ideas. Because activation of the TPN tends to suppress activity in the DMN, an over-emphasis on task-oriented leadership may prove deleterious to social and emotional aspects of leadership. Similarly, an overemphasis on the DMN would result in difficulty focusing attention, making decisions, and solving known problems. In this paper, we will review major streams of theory and research on leadership roles in the context of recent findings from neuroscience and psychology. We conclude by suggesting that emerging research challenges the assumption that role differentiation is both natural and necessary, in particular when openness to new ideas, people, emotions, and ethical concerns are important to success.

Keywords: leadership, roles, neural networks and behavior, DMN, TPN, anti-correlated networks, opposing domains hypothesis

INTRODUCTION

The emergence of two distinct leadership roles, the task leader and the socio-emotional leader, has been documented in the leadership literature since the 1950s (Bales, 1958). The separation of these roles has been seen as pragmatic in applications and is accepted as a finding in behavioral research. However, in practical applications, it leaves an organization with a challenge that can detract from leadership development, succession planning, and organizational flexibility. In this article, we will show that the division between these two types of leadership roles lies far deeper than has traditionally been thought. Recent research in neuroscience suggests that the division between task-oriented and socio-emotional leadership roles derives from a fundamental feature of our neurobiology: an antagonistic relationship between two large-scale cortical networks that is present in every individual.

Neural activity in the task-positive network (TPN) tends to inhibit activity in the default mode network (DMN; Raichle et al., 2001; Fransson, 2005; Raichle and Snyder, 2007; Buckner et al., 2008), and vice versa (Uddin et al., 2009; Jack et al., 2012). The TPN is activated during a broad range of non-social tasks (Fox et al., 2005; Buckner et al., 2008; Uddin et al., 2009; Andrews-Hanna, 2012), and is thought to be important for problem solving, focusing of attention, making decisions, and control of action – in other words for getting things done. However, activation of the TPN also has a deleterious effect on other cognitive functions that are essential to leadership: it suppresses activity in the DMN.

The DMN plays a central role in emotional self-awareness (Ochsner et al., 2005; Schilbach et al., 2008), social cognition (Schilbach et al., 2008; Jack et al., 2012; Mars et al., 2012), and ethical decision making (Koenigs et al., 2007; Bzdok et al., 2012; Jack et al., in press). It is also strongly linked to creativity and insightful problem solving (Subramaniam et al., 2009; Takeuchi et al., 2011). The antagonistic relationship between the TPN and DMN creates a fundamental neural constraint on cognition that is highly relevant to the different roles and capabilities that effective leaders must astutely juggle and deploy. An important consequence of this constraint is that an over-emphasis on task-oriented leadership can prove deleterious to an organization: in particular when openness to new ideas, people, emotions, and ethical concerns are important to success. On the other hand, the over emphasis on relationship oriented leadership may prove deleterious to focus and the execution of clearly defined goals.

We are not the first to note the striking correspondence between the functions of brain networks and leadership. In a recent book, social neuroscientist Matthew Lieberman distinguishes between the social brain and the business brain and does note the antagonistic relationship between the TPN and the DMN (Lieberman, 2013, p. 257). In this paper, we extend Lieberman's preliminary work by providing a more nuanced account of the antagonistic relationship between the TPN and the DMN and their corresponding task and relationship leadership roles. We then extend Lieberman's work by

theorizing strategies that will allow leaders to effectively navigate this fundamental cognitive constraint.

OPPOSING NEURAL DOMAINS

When discussing the functional anatomy of the brain, it is important to appreciate that the literature is less clear than is often acknowledged. The cognitive characterization of the tension between the DMN and the TPN that guides this inquiry is different in important respects from the view that is frequently stated as accepted and uncontroversial (including in the context of leadership, e.g., Waytz and Mason, 2013). Nonetheless, as we will briefly review, the characterization we offer is better supported by the scientific evidence. A number of inconsistencies in the literature facilitate misunderstanding and over-confidence: first, anatomical labels are not always used consistently and sometimes fail to distinguish areas which careful evidence reveals have quite distinct functional roles (Kubit and Jack, 2013). Second, researchers working with different types of cognitive tasks often form quite different views about the primary functional role of a region or a set of regions (i.e., a network). In particular, it is now well acknowledged that researchers have not always been careful to critically evaluate the evidence supporting their inferences about the functional role of brain areas, and sometimes fail to consider evidence about function that derives from a broader view of the literature (Henson, 2006; Poldrack, 2011). Third, networks can be defined according to a number of different criteria.

The issue of how networks can be defined is important to clarify for our purposes. Networks of regions are most often defined (and given a label denoting a provisional functional role) either because: (1) they are frequently found to be activated by a class of cognitive tasks (Corbetta et al., 1998; Duncan and Owen, 2000; Van Overwalle, 2009); or (2) the regions demonstrate strong positive resting state connectivity with each other – a finding which is commonly interpreted as indicating a degree of functional coherence amongst the regions in the network (Fox et al., 2005; Cohen et al., 2008; Vincent et al., 2008; Van Dijk et al., 2010; Yeo et al., 2011). These two criteria are thought to be complementary and broadly consistent with each other, although they do not always yield identical results (Laird et al., 2013).

A third quite different principle that can be used to define a network is through the tendency of a set of regions to be deactivated (i.e., less active than when the participant is at rest) by a class of cognitive tasks (Shulman et al., 1997b). This is how the DMN was originally defined (Raichle et al., 2001). Regions involved in the DMN have also been defined: (a) on the basis of positive resting connectivity between regions in the network, and (b) on the basis of negative correlation (“anti-correlation”) with other regions as revealed by resting functional connectivity. These three ways of defining the DMN (deactivation, positive correlation, and anti-correlation) are broadly consistent and regarded as complementary (Fox et al., 2005; Raichle and Snyder, 2007; Buckner et al., 2008; Uddin et al., 2009; Andrews-Hanna, 2012).

The definition we take as primary for both the DMN and the TPN is their anti-correlation. This follows the original definition of these networks (Fox et al., 2005). An illustration of the two networks, defined in this way, can be seen in **Figure 1**. **Figure 1**

also illustrates a recent state-of-the-art division of the entire cortex into seven networks based on functional coupling between regions, i.e., positive resting connectivity (Yeo et al., 2011). The mapping between Yeo et al.’s (2011) positive connectivity maps and the anti-correlated networks is illustrated in greater detail in **Figures 2** and **3**, for the DMN and TPN, respectively. This reveals the need for some revision of early characterizations of the anti-correlated networks. The broad characterization of the DMN has remained quite stable, and is reasonably consistent using positive and negative correlation criteria (**Figure 2**). However, this is not the case for the TPN (**Figure 3**). It was originally thought (Fox et al., 2005) that the DMN was anti-correlated primarily with the dorsal attention network (Corbetta et al., 1998). However, subsequent work using more data-driven methods (Fox et al., 2005; Chang and Glover, 2009; Chai et al., 2012; Jack et al., 2012) has revealed that the TPN overlaps parts of both the dorsal attention network and the fronto-parietal control network (Vincent et al., 2008). **Figure 3** also illustrates clear overlap between the TPN and the resting state network which Yeo et al. (2011) identify with the ventral attention network (Fox et al., 2006). The ventral attention network is recruited during a variety of demanding attention tasks, however, its precise functional characterization is still subject to debate. It has been characterized as involved primarily in the reorienting of attention, however, more recent analysis suggests that the network as identified by Yeo et al. (2011) can be better characterized as being involved in detecting and responding to task-relevant stimuli (Kubit and Jack, 2013). Hence, particularly for the TPN, it is important to note there is inconsistency between the criteria for defining networks. It appears that DMN is in tension with a set of regions (i.e., the TPN) that lie within a number of different cortical networks that can be distinguished and defined by distinct profiles of positive functional coupling.

THE DEFAULT MODE NETWORK

Until quite recently, the function of the DMN was regarded as largely mysterious. In a comprehensive review, Buckner et al. (2008) noted that “a unique challenge for understanding the functions of the brain’s default network is that the system is most active in passive settings and during tasks that direct attention away from external stimuli.” While these and other researchers acknowledged the difficulty in definitively identifying a function for the DMN, nonetheless a consensus view began to emerge: that the tension between the TPN and DMN could be best explained by a distinction between two kinds of attention, namely externally vs. internally directed cognitive processing. This view was encouraged by some influential early work (Gusnard et al., 2001), by the mistaken view that the DMN was anti-correlated with regions whose primary function was external attention (Fox et al., 2005), and by the paucity of evidence that any externally oriented task could produce activation of the DMN above resting levels (but see Iacoboni et al., 2004).

It is clear that the DMN is reliably engaged by some tasks that involve attention to internal stimuli. Notable examples include: autobiographical recall and prospection (imagining future events; Buckner and Carroll, 2007; Spreng et al., 2009; Spreng and Grady, 2010), self-related processing (Mitchell et al., 2006), and emotion

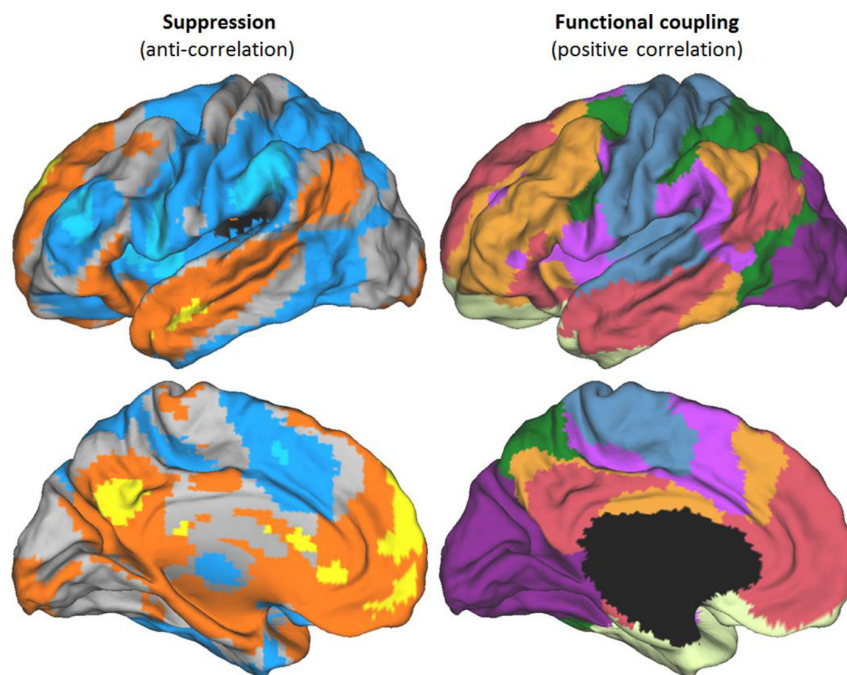


FIGURE 1 | Different criteria for defining brain networks. Functional networks shown on the left hemisphere of the PALS atlas (*top* – lateral view above, *bottom* – medial view). Left panels show anti-correlated networks derived from resting state data. The TPN is shown in blue, the DMN in orange/yellow. Darker colors correspond to anti-correlated networks using a global (whole brain) regressor, brighter colors without a

global regressor (i.e., most strongly anticorrelated areas). Maps derived from data and methods described in Jack et al. (2012). Right panels show the seven network stable solution derived by Yeo et al. (2011) on the basis of positive correlations in resting state data. Area shown in black corresponds to a cross-section through sub-cortical structures, not mapped by Yeo et al. (2011).

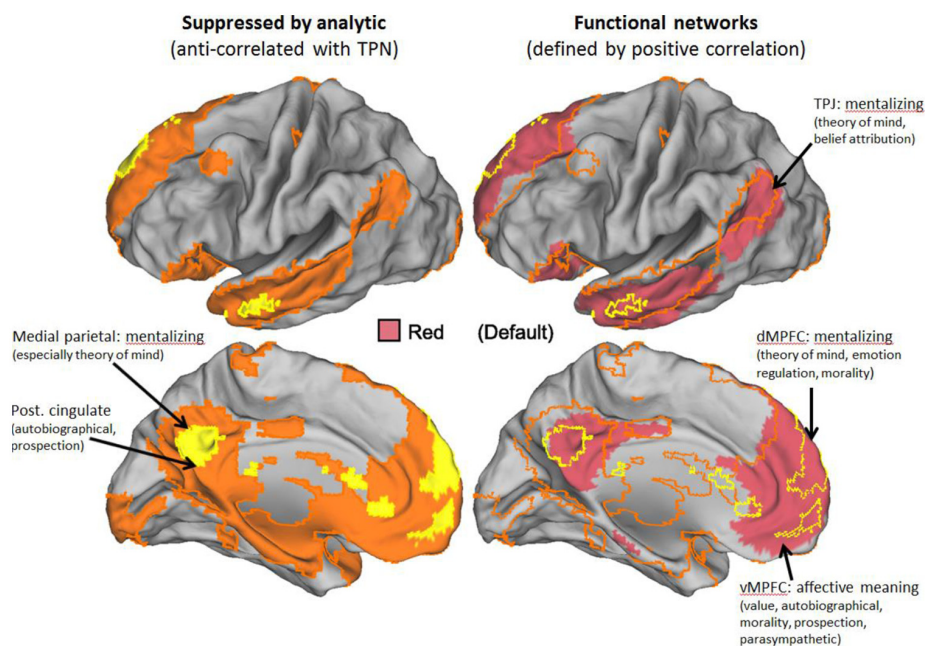
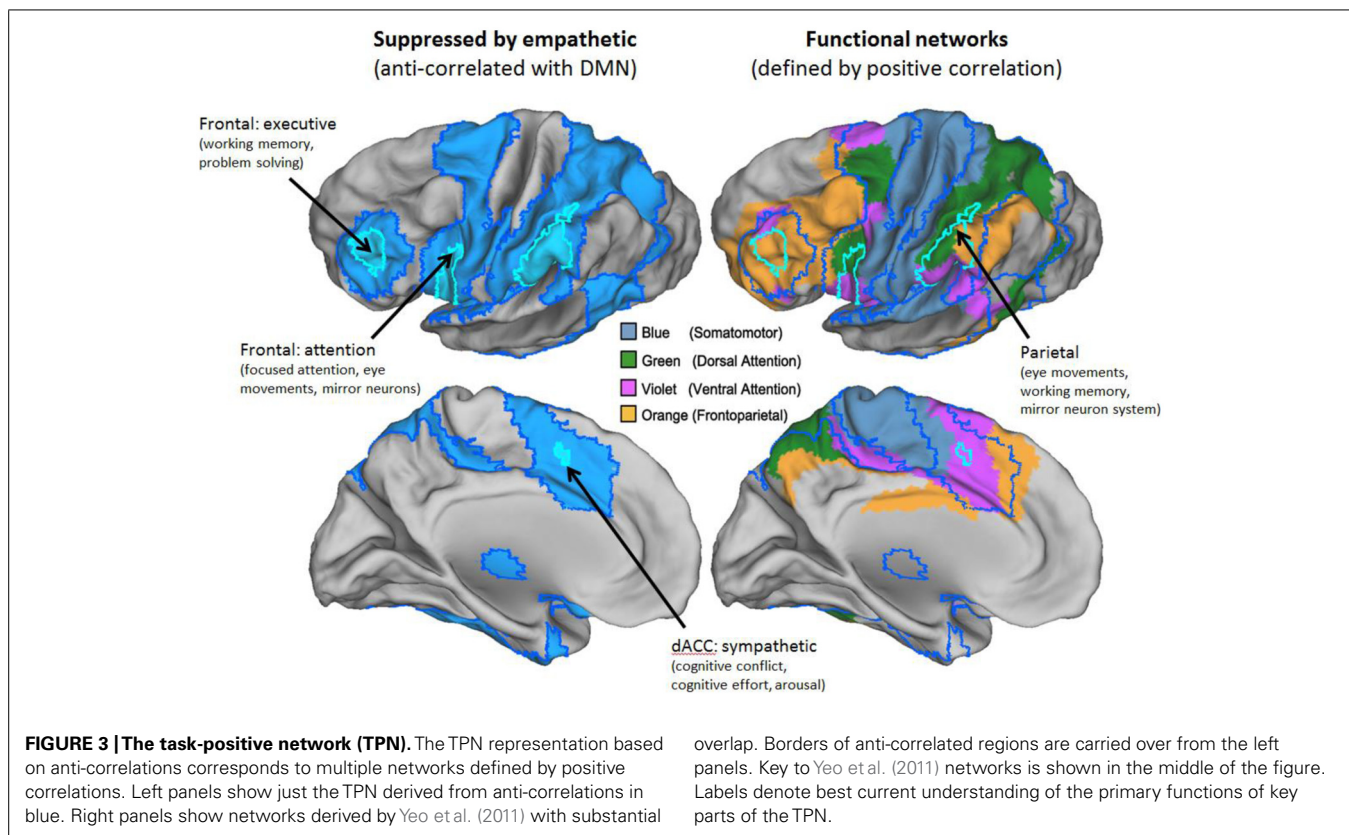


FIGURE 2 | The default mode network (DMN). Strong overlap in the DMN representation based on anti-correlations and positive correlations in resting state data. Left panels show just the DMN derived from anti-correlations in orange/yellow. Right panels show networks derived by Yeo et al. (2011) with

substantial overlap. Borders of anti-correlated regions are carried over from the left panels. Key to Yeo et al. (2011) networks is shown in the middle of the figure. Labels denote best current understanding of the primary functions of key parts of the DMN.



self-regulation (Ochsner et al., 2005). However, the characterization of the DMN as being primarily involved in internal processing glosses over other highly reliable findings which associate DMN activation with externally oriented tasks. These types of externally oriented tasks fall into two broad categories, which correspond to a fractionation of the DMN which can be observed both through meta-analysis of activation findings (Andrews-Hanna et al., 2010) and by resting connectivity analysis (Uddin et al., 2009). More dorsal parts of the midline structures of the DMN, medial parietal and dorsal medial prefrontal cortex (dmPFC) are reliably associated with thinking about the mental states of others, including both their emotional and cognitive (e.g., belief) states (Amodio and Frith, 2006; Schilbach et al., 2008; Van Overwalle, 2009). In contrast, ventral medial prefrontal cortex (vmPFC) is associated with representing the value of external objects (Grabenhorst and Rolls, 2011). Moral decision making tasks, which are again predominantly external in focus, are associated with activity in both dorsal and ventral parts of the DMN (Greene et al., 2004; Bzdok et al., 2012; Koenigs et al., 2012; Jack, in press). Since these findings appear to be inconsistent with the commonly held view that the tension between the TPN and DMN reflects a tension between external and internal attention, we will temporarily set aside that view and return to it in a later section. Instead, the characterization of the DMN we offer here will be guided by a broad view of tasks that are positively associated with DMN engagement.

The DMN may be seen as having two primary circuits. The first is the dorsal portions of the midline structures and the right

temporo-parietal junction (rTPJ), which are most clearly associated with mentalizing, that is, thinking about our own and other's mental states (Ochsner et al., 2005; Amodio and Frith, 2006; Schilbach et al., 2008; Van Overwalle, 2009). It is important to note that the anatomy of this mentalizing circuit is distinct from other regions that make distinct contributions to social cognition. These include: a set of regions primarily involved in perceptual processing of social stimuli such as faces and bodies (Wiggett et al., 2009) and the mirror neuron network, which is involved in both executing and observing actions, and thought to underlie our ability to mimic the actions of others. In contrast, the mentalizing system is thought to be involved not in emotional contagion, but in the cognitive representation of emotion (Lindquist et al., 2012).

The second of the primary DMN circuits is the more ventral portions of the midline structures, which are associated with self-related processing, autobiographical memory and prospection, cognitive representation of emotion, representation of value/reward, emotion self-regulation, and autonomic processing. We endorse the characterization of these processes offered by a recent review (Roy et al., 2012), which concludes: "The vmPFC is not necessary for affective responses per se, but is critical when affective responses are shaped by conceptual information about specific outcomes. The vmPFC thus functions as a hub that links concepts with brainstem systems capable of coordinating organism-wide emotional behavior, a process we describe in terms of the generation of affective meaning." The severe consequence of poor function in this circuit has long

been known through the highly influential work of Damasio (1994) looking at patients with vmPFC damage. These patients exhibit severely impaired social, moral, and decision making behavior, cannot hold down a job, and tend to be shunned by family members, even though they often have high IQs (Anderson et al., 1999). More recent work with moral decision making tasks indicates that they also tend to favor a course of action, which appears to promote the best overall outcome, even when that involves denying individual rights and directly harming others. In other words, they are more utilitarian in their thinking (Koenigs et al., 2007).

With regard to leadership roles, the DMN is the basis for relational roles in which the leader makes sense of their own and other people's emotions and helps to construct a sense of purpose or vision for the group. Given that both subsystems of the DMN are typically deactivated by tasks that activate the TPN, it is troubling to imagine the potential consequences of placing too strong an emphasis on adopting leadership roles that recruit the TPN.

THE TASK-POSITIVE NETWORK

The broadly defined functions of the TPN are agreed in the literature, although some debate persists about the best way to characterize the function of the finer grained functionally coupled networks which it overlaps (Kubit and Jack, 2013). The TPN is activated, and the DMN deactivated, by wide variety of non-social tasks including those involving focused attention, working memory, language, logical reasoning, mathematical reasoning, and causal/mechanical reasoning (Shulman et al., 1997a,b; Duncan and Owen, 2000; Fox et al., 2005; Owen et al., 2005; Van Overwalle, 2011). While the TPN includes some regions of the brain associated with social processes such as the mirror neuron network, it is distinct from the mentalizing network of the DMN both in its location and in the types of tasks that activate it (Van Overwalle and Baetens, 2009; Van Overwalle, 2011; Jack et al., 2012). The TPN includes parts of the dorsal attention system (Fox et al., 2005), the fronto-parietal control network (Vincent et al., 2008), and the ventral attention network (Fox et al., 2006; Kubit and Jack, 2013). Using more relaxed criteria, it can also be seen to overlap the somatomotor network (Figure 3). These networks are broadly associated with focus on, and execution of, well-defined tasks that are non-social in nature. Jack (in press) defines the TPN as “analytical–empirical–critical reasoning, such as mechanical reasoning.” Given our current understanding of the TPN, leadership roles associated with this network are those focused on financial planning, metrics, forecasting, problem solving, as well as strategic social engagement for the purpose of task achievement.

THE OPPOSING DOMAINS HYPOTHESIS

As discussed, it is generally accepted in the cognitive neuroscience literature that the DMN and the TPN are anti-correlated (Greicius et al., 2003; Fox et al., 2005; Fransson, 2005; Golland et al., 2007; Tian et al., 2007; Buckner et al., 2008; Jack et al., 2013b). It is also broadly agreed that a variety of cognitively demanding non-social tasks tend to activate the TPN and deactivate the DMN. There has been less agreement about how best to cognitively characterize the tension between these networks.

The opposing domains hypothesis predicts that activation of the DMN or the TPN is a result of the type of thinking a person engages in to order to complete a given task, regardless of whether the task is externally or internally oriented (e.g., relates to perceived stimuli vs. to information recalled from memory). Personality factors play a role in the deployment of these networks, particularly for tasks where the most productive strategy is unclear or ambiguous. Nonetheless, it is thought that all neurotypical individuals are capable of flexibly deploying these networks, hence tasks which have a clear affordance for one type of processing over the other will tend to engage the relevant network. When a person engages in a cognitively demanding non-social task, they will tend to define their role as having an analytic focus. In this circumstance, both the opposing domains hypothesis and other accounts predict the TPN will tend to be activated and the DMN deactivated. When a person engages in a task that involves mentalizing and/or thinking about affective meaning, and as a result, defines their role as social and/or relational, the opposing domains hypothesis predicts the DMN will be activated and the TPN deactivated. This prediction, which entails that an individual's analytic abilities are suppressed when they are empathically engaged with people, is unique to the opposing domains account.

Jack et al. (2012) used functional magnetic resonance imaging (fMRI) to record brain activity when participants were engaged in social vs. mechanical/analytic tasks. The social tasks required participants to answer questions about the beliefs and attitudes of the characters in emotionally and morally laden text passages or video clips. The mechanical tasks required participants to complete science puzzles, presented either as written passages, or as video clips taken from the Video Encyclopedia of Physics. A rest condition was included, in which participants were only asked to stare at a fixation point, for the purpose of establishing a resting baseline against which both activations and deactivations could be observed.

The findings showed that the neural activation during the social tasks, specifically the activation of the rTPJ, medial parietal/posterior cingulate and the medial prefrontal cortex, was accompanied by the deactivation of the neural networks responsible for mechanical reasoning, specifically, the superior frontal sulcus, lateral prefrontal cortex, and the intraparietal sulcus. Controls were put in place for task and perceptual demands to rule out the alternate hypothesis that the TPN vs. DMN dichotomy can be best accounted for by internal vs. external attention.

Jack et al. (2012) conclude that the anti-correlation between the TPN and DMN “reflects a powerful human tendency to differentiate between conscious persons and inanimate objects in both our attitudes and modes of interaction” (p. 396). Further work (Jack et al., 2013b) looking at humanizing vs. objectifying (where people tend to be viewed as objects) narratives about people provides additional support for the view that these networks are not driven by the surface characteristics of the stimuli, but rather reflect flexible cognitive stances which can be deployed depending on the attitudes and role adopted by the individual. The implications of these findings for leadership and organizational behavior are vast. The duality of task and relationship; inanimate and animate; and social and non-social can be found in

the personality, motivation, group dynamics, socialization, conflict, trust, decision making, mindfulness, and moral reasoning literatures.

A further wrinkle to this account is important to note. While it is very well documented that the TPN and DMN tend to be antagonistic, both at rest and during the performance of tasks, the dichotomy between these networks is not absolute. They can be simultaneously activated and work in cooperation with each other (Fornito et al., 2012; Meyer et al., 2012). Both theory and observation indicates that this occurs when participants are engaged in a type of social reasoning that is highly instrumental, and lacking in genuine empathy. For instance, this pattern is seen more in individuals who are prone to Machiavellian thinking (Bagozzi et al., 2013). It is also the neural signature that is seen when people are animalistically dehumanized, rather than objectified (Jack et al., 2013b).

This recruitment of the TPN during social cognition is likely due to a person thinking critically, strategically, or mechanically about people. Hence, it does not appear to be the case that we can be both genuinely empathetic and analytic at the same time. Instead, our view is that when these networks work co-operatively with each other (Fornito et al., 2012), they realize a different type of cognitive processing from either genuine empathy or pure analytic reasoning. When we engage the analytic network alongside the DMN, this corresponds to a mode of social interaction that is alienating to others. This is reflected in everyday language. When we say that people are being “manipulative” or “calculating,” the metaphor may make sense because they are using TPN brain regions involved in fine motor control and/or mathematical reasoning to operate on social representations (Meyer et al., 2012). Although this cognitive mode involves a sense of social or emotional distance, it is clearly useful to think “strategically” or “politically” in this way on occasion. This is reflected in the observation that strategic social reasoning plays a crucial role in leadership research. For example, Boyatzis and Goleman (2007) make the distinction between emotional intelligence (EI) and social intelligence (SI). EI is defined as the ability of a person to recognize, understand, and use emotional information about oneself or others (Boyatzis, 2006). We expect these competencies will tend to recruit both the DMN and the TPN in tandem. By contrast, SI competencies are non-task focused, for example, acting with compassion, and would therefore primarily recruit the DMN (Boyatzis and Goleman, 2007). Interestingly, Boyatzis et al. (2006) predicted that SI competencies are linked to the parasympathetic nervous system, while focusing on tasks and instrumental use of EI is linked to the sympathetic nervous system. This would suggest that EI competencies would relate to the TPN. Research is currently underway to explore what overlap exists between the divisions of the autonomic nervous system and the TPN and DMN. While the evidence is far from conclusive, early findings based on recent meta-analyses (see, for example, Beissner et al., 2013) indicate that the TPN is more closely linked to the sympathetic nervous system while the DMN is closer to the parasympathetic nervous system. The labels in **Figures 2 and 3** indicate regions which show the closest correspondence between the DMN and TPN and regions implicated in autonomic nervous function (Eisenberger and Cole, 2012).

OPPOSING ROLES OF LEADERSHIP LEADERSHIP ROLES

A role is a constellation of behavior and expectations enacted in a social situation. Mead (1934) claimed that roles were embedded in the situation and therefore were constantly emerging and evolving. As a sociologist and helping to formulate the interactionist theory of roles, Mead (1934) emphasized the expectations of others in the forming and reforming of roles. In this way, roles are distinct from style. Leadership style describes a dispositional comportment of a person as a leader that can vary by situation and demand. Leadership style contributes to role enactment as Biddle (1986) explained from a functionalist theory of roles.

In leadership, a role provides a guide to one's behavior and helps new role occupants become socialized into how they could or should act in a way consistent with the norms and culture of an organization. A leadership role of a person emerges in response to the expectations of others around the leader, especially the followers, and the leader's own style/s, competencies, and values (Boyatzis, 1982). This process of role emergence as a result of the interaction between expectations and behavior has been explained by cognitive role theory (LeMay, 1999).

There appears to be two distinct components of the enactment of leadership roles that parallel the distinction between the TPN and the DMN: task achievement and relationship development. We will place the evolution of this duality of leadership roles in historical context.

FROM TAYLOR TO BASS APPROACHES TO LEADERSHIP ROLES

The centrality of tasks to a leader's role was evident in Cowley's (1928) definition of a leader: “an individual who is moving in a particular direction and who succeeds in inducing others to follow him. . . A leader then, is a person who is going somewhere, who has a motive, who has a program.” (p. 145–146). In short, without a task, leaders do not exist.

Fredrick Taylor's scientific management movement emphasized the task aspect of leadership. Followers were viewed as “machines” to be used efficiently by the leader. In other words, by treating humans as inanimate objects subject to analytical analysis, the role of a leader in the scientific management era was largely reliant on recruitment of the TPN rather than the DMN (Jack et al., 2013b) and therefore discouraged the leader from fostering more meaningful social-emotional connections with followers. The introduction of the “human” side of leadership in the late 1930s gave rise to a multitude of leadership frameworks that reflected the scientific management (task) – human relations (relationship) duality. These frameworks include the autocratic (task)-democratic (relationship) continuum (Tannenbaum and Schmidt, 1958), the Ohio State Leadership Studies on structure (task) and relationship (Shartle, 1950; Fleishman, 1953; Halpin and Winer, 1957), and the Michigan Leadership Studies (Katz et al., 1950) of a production orientation and an employee orientation.

ATTEMPTING TO INTEGRATE TASK AND RELATIONSHIP ROLES FROM THE 1950s TO THE 1970s

When symbolic interaction theory transferred from social to organizational psychology, leadership theory changed to require *both*

relationship building and task attainment. This development parallels the duality of the neural opposing domains: relational leadership competencies are facilitated by the DMN, while the task competencies are facilitated by the TPN. Bales (1958) was instrumental in this theoretical shift in the leadership literature with his claim that a task-oriented group requires two types of leaders to maximize effectiveness; one leader to attend to the task functions of the group (instrumental leader) and another to attend to the emotional needs of the group (expressive leader). The suggestion that two leaders are required in a group stood in stark contrast to the idea that all leadership roles could be carried out by one individual. Given that we now know that the neural networks underlying these two roles are antagonistic, having two leaders in a group presents what initially appears to be a reasonable strategy for relieving the task–relationship tension.

By the 1960s, a consensus began to form that building relationships with followers was a fundamental component of leadership and a critical ingredient in task achievement. Leadership theorists became interested in developing strategies that would enable leaders to integrate these two fundamental leadership roles. The early Ohio State Leadership Studies (Fleishman, 1953) confirmed the conceptual distinction between task-oriented and relationship-oriented leadership and developed a measurement tool for each. Following from this work, task-oriented leadership has been identified as being concerned with production (Blake and Mouton, 1964), goal achievement (Cartwright and Zander, 1960; Bowers and Seashore, 1966), labor allocation, enforcement of sanctions (McGregor, 1960), and creating a context and structure for followers (Shartle, 1950; Fleishman, 1953; Halpin and Winer, 1957). At the individual level, task-oriented leaders were said to have a high need for achievement (McClelland, 1961; Wofford, 1970), to be achievement oriented (Indvik, 1986), and to be cold and aloof to signal their preference for psychological distance from followers (Blau and Scott, 1962). Interestingly, these descriptions are not only consistent with the role of the TPN discussed earlier, but also allude to the suppression of the DMN – in particular, they fit well with our observation that the socially distancing effect of dehumanizing is associated with a shift from DMN to TPN engagement (Jack et al., 2013b).

Conversely, relationship-oriented leaders were described as being focused on follower well-being (Hemphill, 1950), concerned with developing and maintaining relationships (Hersey and Blanchard, 1969), to be more democratic as opposed to autocratic (Bass, 1990), and as placing value on friendships, open communication, and mutual trust. These psychological features fit a profile of DMN activation and TPN deactivation – the neural signature associated with thinking about the experiences of others (Jack et al., 2012) and humanizing (Jack et al., 2013b). Individuals who are humanized experience positive emotions, whereas those who are dehumanized experience negative emotions (Bastian and Haslam, 2011). Correspondingly, research has shown that relationship-oriented leaders are associated with higher job satisfaction and lower turnover in organizations (Bass, 1990; Yukl, 2006).

Yukl (1999) provides the most recent taxonomy of task and relationship oriented leader roles. He also distinguished a third dimension

in his taxonomy, labeled “change orientation” which includes a mix of task and relationship oriented roles. However, in critiquing other’s work, Yukl (1999, 2008) notes the limitations of the task–relationships distinction, specifically, the inconsistent empirical results and the lack of evidence that it is indeed possible to be high in both task and relationship competencies and that being so is related to leadership effectiveness (Yukl, 1999). Research conducted since adds support to Yukl’s critique; specifically, Kaiser and Kaplan (unpublished, as cited in Bass and Bass, 2008) found that in a sample of managers from a consulting firm, 46% were highly task oriented, 19% were highly relationship oriented, and only 6% showed flexibility between the two dimensions. The remaining 29% were low in both task and relationship orientation.

The distinction between task-oriented roles vs. relationship-oriented roles presented in Yukl’s taxonomy appears to closely parallel the distinction made between social and mechanical tasks used to test the opposing domains hypothesis (Jack et al., 2012). Specifically, the task-oriented tasks are, by and large, mechanical and analytical in nature and would therefore activate the leader’s TPN, while the relationship oriented tasks are generally social in nature and would therefore activate the leader’s DMN.

The anti-correlation between these two networks suggests that when a leader is focused on a task-oriented role, their ability and desire to attend to the relationship needs of their followers is diminished. This is not to say that leaders do not have the ability to be both highly analytical and to build effective relationships. In the absence of any task, it is known that the human brain naturally cycles between activation of the TPN and activation of the DMN, activating each several times in a period of a minute (Fox et al., 2005). Hence, it is clearly possible to switch between networks and possibly roles.

However, the evidence from neuroscience does suggest that leaders cannot simultaneously attend to these distinct roles, hence conflicts are likely to arise if leaders get “stuck” in one role, which decreases their ability to switch between the two networks, resulting in the prolonged suppression of one of the networks and associated roles. This trade-off has been noted by a number of scholars. Most recently Yukl (2008) notes that “efforts to improve one performance determinant may have an adverse effect on another performance determinant. . .when leaders are preoccupied with responding to external threats (task), there is less time for people-oriented concerns such as being supportive and developing member skills” (pp. 711–714). The opposing domains hypothesis provides an alternative explanation for why this trade-off occurs. Rather than, or at least in addition to, a simple lack of time and overall cognitive resources, the opposing domains hypothesis suggests that the suppression of the opposing neural network further exacerbates the “adverse effect on another performance determinant.”

The antagonistic relationship between the TPN and DMN may also help us to understand why the type of role a leader adopts moderates the relationship between leadership role (task vs. relationship), task performance and leadership effectiveness respectively. Specifically, Burke (1965) found that a group’s performance of a coding task was completed more effectively under a production-oriented (task) leader while the shared decision-making (task) was carried out more effectively under a

relationship-oriented leader. The opposing domains hypothesis offers two explanations for this finding – the first related to the ability of the followers to perform the task, the second related to the leadership role that the followers' perceived to be effective.

First, followers performed more effectively on the analytical task when the leadership role matched the neural network activated as a result of the analytical nature of the task (the TPN). When a relationship-oriented leadership role was used, the leader's behavior and focus on relationships may have activated the DMN in followers, which we now know to be associated with lapses in attention and performance errors (McKiernan et al., 2003; Mason et al., 2007; Fassbender et al., 2009; Pyka et al., 2009), hence the lower performance on the analytical task. Conversely, the shared decision task, which required interpersonal interaction and therefore would have activated the DMN, was performed more effectively under a relationship oriented leader. A relationship-oriented leader in this task would have allowed for the follower's DMN to be dominant, which is the network required to perform this task effectively. A task-oriented leader would have activated the follower's TPN, which would suppress the DMN resulting in a reduction of human and ethical insight (Jack et al., 2013b, *in press*) and consequently lower task performance.

Second, when completing the coding tasks the followers were predominately engaging their TPN, hence the task-oriented leadership role may have been perceived by followers to be more effective because it was more psychologically resonant. Similarly the relationship-oriented leadership role may have been preferred by followers engaged in the moral decision task because of the resonant emphasis on DMN engagement for both the task and the leadership role.

Further evidence of the interaction between task type and follower preference for a task vs. relationship-oriented leader is offered by Weed et al. (1976). This study found that the only type of task that was a significant moderator between leadership role and task performance was the difficult–ambiguous task. While this study was focused on the difficulty and ambiguity of the task rather than the mechanical or social nature of the task, the authors note that the difficult–ambiguous task was the only task that involved ethical/moral problems and therefore “the significant findings on this task may be partially attributable to the types of skills required to deal with these problems” (p. 65).

Finally, Hersey and Blanchard (1969) developed the Tri-Dimensional Leadership Model that sought to link task and relationship oriented leadership roles to follower perceptions of leadership effectiveness. The Tri-Dimensional Leadership Model suggests that leaders who are highly task oriented will be perceived as “effective” because they know what they want and are able to impose this to accomplish a task without causing resentment. A highly task-oriented leader will be perceived as ineffective when followers' perceive the leader has no confidence in others, is unpleasant, or only shows interest in short-run output. In other words, a highly task-oriented leader will only be seen as effective if they are aware of, and attend to, relationships – rather than dehumanizing their followers – while accomplishing the task.

Similarly, a leader with a high relationship-orientation will be seen as effective by followers when they perceive the leader has

implicit trust in them and is primarily concerned with developing their talents – behaviors associated with humanizing and the DMN. They will be seen as ineffective when followers perceive the leader to be passive and showing little care about the task at hand – behaviors associated sustained activity of the DMN that suppresses the TPN (Mason et al., 2007; Jack et al., 2012). These findings extend the hypotheses derived from the Burke (1965) study with the suggestion that regardless of a leader's preferred role (task-oriented or relationship oriented), the leader must be able to switch fluidly between the opposing neural networks (the TPN and the DMN) in order to be perceived as effective by their followers. Given this, it seems that rather than identifying the individual difference variables and situational variables that are associated with each style in isolation, it may be more important to identify variables that correspond to the ability of a leader to switch between the TPN and the DMN in order to maximize leader effectiveness.

DEALING WITH THE DIALECTICAL TENSION

The previous section has shown that the distinction between task and relationship roles is evident throughout the leadership literature. In this section, we explore potential strategies to resolve, or at least minimize the consequences of the tension that leaders face in developing their roles to attend to task requirements and attending to relationships as a result of the antagonism between the TPN and the DMN.

NEURAL DISPOSITION: MATCHING THE LEADER TO THE SITUATION

As with hormonal disposition, there is some evidence to suggest that humans have a natural disposition toward either analytical–mechanical reasoning and therefore the TPN or social–relational reasoning and therefore the DMN (Jack et al., 2012). While neural disposition is a relatively nascent area, hormonal dispositions are well documented in the literature (see Insel, 1997; Schulkin, 1999). For example, people with higher unconscious power motives are known to have higher resting levels of epinephrine secretion, while people with a higher unconscious Need for Achievement appear to have higher resting levels of vasopressin secretion (Boyatzis and Sala, 2004; Boyatzis et al., 2006). At the behavioral level, neural and hormonal dispositions may underlie certain personality characteristics, learning styles, and perhaps preferred leadership roles (Boyatzis and Sala, 2004).

Considering the opposing domains model, one way to address the tension between the task and relationship leadership roles could be to match a leader's predisposition toward either task or relationship to the type of task they perceive as their primary role and responsibility. In many ways, Bales' (1958) suggestion of the need for two leaders was an attempt to do this. The utility of matching a leader's natural inclination toward either a task or relationship role to the situation has found some empirical support in the literature. For example, Slatter (1955) found that when task demands are high, being liked does not contribute to leadership effectiveness and social or relational skills are not highly valued, whereas in therapy groups, sensitivity training groups, and social clubs socio-emotional skills were important. However, the practical results from dividing the leadership roles have been less than ideal.

Like the old CEO (chief executive officer) and COO (chief operating officer) split, father and mother role split, CO (commanding officer) and XO (executive officer) split in the military, this leadership role differentiation is possible but appears to be less effective in the long-term. Attempts to have two people occupy co-chair, or co-CEO roles have been, at best, confusing. Usually leaders in these roles cannot sustain true status and power equalization over time. In addition, others around them may not allow it and their expectations and preferences push for more status differentiation, not less. Over time, one role dominates the other, and as a result one neural network dominates brain activation (even as an organizational norm) leading the organization down a narrow path of either problem focused decisions with little openness to new ideas or events occurring in the larger environment (like market shifts) OR an organization preoccupied with environmental changes and meeting the various desires of employees that has difficulty executing a strategy consistently over time.

Differentiating the leadership role effectively allows a leader to spend the majority of their time in one of the two neural networks and reduces the need to cycle between them. From the point of view of sustained leadership effectiveness, fluid cycling at rest between the two networks is associated with good mental health and higher IQ, whereas a lessening of the cycling between networks is associated with a variety of mental disorders (Broyd et al., 2009; Andrews-Hanna et al., 2010; Anticevic et al., 2012; Whitfield-Gabrieli and Ford, 2012). While studies of the long-term effects of privileging the engagement of one cognitive mode over the other in task performance have yet to be done, it is plausible that a more balanced approach is associated with better long-term mental health and performance, whereas over-privileging one network for sustained periods leads to mental exhaustion and burn-out – two detrimental effects that are often discussed in the leadership literature. Therefore, role differentiation, while presenting an easier short-term strategy for an organization to accomplish a balance, may prove far less productive if the individual's role remains constant over time.

These considerations suggest a more effective approach would be to train and develop leaders so that they not only possess a high level of competency in enacting both the task and relationship leadership roles, but also have the ability to switch fluidly between them along an awareness of appropriate cues and contexts for doing so (French and Jack, in press), which also requires a perceptual facility with perceiving when each is needed or more appropriate. The actions to invoke a change of role are within a leader's purview. For example, a leader witnessing a competitor take some of their clients or market share could see this as a need for analytic investigation – is there is pricing difference? Are there differences in transportation costs or delivery speed?

Similarly, a leader who is heavily into a task role (and TPN activation) may decide that each day he/she will coach another person to help them develop. In a within subjects study comparing a method of coaching with the positive emotional attractor (PEA; i.e., coaching with compassion) vs. the more typical method of coaching someone to fix them – to the negative emotional attractor (NEA; i.e., coaching for compliance), components of the DMN were significantly activated in the PEA condition more than

the NEA condition (Jack et al., 2013a). Since this neural network allows a person to be more perceptually and cognitively open to new ideas, it may be the process needed to help people become open to switching and engaging both domains with fluidity. By deciding to coach one person each day (formally or informally over coffee or a lunch), *and* to commit to doing it about the person's dreams, vision or values, the leader commits to switching into the relationship role at least once a day and activating the DMN in both himself/herself and the other person. Over time and practice, the switching between the task and relationship roles would likely become easier and help the leader develop more cues as to when one role is more appropriate or possible than the other. Not quite as simple as changing hats or shoes, but it could become as convenient.

NEURAL RESOURCE EFFICIENCY

The opposing domains hypothesis could be framed as presenting a form of “trade-off” between adopting roles favoring task-related leadership activities and therefore activating the TPN and suppressing the DMN and adopting roles favoring relationship building activities and therefore activating the DMN and suppressing the TPN. In this framing, neurological activation is essentially a form of resource that leaders distribute between the task and relationship roles to attain or increase their effectiveness. When a leader expends more neural resources attending to relationships, they consequently have fewer resources to invest in the task role and vice versa. It may be possible that we can change the rate or efficiency of the leader's neural resources, thereby minimizing the extent of activation required to successfully complete the task. Because the TPN and the DMN are antagonistic, minimizing the degree of activation in one network also serves to proportionally decrease the suppression of the opposing network (McKiernan et al., 2003; Pyka et al., 2009).

Task-positive network competencies

We expect that leaders with a high level of cognitive intelligence (g) will show greater ability in analytical or mechanical type tasks. They are also more likely to perceive the need for an analytic leadership role focusing on the TPN and to adopt this role in an organization. When faced with an analytical or mechanical task, we expect leaders with high levels of cognitive intelligence will require less “effort” or neurological resources to successfully complete an analytical or mechanical task than leaders with lower levels of cognitive intelligence (Graham et al., 2010). Similarly, we expect that when faced with an analytical task requiring the strategic use of emotional information, leaders with high EI will require less cognitive effort to engage followers than leaders with low EI. Leaders with higher levels of EI can access the emotional information more easily than those with low EI, even if it is in service of an analytic task. This helps to clarify that emotional labor can be in service of either a task demand or an emotional and social demand.

A leader who shows a high level of familiarity or specialized competence in a given task should also require less neurological resources than leaders with a lower level of familiarity or specialized competence. A high level of task competence will result in the leader experiencing the task with less intensity resulting in a

lower level of activation in the TPN. By the work appearing more routine to a leader using an appropriate role, it may allow a leader to switch roles more easily. Holding competence, experiences, and intelligence constant, more difficult tasks will require more neurological resources than easy tasks (McKiernan et al., 2003; Mason et al., 2007; Pyka et al., 2009).

Default mode network competencies

In similar vein to the reasoning discussed above, when faced with a social or relational task, we expect leaders with high SI (as opposed to EI—see Boyatzis and Goleman, 2007) to require less neurological resources to successfully complete a relational task relative to those leaders with low SI. We would also expect that leaders who possess high levels of empathetic concern and compassion to be in a similar position. These leaders are also more likely to perceive the need for and adopt a relational leadership role.

SWITCHING BETWEEN THE TPN AND DMN

While the idea that a task can be classified as either analytical or social is useful for theoretical purposes, as with most dichotomies, the distinction is rarely so clean-cut in practice. In reality, and particularly in the context of leadership, all tasks have a relational component and an analytical component. Leadership almost always requires consideration of both analytical tasks (TPN) and relationships (DMN), therefore we suspect that the greater ability a leader has to switch between these two modes of reasoning the more effective they will be as a leader. We suspect that minimizing the suppression of the opposing network will make it easier, faster, and less costly for the leader to switch between the two networks. For example, we have already argued that leaders with certain social competencies require less cognitive effort to complete a social task than those without these competencies, resulting in less activation of the DMN and less suppression of the TPN. This reduction in the difference or gap between the two networks should make switching between the two networks faster and less costly.

Along with the ability to switch between the two opposing networks, which we argued may require a reduction in intensity of the dominant network, we also expect the ability to appropriately time the shift from task to relationship to be important both in terms of minimizing disruption for followers and for maximizing the effectiveness of the shift. For example, knowing that activation of the DMN suppresses our analytical-mechanical reasoning abilities (Jack et al., 2012), and that activation of the DMN during analytic tasks is associated with mind-wandering and lapses of attention (Mason et al., 2007; Fassbender et al., 2009), it would appear unwise for a leader to engage followers in activities requiring social or relational reasoning at a time when it is important or urgent to maintain analytic focus. Similarly, in situations requiring social or relational reasoning, for example, during the group's formation period, introducing task-focused activities may inhibit relationship development in the group.

The timing of the switch may also have implications for the timing of feedback. Based on the opposing domains hypothesis, we would expect that the closer the time period between action and feedback, the more congruence there should be between the type of feedback and the type of task. For example, if feedback is

being given while a person is performing an analytical task, the feedback given should be analytical or technical in nature because this is the type of feedback is consistent with the neural network within which the receiver is engaged. If the leader wishes to give feedback that requires the follower to engage in social or relational reasoning, he/she would be better to wait until the receiver has disengaged from the analytical task. The same can be said for giving task-related feedback in an emotionally charged situation. Gottman et al. (2002) documented something every married or partnered person should know. When your spouse or partner is angry and yelling at you, this is not the time to reply by analyzing the situation in emotional distant terms. It does not help and in fact, as Gottman et al. (2002) document, inflames the situation.

Finally, given that the decision to switch from one cognitive domain to another requires reasoning about the emotional state of self and others, we would expect that leaders with greater DMN abilities are more likely to be able to successfully time the shifts than leaders who lack such abilities.

In sum, by using the evidence of these antagonistic neural networks and recent research on activating each of them, we can hypothesize that that most effective leadership requires a combination of three facilitating factors: (a) a decrease in the switching time (or cycle time) between these networks; (b) training people to high levels of competence in enacting the roles requiring each network, so decreasing the cognitive effort required and hence the degree of deactivation of the opposing network; and (c) training leaders to recognize and perceive contexts and cues which require a switch between modes, so they do not remain “stuck in set” and apply an ineffective cognitive strategy for the task at hand (e.g., by privileging analytic thinking when faced with an ethical decision, or intuitive thinking when faced with a logical task where creativity is not helpful).

To make this happen, we conjecture that people would have to be trained in multiple techniques that invoke a tipping point. These techniques would function somewhat like cognitive behavioral therapy, helping leaders to identify external (e.g., follower thoughts and emotional state) and internal (e.g., own thoughts and emotional state) cues and respond appropriately. In particular, people may need to develop the ability to calm the system and lower the intensity when there is a danger they are becoming “stuck in set” — whether that involves preoccupation with social/emotional concerns (over-privileging the DMN) or an overly narrow task focus (over-privileging the TPN).

This emphasis contrasts with current beliefs that to motivate we must increase energy and incentives (whether positive or negative). While that approach may preclude the dualistic swing between these two cognitive modes, and the occasionally conflicting considerations raised by each, it also presents a larger danger: losing sight of important insights, either emotional or analytic. Additionally, the ability to sense the optimal timing and context for switches may also be a critical component in understanding leadership effectiveness. For example, in the context of learning a new task, interruptions can be extremely costly, not only in terms of task outcomes (errors) but also in the ability to “pick up where you left off.” Once a person has gained a higher level of mastery, interruptions will be less costly and following the

interruption, the person will be able to re-engage with the task faster.

Prior research on the intensity of emotions suggests that in order to move a person from a negative emotional state (NEA) to a positive emotional state (PEA), the intensity of the emotion must be reduced to reach a tipping point (Boyatzis, 2013). It seems reasonable to suggest that a similar principle may exist when switching between the TPN and the DMN. Boyatzis (2013) argues that when people are in the PEA they are “more perceptually open and accurate in perceptions of others” (p. 1978; see also Fredrickson and Branigan, 2005; Boyatzis, 2006), which is consistent with the work of the DMN in allowing individuals to engage in reasoning about the emotions of others. In contrast, the NEA is said to be linked to human survival, particularly to defend against threats. NEA also balances “unchecked optimism” through suppressing the DMN, which has been linked to poor investment decisions (Gibson and Sanbonmatsu, 2004) – an analytical task that would require activation of the TPN rather than the DMN. The opposing domains model suggests the NEA’s ability to balance unchecked optimism is achieved through both activating the TPN required for analytical reasoning and suppressing the DMN, which is largely responsible for the overly optimistic state.

The link between the PEA–NEA and the DMN–TPN is also reflected in Fiedler’s (1986) cognitive resources theory. Fiedler and McGuire (1987, as cited in Bass and Bass, 2008) found that under non-stressful conditions, leaders with fluid intelligence (IQ) perform better than leaders with crystallized intelligence (experience); however under stressful conditions, leaders with crystallized intelligence performed better. Cognitive resource theory posits that the reason for this distinction is that under stressful conditions, a leader with fluid intelligence will rely on intellectual solutions to a task even when such solutions are inappropriate. In other words, under stressful conditions, a leader is “stuck” in the TPN and also in the NEA due to the stress condition, which limits their ability to switch into the DMN and the PEA, which enables them to explore more creative and non-intellectual solutions. Leaders with crystallized intelligence (intelligence based on past experience and learning) are likely to experience the same situation with less intensity, thus these leaders will be: (1) closer to the NEA–PEA tipping point; and (2) more able to switch between the TPN and the DMN.

FURTHER CONSIDERATIONS ABOUT MAPPING BRAIN NETWORKS ONTO LEADERSHIP ROLES

In this article, we have focused on mapping a duality which has long been noted at the behavioral level, between different leadership roles, onto a duality in the brain, highlighted by recent research in neuroscience. There appears to be a very promising mapping between these two domains, which suggests a fundamental neurophysiological basis for the observed duality in leadership roles. At the same time, we acknowledge that there is a considerable distance between neurophysiological observations and leadership behavior. Hence, more research is needed to firmly establish the links we highlight, and to elaborate and extend the model sketched here. Our main goal has been to highlight these links as a very promising avenue for further research. With an eye to this future research, in this section, we respond to three

specific questions that naturally arise in response to our proposed mapping.

First, the DMN has been found to exist in many species (Mantini et al., 2011). Further, in humans its function serves as basic index of level of consciousness, even in non-communicative brain-damaged patients (Vanhaudenhuyse et al., 2010). Given that this network appears to have such basic functions, it may seem surprising that we are suggesting it plays a key role in effective leadership, which would appear a higher level function. However, we regard this as consistent with our account, which is based on the view that the default network originally evolved to play a basic role in visceral awareness and emotion self-regulation, and that these functions expanded and evolved so that in the human this cortex additionally supports complex representations of value and the mental states of others (Jack et al., 2012, 2013b, in press). This fits with evidence that the default network is considerably expanded in the human compared to other species, even when its size is considered relative to overall cortical volume – which is massively expanded in the human compared to other primates (Jack et al., in press; **Figure 1**).

More broadly, our review indicates that we see the default network as critically involved in self-management, in particular mindfulness, motivation, and affective meaning. We see relational aspects of leadership as an extension of these functions which arises through coupling of them with our capacity to metalize. In summary, we suggest it quite natural to view the relational aspects of effective leadership as a skillful cognitive blending of our basic capacities for emotional self-regulation and social cognition. This view sits very well with what is known about the function and evolution of the DMN, and is not contradicted by findings which indicate the DMN plays a role in more basic functions.

Second, we admit and welcome the possibility that there are likely to be additional mechanisms, beyond the DMN/TPN duality we highlight, which are critical for understanding leadership. For example, we have highlighted a duality which places two much discussed systems involved in social cognition in opposition: the mirror neuron system lies within the TPN, and hence there is a general tendency for it to be deactivated when the metalizing system of the DMN is activated, and vice-versa. The mirror neuron system is thought to play a role in “emotional contagion” (Hatfield et al., 1994) – a key mechanism used by leadership scholars to explain the transfer of emotion between leader and follower (Bono and Ilies, 2006; Johnson, 2008; see also Sy et al., 2005) and from followers to the leader (Dasborough et al., 2009). Additionally, parts of both the mirror neuron network and the DMN were activated in older executives when remembering specific moments with resonant vs. dissonant leaders in their past (Boyatzis et al., 2012). In summary, it is not our claim that the DMN/TPN dichotomy highlighted here represents an exhaustive description of the neural processes involved in effective leadership. We look forward to future research that may clarify different types of neural interaction. In particular, we acknowledge the importance of looking at ways in the DMN and TPN work cooperatively in addition to our focus here on the “default” tendency for them to work competitively (Fornito et al., 2012). Such cooperative interactions between the networks need not always be anti-social in effect, although we document evidence above that some

modes of cooperation are associated with a greater sense of social distance.

Finally, the methodological concern might be raised that our analysis depends on reverse inference (Poldrack, 2011). That is, since brain imaging evidence is essentially correlational in data, it is not clear that the DMN and TPN are essential to the specified roles in effective leadership. We acknowledge this concern, which applies to all neuroimaging data. One important way to mitigate faulty inferences of this type is to conduct broad analyses of the literature in order to justify the claimed association between a specific brain area and a specific function (Poldrack, 2011). Another important step is to conduct critical tests of the hypothesized account against other accounts.

We have taken both these steps, using both meta-analysis (Jack et al., in press) and critical tests of our theory (Jack et al., 2012, 2013b) to justify our view that the DMN vs. TPN dichotomy reflects a tension between empathetic vs. analytic reasoning, as opposed to the more broadly stated view that it reflects a tension between internal vs. external attention. Nonetheless, we agree that further testing is wanted. Ideal tests would involve directly up or down-regulating one of the networks, or modifying the ability to switch between them, and then assessing the impact on naturalistic leadership behavior. As noted, there is already evidence suggesting that patients with vmPFC damage perform poorly in relational leadership roles (Anderson et al., 1999), however it would be ideal to manipulate neural processing and study effects within individuals. While this is challenging to do directly, some more indirect tests along these lines may be possible. For instance, oxytocin administration appears to up-regulate DMN function (Bethlehem et al., 2013), hence we would predict oxytocin administration should improve performance in relational leadership roles and deteriorate performance in task-oriented roles. Alternatively, it has been shown that different forms of meditation tend to either increase (focused meditation) or decrease (non-dual awareness meditation) anti-correlations between the DMN and TPN (Josipovic et al., 2012). The former should increase leadership flexibility (i.e., the ability to switch between different roles and perform well in both), the latter decrease it. Exploring these and other potential manipulations of neural processing is an important area for further research.

CONCLUSION

The emergence of two distinct leadership roles, the task-oriented leader and the relationship-oriented leader, has been documented in the leadership literature since the 1950s (Bales, 1958). Recent discoveries in neuroscience that the TPN, which allows us to focus on problem-solving and analytic work, is antagonistic with the DMN, which allows a person to be socially engaged and open to new ideas, creates a dialectical tension that reverberates throughout the leadership role literature and raises questions as to how leaders can effectively fulfill both roles.

RESEARCH, THEORY, AND PRACTICAL IMPLICATIONS

This paper has identified a key pattern in the leadership literature and linked this pattern to cutting edge research in the neuroscience domain. In doing so, we have raised a number of questions

regarding our treatment of the task and relationship distinction in the literature to date, particularly the assumption that leaders are able to attend to both leadership roles simultaneously. Additionally, we have been able to add further explanation to some historical findings attempting to understand the interaction between task, leadership roles, and leadership effectiveness. Finally, we suggested an array of conceptual implications that might extend our current conceptualization and operationalization of leadership effectiveness.

From a practical standpoint, this paper suggests that developing a leader's analytical and relational abilities may be an important way to offset the costly effects of the antagonistic relationship between the TPN and the DMN. Increasing a leader's abilities in each role should facilitate the ability faster and more fluidly between the task and relationship roles by reducing the cognitive effort, and consequently the differential activation between the TPN and the DMN, required to perform effectively in each respective role. We believe that the ability to switch between these networks and corresponding leadership roles may be a key component of leadership effectiveness.

Additionally, knowing that engagement in analytical tasks inhibits our ability to engage in social or relational reasoning and vice versa may have important implications for organizations in terms of how they structure and order tasks that have analytical and relational components. For example, when giving feedback, managers should consider if the feedback is analytical or task related in nature or interpersonal in nature and time the delivery of that feedback accordingly. The same may be said for the ordering of meeting agendas and the time and structure of performance review meetings.

While this paper has focused specifically on the implications of the opposing domains hypothesis for leadership roles, we believe that the distinction and antagonistic relationship between analytical-mechanical reasoning and social reasoning exists in many other areas in the organizational behavior domain. These areas include, but are not limited to, leadership styles, conflict management, trust, and moral reasoning. For example, distinctions in the literature have been made between cognitive and relational trust (Lewis and Weigert, 1985); cognitive conflict and affective conflict (Jehn, 1997; De Dreu and Weingart, 2003); empathy and dehumanization (Haslam, 2006).

Relevant to the leadership domain specifically, further testing is needed in order to understand if individual difference variables play a role in facilitating the ability to switch between the two networks. Research is currently underway to address this question by surfacing the opposing domains at the behavioral level and linking individual difference variables and abilities to the speed at which an individual is able to switch between tasks requiring analytical and tasks requiring relational reasoning. Once we have more information on this we will be able to target these variables in leadership development training programs. Additionally, manipulation of situational characteristics within each type of task, for example, task difficulty and routineness for analytical tasks, and prior relationship quality for social tasks, will allow us to isolate the key situational variables at play. Finally, further research on the link between hormonal systems and neurological systems would allow us to understand how

tipping points in hormonal systems influence neurological tipping points.

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Redefining neuromarketing as an integrated science of influence

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Multiple transformative forces target marketing, many of which derive from new technologies that allow us to sample thinking in real time (i.e., brain imaging), or to look at large aggregations of decisions (i.e., big data). There has been an inclination to refer to the intersection of these technologies with the general topic of marketing as “neuromarketing.” There has not been a serious effort to frame neuromarketing, which is the goal of this paper. Neuromarketing can be compared to neuroeconomics, wherein neuroeconomics is generally focused on how individuals make “choices,” and represent distributions of choices. Neuromarketing, in contrast, focuses on how a distribution of choices can be shifted or “influenced,” which can occur at multiple “scales” of behavior (e.g., individual, group, or market/society). Given influence can affect choice through many cognitive modalities, and not just that of valuation of choice options, a science of influence also implies a need to develop a model of cognitive function integrating attention, memory, and reward/aversion function. The paper concludes with a brief description of three domains of neuromarketing application for studying influence, and their caveats.

Keywords: neuromarketing, neuroeconomics, marketing communications, neuroimaging, scaling, influence, choice

INTRODUCTION

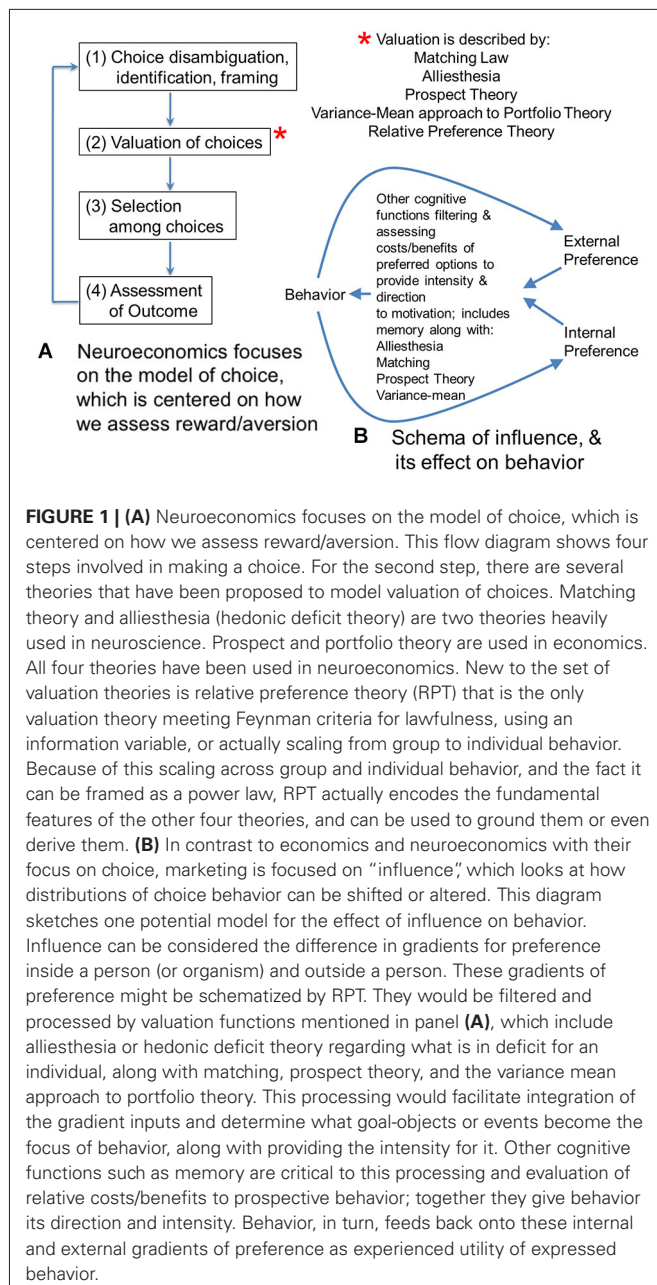
Marketing has been dominated for over a century by models that assume a rational process of persuasion, which follows a sequence from awareness through purchase that consumers can consciously articulate. While this approach fits with traditional research methodologies, it hasn't always explained or predicted purchase behavior. Recent developments suggest that a new perspective may be emerging. In particular, marketers have sought to integrate ideas about non-rational and rational processes (Kahneman, 2011), and ideas related to social neuroscience vs. individual decision-making (Lee et al., 2007; Senior and Lee, 2008), as well as using methods and technologies aligned with neuroscience (Ioannides et al., 2000; Braeutigam, 2005; Vecchiato et al., 2011; Plassmann et al., 2012). Some have been quick to label—not always in a complimentary manner—such developments as “neuromarketing” (e.g., Laybourne and Lewis, 2005¹).

To date, neuromarketing has lacked a solid theoretical framework. As such, the term “neuromarketing” itself runs the risk of confusing more fundamental scientific research with commercial applications (Lee et al., 2007; Javor et al., 2013). In this paper, we seek to extend existing work (e.g., Fugate, 2007; Hubert and Kenning, 2008; Senior and Lee, 2008; Wilson et al., 2008; Fisher et al., 2010), to clarify a framework for neuromarketing as an integrated science of influence. We start by contrasting neuroeconomics to neuromarketing. We then consider the concept of influence across individuals, groups, communities and markets, along with its dependency on an integrated model of mental function, along with some key—often unrecognized—caveats that must be considered by neuromarketing researchers.

INFLUENCE VS. CHOICE

It is helpful to compare neuromarketing to neuroeconomics, with which it may appear to overlap. Neuroeconomics tends to focus on individual and group choice, or judgment and decision-making in the context of consumables or markets

¹ See Brain scam? (2004). *Nat. Neurosci.* 7, 683. doi:10.1038/nn0704-683; and Neuromarketing: beyond branding (2004). *The Lancet Neurol.* 3, 71. doi:10.1016/S1474-4422(03)00643-4.



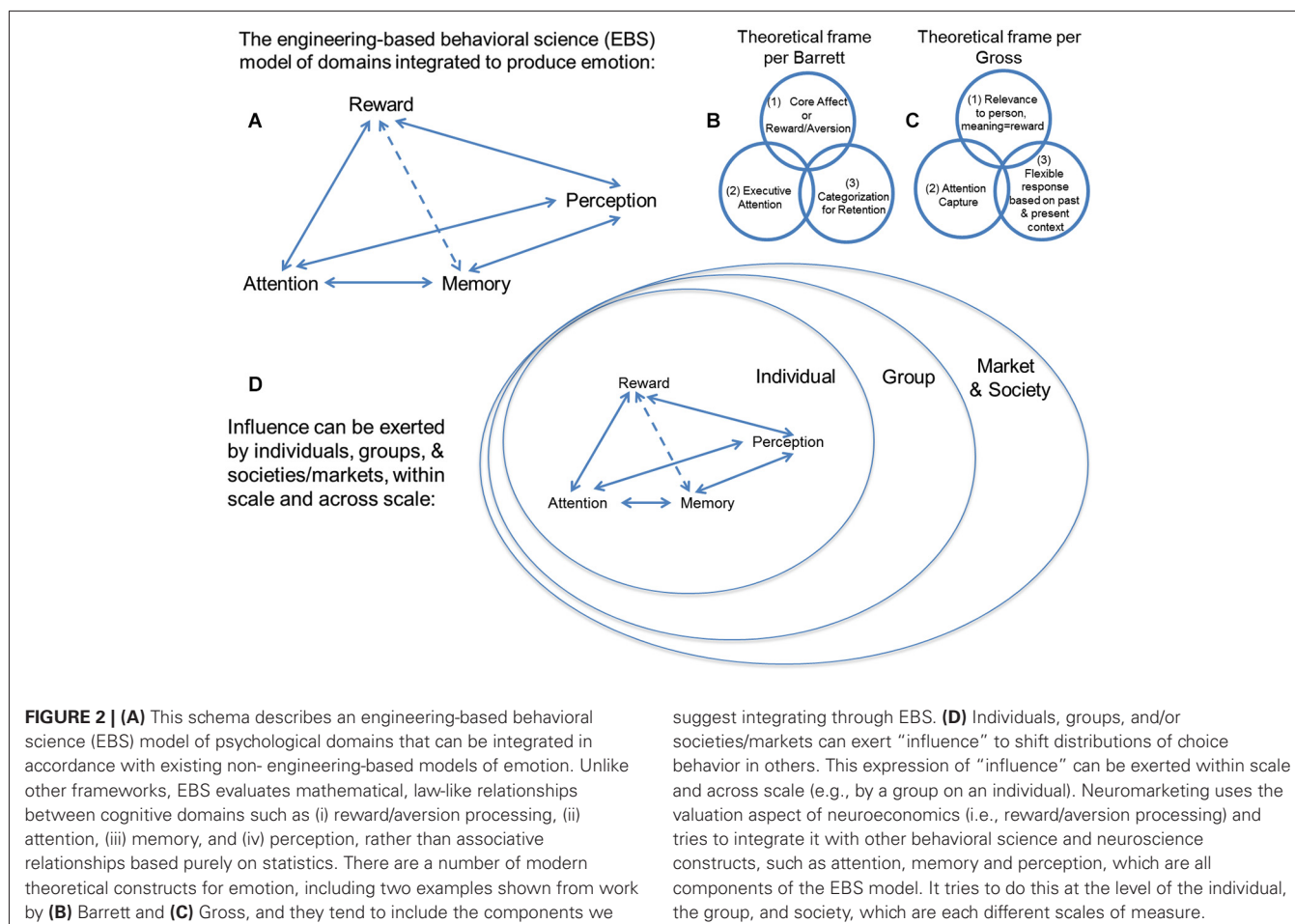
(Figure 1A; Camerer, 2008). This focus on choice is distinct from the focus in neuromarketing on the issue of how individuals and groups might be shifted from one pattern of decisions to another pattern, or to change their *distribution of choices*.

Much neuromarketing research to this point has been focused on optimal methods to shift the distribution of choices (e.g., Ambler et al., 2004; McClure et al., 2004; Ohme et al., 2009; Santos et al., 2011). The use of “neuro” as a prefix has thus followed a similar rationale to that of neuroeconomics, whereby study of the neural processes provides a tool for describing behavioral change that was not available by the study of behavior alone (Ariely and Berns, 2010).

Such a view of neuromarketing ignores the broader perspective on what might be called “influence,” which is the primary issue involved with marketing, advertising, engineering design, teaching, or behavioral change in medicine. All of these categories of “influence” focus on how to get people to engage in a behavior preferred by a corporation, government, trade-group, culture or other entity. From an ethical perspective, discussions regarding consumer rights, for example privacy, are key when considering the influencing of behavior by interest groups, and neuromarketing research has been a subject of some interest in this regard (e.g., Murphy et al., 2008; Wilson et al., 2008). Nonetheless, influence doesn’t just shift the distribution of choices to one favored by the interest group in question, but balances between internal and external forces on behavior. Influence might be considered a balance between gradients of preference within an individual or group that influence events outside of them, and gradients of preference outside the individual or group that influence events inside of them.

Such gradients of preference could be schematized by patterns of approach and avoidance decisions (i.e., the distribution of choice) as described by relative preference theory (RPT; Breiter and Kim, 2008; Kim et al., 2010), an empirically-based account of reward/aversion resembling prospect theory (Kahneman and Tversky, 1979; Breiter et al., 2001) but grounded in information theory (Shannon and Weaver, 1949) to account for patterns in decisions that can be connected to reward/aversion circuitry and genetic polymorphisms (e.g., Perlis et al., 2008; Gasic et al., 2009). Using RPT, internal and external gradients of preference would involve variables quantifying (a) the pattern of approach decisions; and (b) the pattern of avoidance decisions. In the case of internal preferences, these would characterize the individual, whereas in the case of external preferences these might characterize a group of people external to the individual (or a preference gradient from just one other external person). RPT allows individual and group preferences to be readily characterized in a quantitative, lawful fashion that scales between individual and group. The integration of internal (e.g., individual) and external (e.g., group) gradients of preference would then be given direction in distinct decision/planning/problem solving situations by the processes briefly schematized in Figures 1A,B. Gradients of preference given direction by hedonic deficit theory (i.e., alliesthesia; Cabanac, 1971; Paulus, 2007) and other valuation processes (necessary for incorporating probabilities related to goal-objects, Kahneman and Tversky, 1979; relative valuations across goal-objects, Herrnstein, 1961; and variance in valuation, Markowitz, 1952) would constitute the combined intrinsic and extrinsic motivation described by Deci and Ryan (1985), leading to behavior, which in turn feeds back into gradients of preferences based on the experienced utility in individuals involved (see Kahneman et al., 1997). Such a schema is shown in Figure 1B as one of many possibilities for how internal and external gradients are balanced through their effects on behavior, and can shift distributions of choice.

In considering the balance between internal and external preference, cognitive processes thought to be separate from that of the valuation of options come into play, such as perception, attention,



and memory (Ioannides et al., 2000; Ariely and Berns, 2010). At this time, no theoretical schema and little empirical data exist for how these theoretically independent cognitive processes interact, but cognitive processes for *perception* of outside stimuli exerting influence, *attention* to their features, and *memory* for comparison of such features to prior percepts are necessary operations for processing “influence”. Exerting “influence” to change another’s behavior, or being the subject of outside “influence” to change your own behavior thus need to be considered in a much broader construct of mental operations (see **Figure 2A**). One must also recognize that this ensemble of operations (i.e., perception, attention, memory, reward/aversion processing) have been extensively theorized to be core processes for emotion (Breiter and Gasic, 2004; Barrett, 2006; Gross, 2009, 2013; Kuppens et al., 2013; Lindquist et al., 2013). Specific examples of this are schematized in **Figures 2B,C** for the models of Barrett (2006) and Gross (2009, 2013).

The balance between internal and external forces on behavior (e.g., respectively, internal emotional experience (or internal preference gradient) vs. emotional expression by entities outside the individual (or external preference gradient)) must also be apparent at the neural level of measurement, given that “brain and mind are one”, a fundamental hypothesis of neuroscience (e.g., Breiter and Rosen, 1999; Breiter and Gasic,

2004; Breiter et al., 2006). This view of neuromarketing thus has as its focus an understanding of the balance between internal and external preferences (emotional experiences), on individuals and groups. Neural measures of one individual or interacting individuals (e.g., as with joint trust games; King-Casas et al., 2005; Tomlin et al., 2006) can be made in parallel with behavioral ones to confirm that observations made at the behavioral level affect those at other levels of spatiotemporal organization, or actually scale across levels of spatiotemporal organization (i.e., group behavior, individual behavior, distributed neural groups, neural group, etc.). Influence can thus be thought of as being present across multiple spatiotemporal levels of measurement, from group measures to measures of individual behavior to neural groups, etc. The issue of scaling might be considered as a “layering of influence” and warrants further discussion.

LAYERS OF INFLUENCE AND COMMUNITIES AFFECTED

Scaling is rarely discussed in experimental psychology and other behavioral disciplines, and was not formally introduced into behavioral science and neuroscience until the 1990s by Sutton and Breiter (1994). In its adaptation to biology and behavior, scaling refers to how measures made at one level of spatiotemporal organization, relate in a principled, lawful manner to measures at

other spatiotemporal levels of organization (Sutton and Breiter, 1994; Perelson et al., 2006; Savage and West, 2006). This relationship does not represent a statistical one where a certain amount of the variance at one level of measure can predict the variance at another level, or how some information at one layer of organization can specify some extent of information at another layer (Adami, 2004; Szostak, 2004). Instead, it is causal (i.e., mechanistic) in that the same patterns of behavior measured at one layer are also measured at a neighboring level, and there is a necessary relationship (Sutton and Breiter, 1994; Breiter and Gasic, 2004; Breiter et al., 2006). Given that it has not been a major topic in behavior science or neuroscience, few biological measures have yet been shown to scale. One behavior that does show scaling is that of circadian rhythms, which show measures that scale from behavior to distributed groups of neurons to individual neural groups to cells and molecular biology. The other is approach/avoidance behavior described by RPT, scaling from group behavior to individual behavior, and potentially to other scales (Breiter and Kim, 2008; Kim et al., 2010). To date, few behavioral constructs outside of RPT have been tested to Feynman criteria for lawfulness, which includes scaling (Feynman et al., 1963).

Scaling has become an important metaphor/analogy in considering the statistical association of measures made at one spatiotemporal scale vs. another, as with the Research Domain Criteria project (RDoC) sponsored out of the National Institutes of Health (NIMH; Insel et al., 2010; Morris and Cuthbert, 2012; Cuthbert and Insel, 2013). The RDoC project and projects sponsored out of the National Institutes of Health Connectome Project (Van Essen et al., 2012; Barch et al., 2013) focus on measures at different spatiotemporal scales that can predict some degree of variance in each other. Both the RDoC and Connectome projects are directly modeled after the Phenotype Genotype Project in Addiction and Mood Disorders (PGP),² which successfully discovered measures that scale across levels (i.e., RPT; Breiter and Kim, 2008; Kim et al., 2010).

While scaling is a *sine qua non* of classical science across levels of spatiotemporal organization, constructs that have become fundamental to more contemporary approaches to science have also become active considerations in neuroscience, in particular the issue of uncertainty (Kahneman and Tversky, 1979; Knill and Pouget, 2004; Gallistel and King, 2009; Kim et al., 2010; Vilares and Kording, 2011). Scaling and uncertainty are of interest with regard to neuromarketing, in that there is a common intuition that influence occurs between individuals, between individuals and a group, and between groups. As schematized in **Figure 2D**, influence is thought to occur in the interaction between individuals, who are embedded within groups, so that they affect their respective groups, and the larger framework (e.g., society, market) in which that group exists. This embedding of individuals/groups can be directly analogized to the embedding of networks (Sutton and Breiter, 1994).

This model of influence across scales of organization (e.g., individual, group, society/market) also relates to issues of uncertainty due to information loss in the communication between individuals/groups, or the uncertainty related to imprecision in the interpretation of communicated emotions (e.g., **Figures 2B–D**). Characterizing influence by scaling and uncertainty has some appeal, but begs the issue of what influence is in this context. When one considers influence in this model, it comes across as resembling a field of sorts, with a gradient of effects as two entities wielding influence come in greater proximity to each other (**Figure 1B**). To date, there has been no formal definition of influence, either through axiomatic derivation, or through iterative modeling (Banks and Tran, 2011) of behavior data to show a specific mathematical formulation of a pattern in a graph. Such work is clearly needed, and likely will depend on the cognitive processes identified to underlie this “field” of influence, such as those involved with emotion, discussed previously.

One might consider influence, and its potential scaling and effects of uncertainty, as a product of human psychology and the sub-processes underlying human information processing. Such considerations point to the importance of having a complete model of mental functioning, which is as yet lacking. Neuromarketing investigations can have a major input into the development of this integrated model, if they are conducted from a consistent and coherent theoretical base as discussed herein.

BASING INFLUENCE ON AN INTEGRATED MODEL OF MENTAL FUNCTION

At this time, we have no unified model of the mind, which shows how sub-processes such as attention, memory and reward/aversion processing are integrated and function concurrently for decision-making, planning, and problem solving. When one opens any cognitive science/biological psychology textbook, one finds chapters on information theory, perception, attention, decision-making, etc., but nothing integrating them. Even the use of the term information theory—although considered the basis of cognitive science—was never used in its mathematical framework in cognitive science until approximately 4–6 years ago (Breiter and Kim, 2008; Tononi, 2008; Gallistel and King, 2009; Kim et al., 2010). For the most part, marketers have relied on thinking about judgment and decision-making in terms of cognitive biases and mental functions involved with choice.

Recently, attention has been given to the building of such an integrated model of mental processing, starting with efforts to look at the input end of cognitive function, and to consider how quantitative descriptions of processes for reward/aversion, attention, and memory might work together. This work has led to research (Viswanathan et al., Under review) integrating parts of RPT (representing reward/aversion) with variables from signal detection theory (representing attention), and combining signal detection theory with Ebbinghaus memory functions to unpack sub-processes mediating working memory (Reilly et al., Under review). This early work argues that cognitive science constructs can be integrated, and points to the large amount of work needed to develop a comprehensive merger of domains in

²Lawler, A. “White house stirs interest in brain-imaging initiative”, Science, News, August 2, 2002; Abbott A. “Addicted”, Nature’s Senior European Correspondent, Nature, News Feature, October 31, 2002; and <http://pgp.mgh.harvard.edu>

cognitive science, including domains such as decision-making, planning, and problem solving, along with output of the system in terms of motor behavior, language, and autonomic functions.

The ultimate integration of these cognitive functions can be analogized to a wall chart in biochemistry where all chemical pathways underlying biological metabolism are organized. We are a long way from having such an integrated platform for mental operations, particularly since such integrated systems as in biochemistry also convey mechanism and allow causal inference. In the short term, the viability of such an effort can start with developing complete constructs for attention, memory, and reward/aversion processing. Complete constructs for attention, for instance, would necessitate the mathematical description of the relationship between focused, selective, sustained, divided, and alternating attention. The potential for such complete constructs to be integrated across functions (i.e., perception, attention, memory, and reward/aversion processing) would then be a necessary second step in testing the viability of developing a general model of the mind.

Development of such a general model of mental function would allow us to theorize and empirically test what set of functions together respond to influence from another individual/organism, and exert influence on individuals/organisms outside of the person. With an integration of, at minimum, the functions thought to comprise emotion and memory thereof, cognitive psychology would likely be able to begin defining a quantitative model of influence. Such an effort will also depend on parallel assessments of the integrated cognitive model through approaches that (1) assess how well the integrated cognitive construct fits with neuroscience measures; (2) determine if important features of the construct can be derived axiomatically (an approach used extensively in traditional economics); and (3) test if the integrated cognitive construct facilitates the analysis of large data sets of human consumption and media use (referred to as “big data”), which should show features of human cognitive function.

Even so, efforts devoted towards developing neuromarketing as a science of influence, and towards a general model of mental function must remain cognizant of the risks inherent in such research, particularly given the persuasiveness of brain imaging (Roskies, 2008). Such risks are well covered in other foundational literature (e.g., Senior et al., 2011), but it is worth noting here that the subtractive and reverse inferential methodologies—predicated on observing specific brain region activity associated with specific tasks—are unable to conclusively confirm either the necessity of that specific region for that specific task, nor the lack of involvement of other regions, particularly in complex tasks (Friston et al., 1996; Poldrack, 2006, 2008). Confounds can also arise in neuroscientific studies of behavioral change (i.e., influence). It is a mistake to assume that one wants changes in both behavior and brain signal to interpret the effect of any influence. Such circumstances only lend themselves to interpretation when there is a parametric variation in both variables, which in turn can lead to a power problem. Rather, it is usually preferable for variables in *either* behavior or neuroimaging change, assuming the (often unrecognized) issue that baseline

or comparative conditions remain unchanged also. Similarly, one must control for hormonal and demographic variables, which have been shown to influence key neuroimaging variables (Goldstein et al., 2005, 2010; Breiter et al., 2006). A final caveat is that we still do not understand the processes by which distributed groups of cells “process information” (e.g., Freeman, 2001). The functional domains of biochemistry, molecular biology, and genetics are quite distinct from those we hypothesize for behavior (e.g., attention, memory, reward/aversion processing, etc.), and how distributed neural groups produce functional domains and interact is far from understood. As such, all neural signals must be looked at as providing ancillary support for measures made at other spatiotemporal scales (e.g., behavior or genetics).

There also remain key issues in the use of “big data” approaches to neuromarketing. In particular, the high-dimensionality and huge size of data sets in this context can lead to inferential problems of their own—particularly spurious correlations, noise accumulation, and incidental homogeneity (e.g., Fan and Fan, 2008; Fan et al., 2013). The often uncontrolled and naturalistic collection of such data sets also has the potential to raise issues of public interest regarding the ethics of social research (e.g., Kramer et al., 2014). That said, as long as researchers approach their work in light of such caveats, big data provides opportunities for neuromarketing as a science of influence, in particular due to (i) its cohort sizes; (ii) its attention to demographic and socio-economic variables; and (iii) its broad array of variables that can be aligned to neuroscience variables.

SUMMARY

This manuscript provides a theoretical framework for neuromarketing based on the process of influence, and how it shifts distributions of choice across many scales of measurement, from individual to group/market and society. As opposed to issues of choice, issues of influence encompass a broader array of behavioral science domains, pointing to the importance of developing a rigorous quantitative model of mental function, which can provide testable hypotheses for how distributions of choice are shifted across scale and within scale (i.e., from individuals to groups/market to society and back again). However, a tremendous amount of work is needed to get to this point, and this work will need to meet the highest of academic standards if it is to change standards of practice and have real relevance for the marketing community and those involved with influence or behavior change, whether that be in education, medicine, business, marketing communications, design, or political policy.

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Age-related striatal BOLD changes without changes in behavioral loss aversion

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Loss aversion (LA), the idea that negative valuations have a higher psychological impact than positive ones, is considered an important variable in consumer research. The literature on aging and behavior suggests older individuals may show more LA, although it is not clear if this is an effect of aging in general (as in the continuum from age 20 and 50 years), or of the state of older age (e.g., past age 65 years). We also have not yet identified the potential biological effects of aging on the neural processing of LA. In the current study we used a cohort of subjects with a 30 year range of ages, and performed whole brain functional MRI (fMRI) to examine the ventral striatum/nucleus accumbens (VS/NAc) response during a passive viewing of affective faces with model-based fMRI analysis incorporating behavioral data from a validated approach/avoidance task with the same stimuli. Our *a priori* focus on the VS/NAc was based on (1) the VS/NAc being a central region for reward/aversion processing; (2) its activation to both positive and negative stimuli; (3) its reported involvement with tracking LA. LA from approach/avoidance to affective faces showed excellent fidelity to published measures of LA. Imaging results were then compared to the behavioral measure of LA using the same affective faces. Although there was no relationship between age and LA, we observed increasing neural differential sensitivity (NDS) of the VS/NAc to avoidance responses (negative valuations) relative to approach responses (positive valuations) with increasing age. These findings suggest that a central region for reward/aversion processing changes with age, and may require more activation to produce the same LA behavior as in younger individuals, consistent with the idea of neural efficiency observed with high IQ individuals showing less brain activation to complete the same task.

Keywords: loss aversion, aging, nucleus accumbens, reward, fMRI, neurocompensation

Introduction

Age is among the most commonly used variables in marketing and consumer research. While age is a deceptively simple variable, the underlying construct of biological age and how it relates to behavior is not always clear. One age effect supported by a number of social psychology studies is that older adults put more weight on avoiding potential negative outcomes, as evidenced by an aversion to change (Botwinick, 1978) and nostalgia for early experience (Schindler and Holbrook, 2003). Aging research points to an association of age with making less risky decisions (Johnson and Busemeyer, 2010), and suggests that older individuals generally avoid losses to a greater extent than younger individuals (e.g., Heckhausen, 1997). A fundamental way to quantify this perspective is with the concept of “loss aversion” (LA), in which negative stimuli have a disproportionate psychological impact relative to positive ones (Kahneman and Tversky, 1979), and can be defined mathematically by the ratio of valuation of monetary losses relative to valuation of gains (Tversky and Kahneman, 1991), or in more general terms, as the ratio of avoidance to approach measures (Abdellaoui et al., 2007). LA has become an important variable in consumer research (Ariely et al., 2005; Paraschiv and L’Haridon, 2008) and is consistent with the observation that older individuals are more focused on goals pertaining to maintenance and regulation of loss (Ebner et al., 2006). Cole et al. (2008) suggest, based on “regulatory focus theory” (Avnet and Higgins, 2006), that older individuals would be more prevention-focused i.e., avoid losses, than promotion-focused i.e., pursuit of gains.

Neuroscience studies have examined the biological basis for age-related changes in cognitive function (Hedden and Gabrieli, 2004; Mohr et al., 2010), which might affect biases in decision-making such as LA. For instance, Raz (2000) found a steady decline in the prefrontal cortex (PFC) structures starting from the age of 20 along with a decline in the striatal volume over the lifespan of an individual. In many studies, the biology of age-related changes in the brain goes in the same direction as behavior (Good et al., 2001), as for instance in the domain of episodic memory, where older adults have demonstrated decreased activation of various sites in the left and right prefrontal cortices correlating with decreased performance on the task relative to their younger counterparts (Grady et al., 1995, 1999; Cabeza et al., 1997; Madden et al., 1999; Grady and Craik, 2000; Reuter-Lorenz, 2002; Stebbins et al., 2002). An alternate outcome is also possible, wherein alterations in brain activity are not associated with an alteration of behavior, namely, increasing amounts of activation are needed to produce the same behavior (e.g., neurocompensation; Cabeza et al., 2002; Park and Reuter-Lorenz, 2009; Daselaar et al., 2015).

These neuroimaging and behavioral studies thus suggest at least two potential hypotheses regarding LA, its underlying neural substrate, and aging: (1) LA behavior may parallel changes in neural processing, specifically, LA behavior may increase with age along with increased activation in tissue required to process it; or (2) LA behavior may increase more

slowly than the compensatory activity in tissue processing it (i.e., there may be small differences in LA behavior with age, and strong brain activity differences during its processing). This latter possibility finds support from an early functional MRI (fMRI) study that reported decreases in either performance or IQ were associated with increased brain activation during cognitive function (Seidman et al., 1998), and the observation of potentially compensatory activity in older individuals (Meunier et al., 2014). Two recent studies of LA specifically support option (2) above, in that they report LA behavior does not change between young adults and old adults (Li et al., 2013) or between adolescents and young adults (Barkley-Levenson et al., 2013). One of these studies also evaluated neural processing of LA, and found differences between adolescents and young adults in large decision-making networks, further supporting option (2) (Barkley-Levenson et al., 2013).

In the current study we sought to test these hypotheses evaluating subject age against (1) the relative overweighting of behavioral responses to negative vs. positive stimuli (i.e., LA behavior) using a validated keypress measure (Kim et al., 2010); and (2) neural differential sensitivity (NDS; Tom et al., 2007) within the ventral striatum/nucleus accumbens (VS/NAc) to the same stimuli used in the behavior task. Given the substantial involvement of the VS/NAc in motor preparation (e.g., Florio et al., 1999) and abnormality with motor illnesses such as Parkinsonism (e.g., Aarts et al., 2014; Payer et al., 2015), we sought to avoid the motoric contamination inherent with cognitive imaging studies of the VS/NAc using monetary choice paradigms (Tom et al., 2007; Canessa et al., 2013). Since the motor responses for the keypress task would not be separate from reward/aversion assessments (the amount of VS/NAc activation could just reflect how much an individual was keypressing to approach or avoid a stimulus, or reflect the urgency of their responses), the keypress task was done outside the MRI, and the outcome of keypress responses used for model-based analysis of VS/NAc signal during passive viewing of the same stimuli; such a model-based approach to fMRI has been used with this task (Aharon et al., 2001) and fMRI-based imaging-genetics used with these stimuli and task before (Perlis et al., 2008; Gasic et al., 2009), consistent with the framework for model-based imaging discussed by others (e.g., Mittner et al., 2014; Wang and Voss, 2014; White et al., 2014; Xu et al., 2015). The implicit assumption in this model-based application was that the emotional response to faces in the scanner, and the behavior based on emotional response to the same stimuli outside of the scanner would be related, as suggested for studies of emotion-based processing by other investigators (Hayes and Northoff, 2012).

To examine the underlying physiological effects of age on LA, we performed whole brain fMRI to monitor activity within the VS/NAc, using a passive viewing paradigm with affective faces known to evoke positive and negative valuations (Strauss et al., 2005), given the VS/NAc is a central region for reward/aversion processing (Breiter et al., 1997; Blood et al., 1999; Breiter and Rosen, 1999; Hayes and Northoff, 2012), and has been shown to activate to both positive and

negative stimuli (Aharon et al., 2001; Berra et al., 2001; Breiter et al., 2001; Kober et al., 2008; Hayes and Northoff, 2012) and to track LA for the choice and anticipation phases of decision making (Tom et al., 2007; Lee et al., 2012; Canessa et al., 2013). For a behavioral index of LA, we used the same affective faces (Ekman and Friesen, 1976) with a keypress task performed outside the MRI that allowed the subject multiple potential decisions: (1) to do nothing about the default viewing time of a picture; (2) to view the picture for longer (approach); or (3) to view the picture for shorter (avoidance) time. The keypress data was analyzed to produce a value function (Breiter and Kim, 2008; Kim et al., 2010) for each subject that is analogous to a prospect theory value function or utility curve (Kahneman and Tversky, 1979), but unlike any other reward/aversion construct actually uses an entropy variable representing information (Shannon and Weaver, 1949). The slopes of the negative and positive portions of this curve can be readily sampled to yield a measure of LA in a general framework for LA as an overweighting of aversion (toward negative stimuli) relative to approach (toward positive stimuli) as discussed by Abdellaoui et al. (2007). For the model-based fMRI analysis, we explicitly required that (i) relative activation to negative (avoidance) stimuli vs. positive (approach) stimuli (i.e., the NDS of avoidance vs. approach) would occur in the VS/NAc; and (ii) that NDS-related fMRI signal in the VS/NAc would significantly correlate with LA behavior across subjects. If this were observed, we then sought to evaluate if VS/NAc NDS would increase with age, and whether or not it would parallel any relationship of LA behavior to age, supporting either the first or second hypothesis regarding the interaction of LA, its underlying neural substrate, and aging.

Methods

Subjects

Healthy control subjects were aggregated for an exploratory analysis on an available sample of subjects with complete behavior and imaging data from three paradigms for which LA parameters could be computed and evaluated. The resulting sample of 17 subjects was compiled for use with another project testing if the negative component of LA could explain aspects of amygdala function across the three paradigms and connect it to structural measures (Lee et al., 2012); the current study focused just on the emotional faces paradigm given the value function curves from keypressing to these stimuli had never been published, nor evaluated against NDS or age. These 17 subjects were recruited by advertisement and were part of a larger phenotype genotype project in addiction and mood disorder (PGP)¹. Subjects were free of any psychiatric, neurological, or medical issues per psychiatrist-based SCID for DSM-IV diagnoses, medical review of systems and physical evaluation including blood chemistry. Race was determined by individual self-identification using a standardized form (Benson and Marano, 1998), and

handedness via the Edinburgh Handedness Inventory (Oldfield, 1971). Participating subjects were without any current or lifetime DSM-IV Axis I disorder or major medical illness known to influence brain structure or function, including neurologic disease, HIV, and hepatitis C. Subjects were scanned at normal or corrected normal vision. Women were scanned during their mid-follicular phase based upon self-reported menstrual history, with confirmation at the time of scanning based on hormonal testing with a urine assay.

Participants in the study were adults (10 males, 7 females; 5 African Americans and 12 Caucasians) between the ages of 20 and 55 with a mean (\pm SE) age of 35.8 ± 2.7 years, with no significant difference between men and women ($F_{(1,15)} = 1.81$, $P < 0.20$). They had a mean educational history of 15.4 ± 1.9 years, with no significant difference between men and women ($F_{(1,15)} = 2.78$, $P < 0.12$). Fifteen of subjects were right-handed.

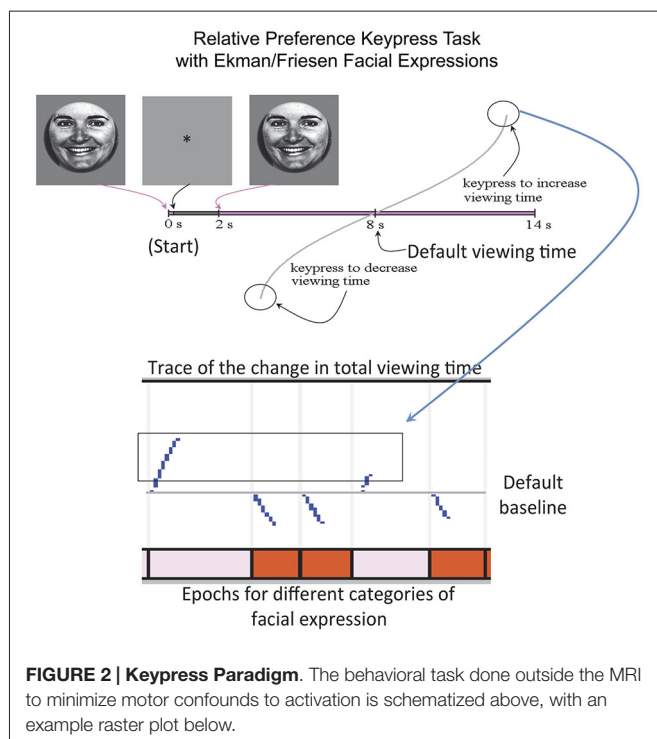
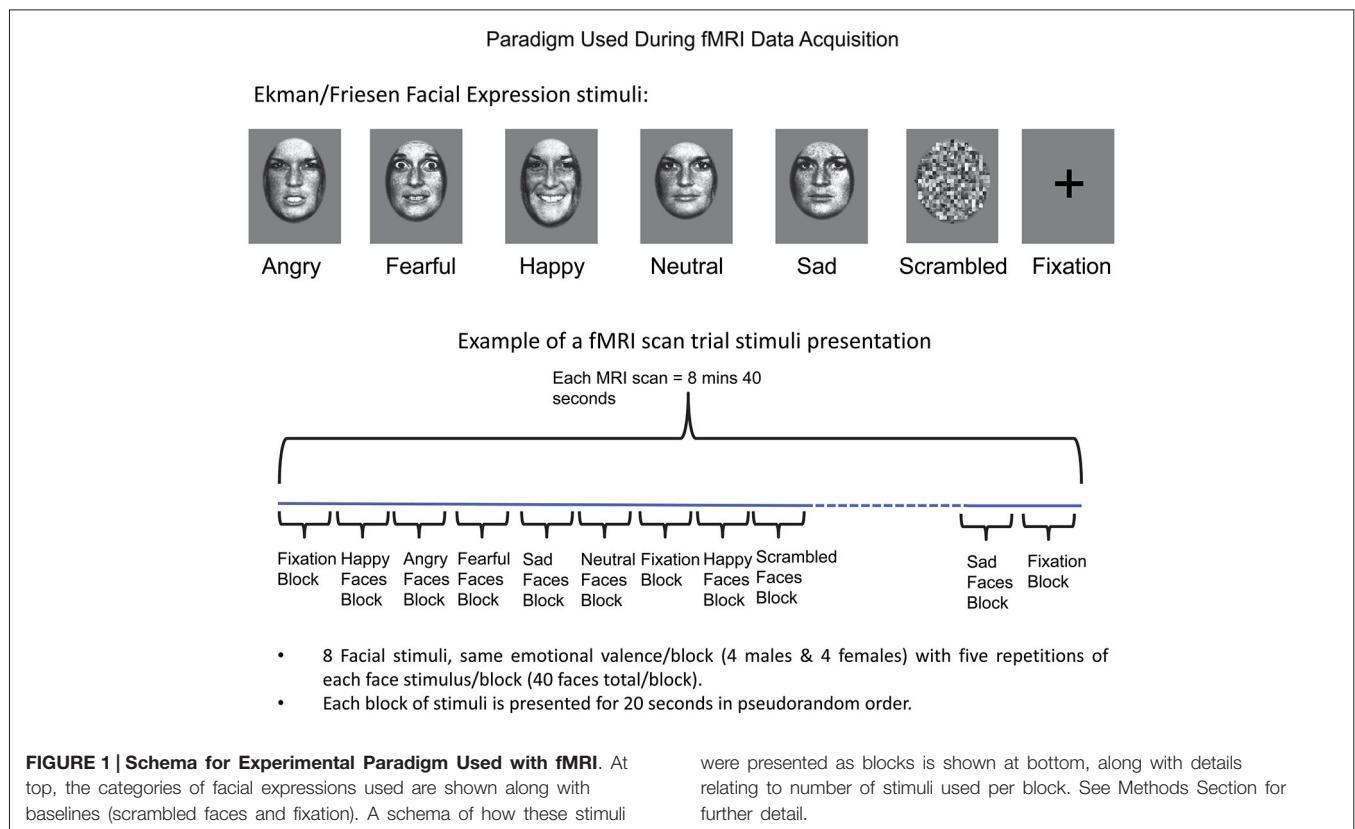
Experimental Paradigm and Offline Behavioral Testing In Scanner

Two fMRI scans were acquired (8 min 40 s each), each consisting of 20-s blocks of the following seven experimental conditions: angry, fearful, happy, sad, neutral expressions (Ekman and Friesen, 1976), along with phase-scrambled stimuli and fixation (**Figure 1**). During each scan, the seven conditions (blocks) were presented in a counterbalanced order such that no condition followed or preceded another more than once. This produced a sequence of 25 blocks for the first run, and 24 plus one blocks for the second run, with the extra block in the second run being equivalent to the last block in the first run, placed at the beginning to maintain counterbalancing across all conditions. Each facial expression block included standardized images of faces of eight individuals (four males) in a pseudorandom order (Breiter et al., 1996; Strauss et al., 2005). Each face was displayed for 200 ms with a 300 ms interstimulus interval during which a fixation cross was displayed, with five repetitions of each face stimulus per block (40 faces total per block). Face stimuli (Ekman and Friesen, 1976) were previously normalized at the MIT Media Lab (Breiter et al., 1996). The face stimuli were projected via a Sharp XG-2000V color LCD projector through a collimating lens onto a hemispherical tangent screen and viewed by the subject via a mirror affixed to the head coil. Subjects were instructed to simply look at the faces, keeping their eyes focused on the center of the picture at the location of the cross-hair. After completion of scanning, subjects performed a memory task in which they were asked to identify faces and facial expressions they had seen during the scanning session.

Offline Behavioral Testing

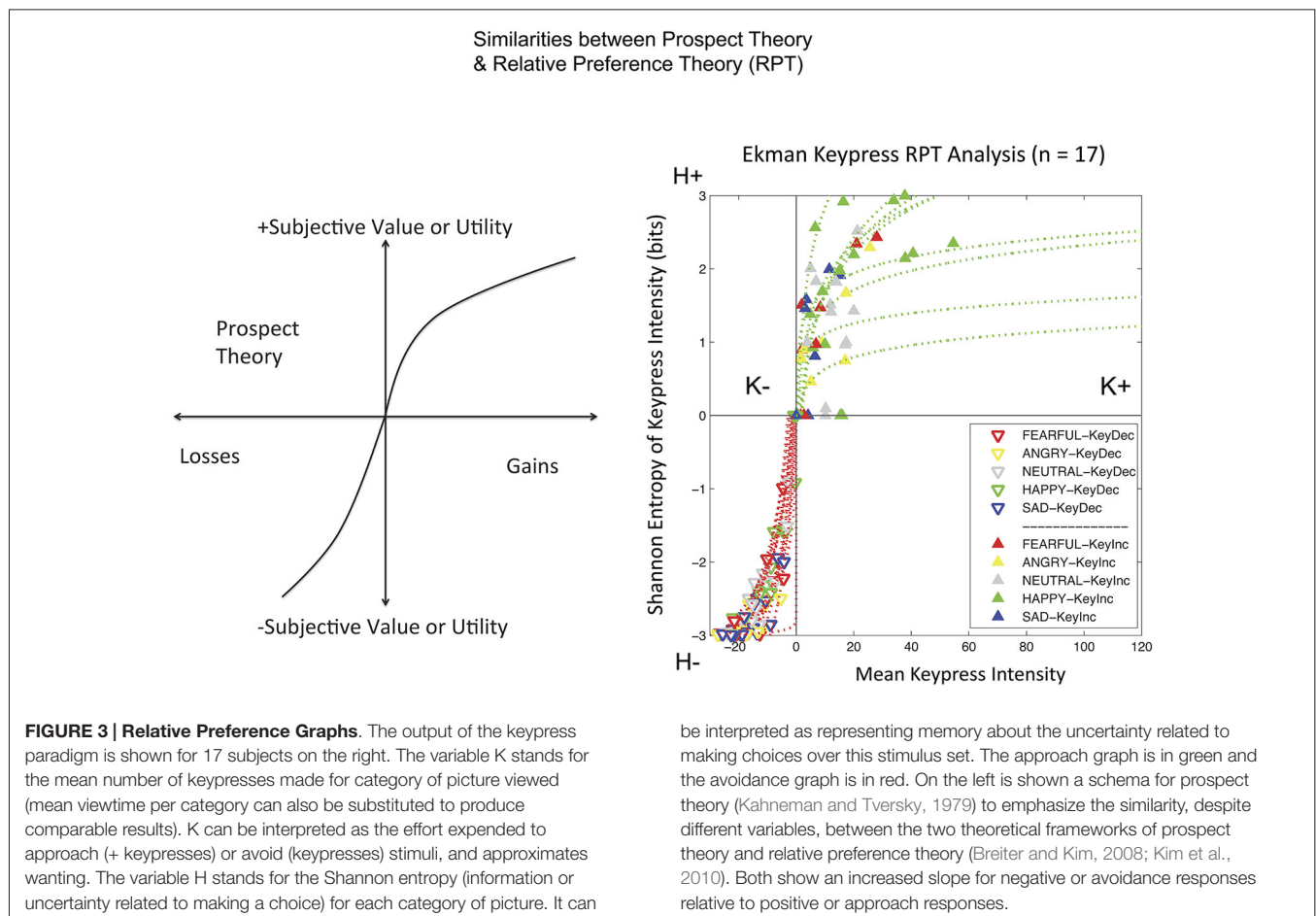
This experiment utilized a keypress task to determine each subject's relative preference toward the ensemble of faces (Aharon et al., 2001; Elman et al., 2005; Strauss et al., 2005; Levy et al., 2008; Makris et al., 2008; Perlis et al., 2008; Gasic

¹<http://pgp.mgh.harvard.edu>



separation of passive viewing and keypress response allowed the fMRI component to be free of motoric elements, which would otherwise confound interpretation of the fMRI results (please see Introduction Section). The keypress procedure was implemented with MatLab software on a PC (i.e., a personal computer). This task captured the reward valuation attributed to each observed face, and quantified positive and negative preferences involving (i) decision-making regarding the valence of behavior; and (ii) judgments that determine the magnitude of approach and avoidance (Breiter et al., 2006; Perlis et al., 2008; **Figure 2**). The objective was to determine how much effort each subject was willing to trade for viewing each facial expression compared to a default viewing time. Subjects were told that they would be exposed to a series of pictures that would change every 8 s (the default valuation of 6 s + 2 s decision block; **Figure 2**) if they pressed no keys. If they wanted a picture to disappear faster, they could alternate pressing one set of keys (#3 and #4 on the button box), whereas if they wanted a picture to stay longer on the screen, they could alternate pressing another set of keys (#1 and #2 on the button box). Subjects had a choice to do nothing (default condition), increase viewing time, decrease viewing time, or a combination of the two responses (**Figure 2**). A “slider” was displayed to the left of each picture to indicate total viewing time. Subjects were informed that the task would last approximately 20 min, and that this length was independent of their behavior, as was their overall payment. The dependent measure of interest was the amount of work, in number of keypresses, which subjects traded for face viewtime.

et al., 2009; Yamamoto et al., 2009; Kim et al., 2010), which had been used for passive viewing during scanning. The



Magnetic Resonance Imaging

All functional MR imaging was performed on a Siemens Trio 3 Tesla MRI system using an eight-channel phased-array receive-only RF coil. Subjects were positioned in the MRI scanner and their heads stabilized using foam pads and adjustable paddles fixed to the RF coil assembly. Blood oxygenation level-dependent (BOLD) functional images were acquired using gradient-echo EPI (TR/TE/ α 2.5 s/30 ms/90°, 3.125 mm \times 3.125 mm \times 3 mm resolution), with slices situated parallel to the AC-PC line, and parallel to the inside curve of the FOC to minimize signal distortion in this region (Deichmann et al., 2003). Structural images were acquired using a high resolution T1-weighted MPRAGE sequence (192 sagittal slices over the full head volume, matrix = 224 \times 256, FOV = 224 \times 256 mm², thickness = 1 mm, no gap) before functional scanning. Details of the imaging parameters and protocol have been reported previously (Perlis et al., 2008; Gasic et al., 2009).

Data Analysis Behavioral Data

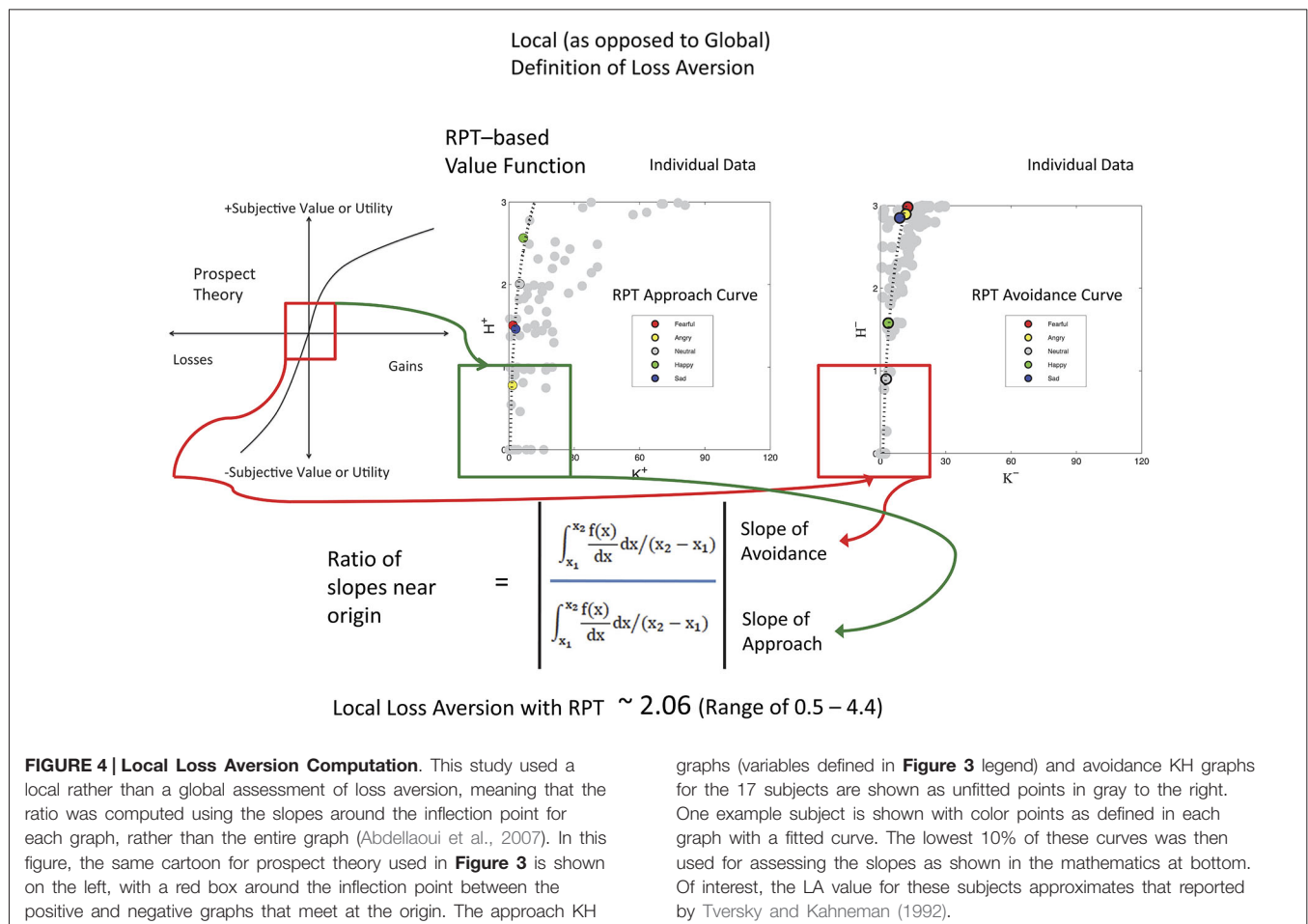
Keypress data were checked by a relative preference theory analysis of each subject, using previously validated procedures (Breiter and Kim, 2008; Kim et al., 2010; **Figure 3**). These procedures produce a valuation graph with variables K

and H that encode mean keypress number and Shannon entropy (i.e., information) (Shannon and Weaver, 1949). This valuation graph has been interpreted to relate “wanting” of stimuli (Aharon et al., 2001) to the uncertainty associated with making a choice (Kim et al., 2010). Using a local and general definition of LA (Abdellaoui et al., 2007), we computed the slope of the negative value/utility function (s^-) and the slope of the positive value/utility function (s^+), to produce s^-/s^+ (**Figure 4**). Specifically, s^- and s^+ were computed by the integral of the curve-fit slope over the 10% of the curve closest to the inflection point or origin (**Figure 4**). An absolute value of s^-/s^+ was then computed for each subject. With the full dataset of these subjects we then assessed the association of LA (i.e., $|s^-/s^+|$) with age using linear regression; given this test was done in parallel with another test against age (see NDS and age below), there was a correction for multiple comparisons imposed of $p < 0.05/2 = 0.025$.

Imaging Data

fMRI data were analyzed using the FSL platform (FMRIB's Software Library, v4.1.9)², and followed signal processing and

²<http://fsl.fmrib.ox.ac.uk/fsl/fslwiki>



statistical analysis procedures we have detailed elsewhere (Perlis et al., 2008; Gasic et al., 2009). Stimuli were grouped based on keypress responses into stimuli subjects avoided (Angry, Fearful, and Sad faces) and stimuli subjects approached by using the keypress task to increase viewing time (Happy faces). These two stimuli classes were contrasted in order to determine brain areas that responded more highly to negative (avoidance) than to positive (approach) stimuli [i.e., the β slope for the negative activation (or PE for the -COPE) was greater than the β slope of the positive activation (or PE for the +COPE)]. Statistical maps of NDS to losses relative to gains ($- > +$) were constructed as a group map, and voxels selected above a whole brain correction for z -stat = 2.3 that overlapped the VS/NAc segmentation volumes from the ICBM152 T1 template (Perlis et al., 2008; Gasic et al., 2009; **Figure 5**). VS/NAc segmentation followed previously published parameters for its boundaries (Breiter et al., 1997), using processes that have been well validated (see Breiter et al., 1994; Makris et al., 2004). As a second step in our model-based fMRI analysis, we assessed the correlation of NDS [(Angry, Fearful, and Sad $>$ Happy)] in the VS/NAc to LA, as described by Tom et al. (2007), using a subset of the 17 subjects who were not statistical outliers (**Figure 6**). For this isolated correlation, significant effects had to meet $p < 0.05$. With the

full dataset of these subjects we then assessed the regression of NDS with age (**Figure 7**), and LA with age. Given two assessments against the age variable, significant effects had to meet $p < 0.05/2 = 0.025$.

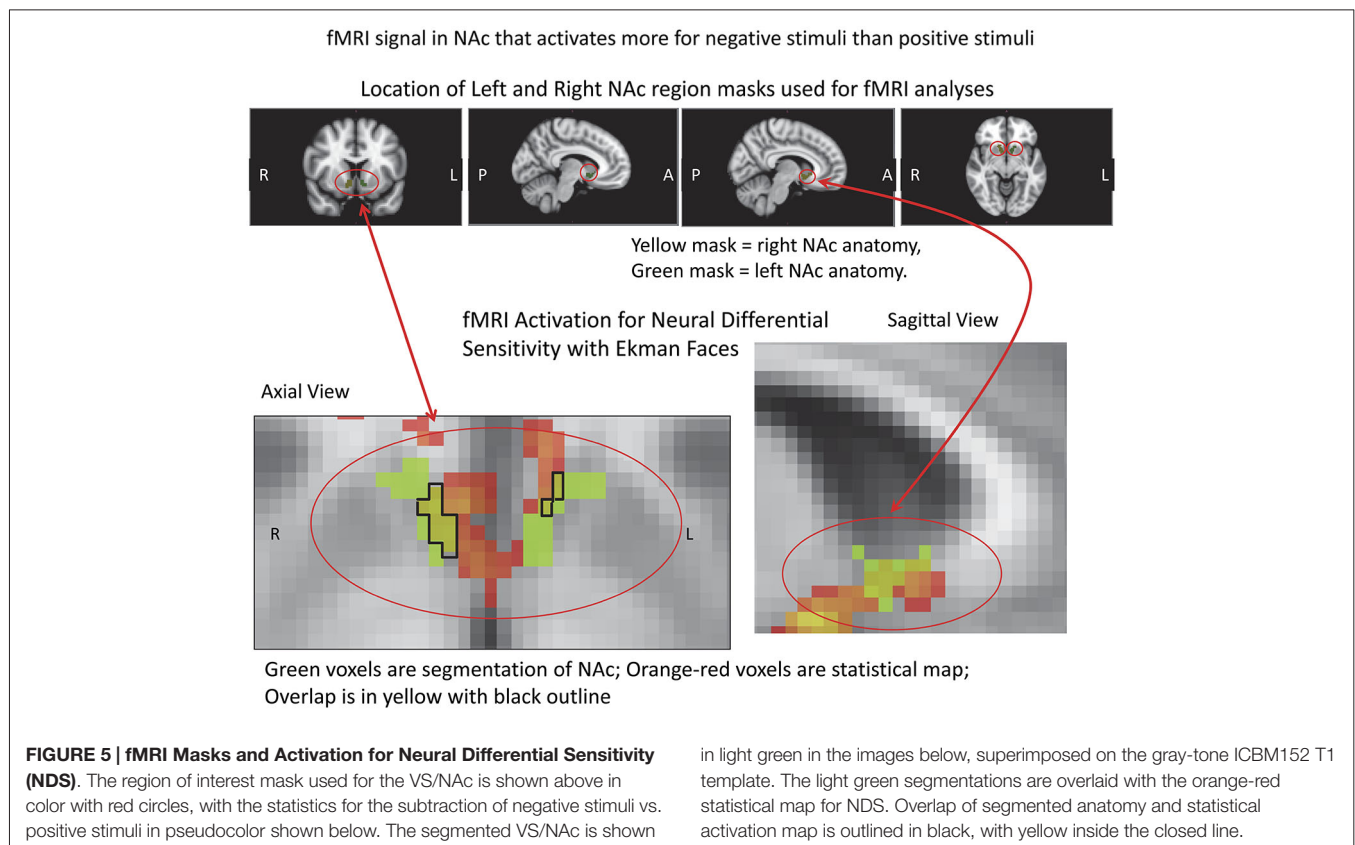
Results

Behavioral Data

All 17 subjects produced keypress data with value function graphs consistent with relative preference theory (Breiter and Kim, 2008; Kim et al., 2010; **Figures 3, 4**). All graphs produced LA computations (**Figure 3**), although five subjects had s-/s+ ratios that were > 2 standard deviations above or below the cohort mean, and thus were considered outliers. The LA estimate for remaining subjects was 2.06 ± 0.36 (mean \pm SE) (**Figure 4**), and the confidence interval of this group overlapped the LA mean of 2.25, published by Tversky and Kahneman (1992). The regression of LA to age showed a non-significant relationship ($p > 0.1$).

Neuroimaging Data

fMRI data showed significant motion artifacts in two subjects. In the remaining subjects, significant fMRI activation was observed in the VS/NAc bilaterally in the majority of



subjects (see segmentation-based masks of the VS/NAc and group statistical map in **Figure 5**). In individuals, voxels of activation with $p < 0.05$, $z = 1.96$ that overlapped segmentation of the VS/NAc were used to sample BOLD signal representing NDS to losses relative to gains. Across subjects, we found that activation to negative stimuli in left and right NAc was significantly greater than activation to positive stimuli (**Figure 5**). This signal was used for a control analysis of the correlation of NDS relative to behavioral LA ($r_{(2,11)} = 0.64$, $p < 0.04$). Without outliers (>2 SD from mean NDS), we found the same relationship (**Figure 6**) reported by others (Tom et al., 2007). When we assessed the relationship of NDS in the VS/NAc to age, we observed a significant positive correlation ($F_{(2,16)} = 9.01$, $p < 0.009$) (**Figure 7**).

Discussion

Synopsis

This study showed that a validated keypress paradigm that allowed subjects to trade effort for view-time of emotional faces (Ekman and Friesen, 1976), produced a relationship between the mean (K, **Figure 3**) and pattern of keypressing (H, **Figure 3**) consistent with previous reports using a beauty stimulus set, the International Affective Picture Set, and food stimuli (Breiter and Kim, 2008; Kim et al., 2010). This relationship from the picture-based keypress task produced a ratio between the slope of the avoidance value function (s-) and slope of the

approach value function (s+) as a LA measure quite close to that reported by Tversky and Kahneman (1992), who used a monetary decision task.

The keypress-based LA measure correlated with a measure of NDS from the VS/NAc, in similar fashion to that reported by others using a monetary choice task (Tom et al., 2007), and meeting our two criteria for model-based fMRI effects. Although correlation of LA with age was non-significant, the correlation of NDS with age showed a significant positive relationship. Two sides of the three-way correlation test between LA, NDS, and age were significant, suggesting that as individuals age their NDS also increases but their behavioral index of LA does not. The discussion that follows will evaluate potential hypotheses and implications of these findings, along with important caveats.

Neurocompensation and Other Hypotheses

The relationship between age and NDS in the absence of a significant relationship between age and behavioral LA suggests interesting hypotheses about the neural processing of LA in relation to age. First, Seidman et al. (1998) have shown that subject IQ is inversely related to brain activation levels across individuals, suggesting that the brain compensates with greater neural activity when functional capacity is lower. Given that aging is known to be associated with brain atrophy (e.g., Raz et al., 2005) and cognitive decline (e.g., Kensinger and Corkin, 2008), it is inferred that the functional capacity of the brain declines with age. The findings in this study suggest

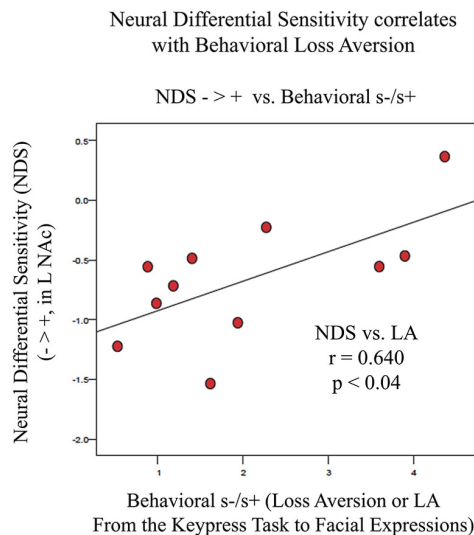


FIGURE 6 | Association between LA and NDS from BOLD signal collected by fMRI. NDS represents the difference between BOLD signal in the left VS/NAc for negative stimuli (Angry, Fearful, and Sad faces) minus positive stimuli (Happy faces). LA is represented as the absolute value of s-/s+ from the relative preference graphs of each subject as shown in **Figure 3**. The line of best fit is shown from this association.

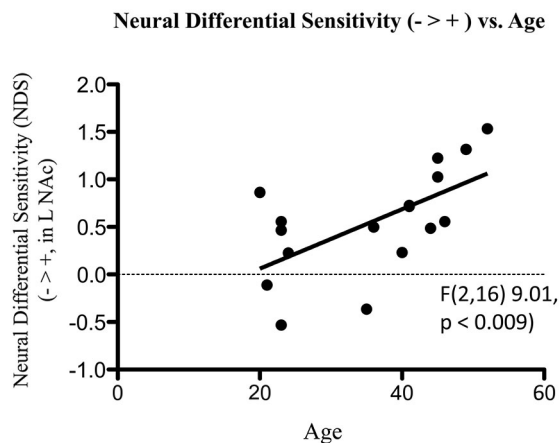


FIGURE 7 | Association of NDS from BOLD signal collected by fMRI with age. The line of best fit is shown from this association.

the hypothesis that as an individual ages, the neural differential between losses and gains increases to achieve the same level of behavioral LA. This perspective is consistent with recent research on aging wherein preserved cognitive function in the context of age-related brain activity may be thought to represent a neurocompensation mechanism (Meunier et al., 2014). Consistent with the neural efficiency (neurocompensation) hypothesis, age-related differences in reward processing have led to evolutionary theories about the changing costs and need to acquire resources over the lifespan. Namely, youth have optimal health and a lack of resources, which may drive the early aggressive pursuit of rewards (Spear, 2000; Somerville

and Casey, 2010); while as age progresses, biological decline drives the need to minimize effort and protect what has been acquired (Heckhausen, 1997; Ebner et al., 2006; Heckhausen et al., 2010).

Consistent with these observations, age-related brand loyalty (Lambert-Pandraud and Laurent, 2010) has been attributed to an increased aversion to risk associated with change (Montgomery and Wernerfelt, 1992; Erdem et al., 2006) leading to investigations of age-related changes in decision making and reward processing across the lifespan (Mata and Nunes, 2010; Eppinger et al., 2011, 2012; Mata et al., 2011; Weller et al., 2011; Paulsen et al., 2012a,b; Barkley-Levenson et al., 2013). In the current study, we observed no significant differences in LA behavior, but did find relatively early (i.e., range 20–55 years old) age-related increases in NDS. The parametric increase in NDS with age may indicate additional neural effort is required to obtain the same behavioral outcomes as one ages. Previous studies support this notion; for example, aging populations show bilateral activation patterns within homologous areas of the PFC while their younger counterparts achieve the same performance with singular lateralized activations (Reuter-Lorenz et al., 1999; Cabeza et al., 2002), suggesting compensatory mechanisms in response to neural senescence (Cabeza et al., 2002; Park and Reuter-Lorenz, 2009; Daselaar et al., 2015). In addition, recent imaging work on cognitive function suggests that behavioral outcomes reflect interactions between age, neural efficiency and processing load (Cappell et al., 2010; Vallesi et al., 2011; Turner and Spreng, 2012).

Alternative hypotheses might consider additional age-related asymmetries in the larger decision making network that interact with the VS/NAc in such a way that the response to LA is either uninhibited or amplified. For example, on the other end of the age spectrum, recent imaging work has shown asynchronous developments of the VS/NAc and PFC parallels adolescents' predisposition to engage in high-risk behaviors (Steinberg, 2008; Van Leijenhorst et al., 2010; Blakemore and Robbins, 2012; Barkley-Levenson and Galván, 2014), however the relationship only becomes apparent when the asynchronous trajectories of PFC and VS/NAc interact within a specific window of development. The observed VS/NAc response to LA may reflect a similar interaction, albeit in areas that did not reach thresholds of activation that changed behavior in the current experiment, either because of the age group examined, sensitivity of the task, or sensitivity of the imaging paradigm. For example, given the limitations of imaging relatively small and deep subcortical structures, particularly in small sample sizes, additional areas may also contribute to age related changes in processing LA, such as functional differences between the dorsal and ventral striatum, where activations in the dorsal striatum may have been sub-threshold in our data, or may only be associated with anticipation paradigms (Tom et al., 2007) related to LA.

Limitations

The differences in the relationship between age and neural responses vs. age and behavior suggests future work might benefit from examining VS/NAc response against other regions implicated in decision making, which appear to contribute to

LA processing (e.g., consider the amygdala findings in Lee et al., 2012, RO1 submission MH098867, and Canessa et al., 2013). In addition, while the sample size for this study is comparable to similar such work (e.g., Tom et al., 2007), much more needs to be done to develop a better understanding of age effects. In this study, we have a sample size of 17 subjects in the age range of 20–55 years. Future studies might include a wider age range to facilitate determining if there are distinct clusters of subjects supporting one or both of the hypotheses regarding age and neural function, and increase the number of participants to obtain a more densely packed gradient of age distributions. With a more comprehensive and dense parametric gradient of age, we speculate that we would see stronger correlations with VS/NAc activation, however we may also find non-linear functions, or a step function based on plateaus within certain groups of ages.

The use of a model-based approach to fMRI in this study also needs to be carefully considered in terms of its pros and cons. Given concerns about VS/NAc involvement with motor preparation (e.g., Florio et al., 1999) and alteration with motor illnesses such as Parkinsonism (e.g., Aarts et al., 2014; Payer et al., 2015), we sought to avoid motoric influence in cognitive imaging studies of the VS/NAc as occurs by definition with monetary choice paradigms (e.g., Tom et al., 2007; Canessa et al., 2013). The implicit assumption in our model-based approach was that emotional responses would drive keypress behavior, and thus the keypress responses would reflect the assessment of the faces being passively viewed in the scanner (see Perlis et al., 2008; Gasic et al., 2009). Such considerations about the use of valuation systems for processing even passively presented stimuli have been discussed by others (e.g., Hayes and Northoff, 2012), and similar considerations have been employed in other model-based fMRI analyses (e.g., Mittner et al., 2014; Wang and Voss, 2014; White et al., 2014; Xu et al., 2015). In this study, the model had two components: (i) testing if NDS would occur in the VS/NAc; and (ii) assessing if NDS-related fMRI signal in the VS/NAc correlated significantly with LA behavior across subjects. It is important to note that the behavioral process studied is one of only two behavioral models (the other being circadian rhythms) that have been tested to Feynman criteria for lawfulness (Kim et al., 2010). Even with such considerations, there is always the possibility that our implicit assumption does not hold, and the keypress behavior outside the scanner relates to a completely different cognitive function than that occurring in the scanner to passive viewing, such as might be involved with the default network.

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Conclusion

In this study we used a more general interpretation of LA, as an overweighting of aversion (toward negative stimuli) relative to approach (toward positive stimuli), and found close concordance with prior published LA measures (Tversky and Kahneman, 1992; Abdellaoui et al., 2007). This LA measure correlated significantly with the differential processing of negative outcomes relative to positive ones by the brain consistent with other studies (Tom et al., 2007; Lee et al., 2012; Canessa et al., 2013). The absence of LA correlation with age, but presence of age correlation with brain differential sensitivity (i.e., NDS) supports a neural efficiency or neurocompensation hypothesis regarding the effects of age on the process of LA. The data from this study may have implications for future research using non-monetary stimuli, such as consumables, marketing options, or market communications. Crossing this consideration with the aging data, the results of our study suggest that marketing communications and brands research that target older adults might focus on the cost of neural processing in marketing communications. Future fMRI work might specifically target an older adult population in order to examine how brain circuits underlying decision-making may be altered in persons over the age of 65. Future fMRI work might also examine the interactions of the nature of information with other variables such as amount of information (Mata and Nunes, 2010) and uncertainty, and thus give us a better understanding of the sub-processes that occur when older adults make decisions.

Acknowledgments

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On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note

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EEG Hyperscanning is a method for studying two or more individuals simultaneously with the objective of elucidating how co-variations in their neural activity (i.e., hyperconnectivity) are influenced by their behavioral and social interactions. The aim of this study was to compare the performance of different hyper-connectivity measures using (i) simulated data, where the degree of coupling could be systematically manipulated, and (ii) individually recorded human EEG combined into pseudo-pairs of participants where no hyper-connections could exist. With simulated data we found that each of the most widely used measures of hyperconnectivity were biased and detected hyper-connections where none existed. With pseudo-pairs of human data we found spurious hyper-connections that arose because there were genuine similarities between the EEG recorded from different people independently but under the same experimental conditions. Specifically, there were systematic differences between experimental conditions in terms of the rhythmicity of the EEG that were common across participants. As any imbalance between experimental conditions in terms of stimulus presentation or movement may affect the rhythmicity of the EEG, this problem could apply in many hyperscanning contexts. Furthermore, as these spurious hyper-connections reflected real similarities between the EEGs, they were not Type-1 errors that could be overcome by some appropriate statistical control. However, some measures that have not previously been used in hyperconnectivity studies, notably the circular correlation co-efficient (CCorr), were less susceptible to detecting spurious hyper-connections of this type. The reason for this advantage in performance is discussed and the use of the CCorr as an alternative measure of hyperconnectivity is advocated.

Keywords: electroencephalography, hyperscanning, phase synchronization, social neuroscience, inter-brain connectivity, Phase Locking Value

INTRODUCTION

Over the last decade, the development of techniques that allow the measurement of neural activity from two or more individuals simultaneously, known as hyperscanning, has been heralded with some justification as a promising new field in social neuroscience (Dumas, 2011; Dumas et al., 2011; Sanger et al., 2011; Babiloni and Astolfi, 2012; Konvalinka and Roepstorff, 2012). Hyperscanning methods have been used in many different social contexts but all involve the simultaneous recording of brain activity from two or more individuals with a view to determining how co-variation in their neural activity is related to their behavioral and social interactions and this work has resulted in multiple claims that neural coupling between people is increased during social interaction. In contrast, there has been little attempt to determine how valid the methods used to measure connectivity are in this context and this paper is one attempt to redress that omission.

The first true hyperscanning study was reported by Montague et al. (2002) using two linked fMRI scanners with two individuals playing a variant of the children's guessing game, "handy-dandy." Other studies have used near-Infrared Spectroscopy (Funane et al., 2011) and there is also a single case study demonstrating

the feasibility of hyperscanning using magnetoencephalography (Baess et al., 2012). Most studies, however, have relied upon EEG which, is not only more readily available than other methods but is also better suited for use in naturalistic social settings, and these are the focus of this paper.

The first EEG hyperscanning study was reported by Babiloni et al. (2006) and involved sets of four individuals playing Tressette, a bridge-like game. Since then, there have been 30 more EEG publications that meet the definition of hyperscanning coming from more than 20 independent studies have claimed increased neural coupling between people engaged in social interaction (Babiloni et al., 2006, 2007a,b, 2011, 2012; Flexer and Makeig, 2007; Tognoli et al., 2007, 2011a,b; Chung et al., 2008; Tognoli, 2008; Yun et al., 2008; Astolfi et al., 2009, 2010a,b,c, 2011a,b, 2012; Lindenberger et al., 2009; Dumas et al., 2010, 2012a,b; Fallani et al., 2010; Dodel et al., 2011; Lachat et al., 2012; Naeem et al., 2012a,b; Sanger et al., 2012, 2013; Yun et al., 2012; Kawasaki et al., 2013). The methods used to establish neural coupling between people have been very consistent and nearly all studies have used one of three methods: (i) covariance in amplitude or power, (ii) Partial Directed Coherence (PDC); (Baccala and Sameshima, 2001), and (iii) phase synchrony, mostly the

Phase-Locking Value (PLV) (Lachaux et al., 1999) or a variant thereof.

The most frequently used method for demonstrating brain-to-brain coupling between socially interacting individuals, used in 12 reports, has been to show that there are contiguous, or near contiguous changes in EEG amplitude or power (Babiloni et al., 2007b, 2011, 2012; Tognoli et al., 2007; Yun et al., 2008; Astolfi et al., 2009; Dumas et al., 2012b; Lachat et al., 2012; Naeem et al., 2012a,b; Yun et al., 2012; Kawasaki et al., 2013). In most cases, this EEG amplitude/power has been estimated from event-related changes or from FFT. Showing that there are co-variances in EEG power is a weak form of association and although it is suggestive of neural coupling, it is by no means conclusive.

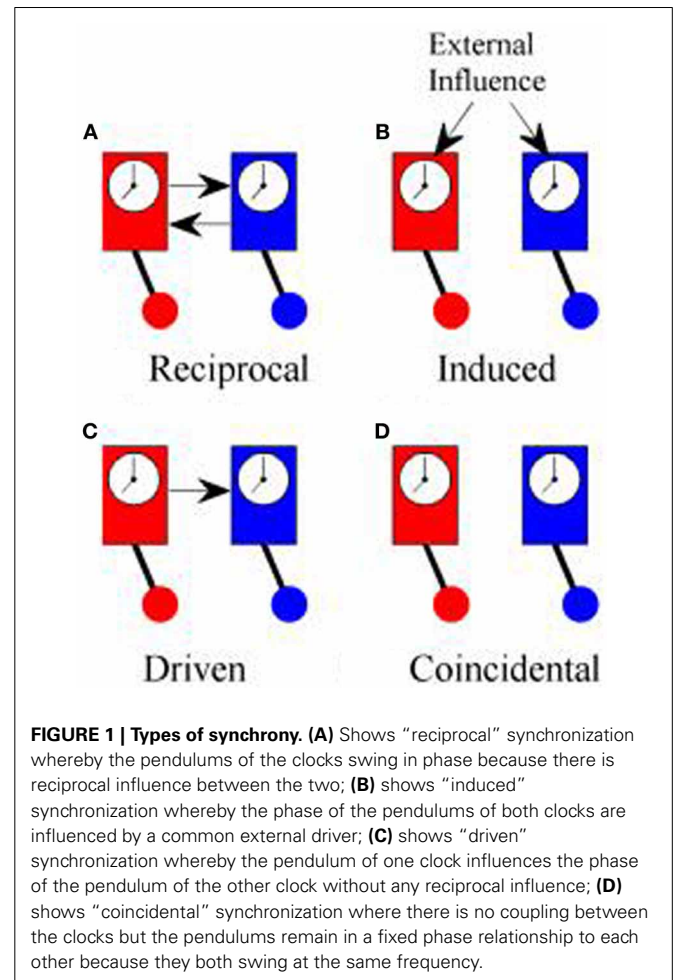
The second most commonly used method has been that of PDC which was the approach used in the very first EEG hyperscanning study (Babiloni et al., 2006) and has been used in at least nine further studies since (Babiloni et al., 2007a,b; Astolfi et al., 2010a,b,c, 2011a,b, 2012; Fallani et al., 2010). PDC is based on multivariate autoregressive modeling and Granger Causality and is designed to be able to show the direction of flow of information (linear) between two systems (Baccala and Sameshima, 2001). As such, PDC seems ideally suited to role of identifying inter-brain coupling in hyperscanning studies, at least in those cases where when one person's behavior is driving another's. However, both PDC and Granger causality are not without their critics. Friston (2011), for example, provides a critique of the use of Granger causality in fMRI research and, some of the limitations he mentions apply equally well to EEG research. It is certainly the case that, as Konvalinka and Roepstorff (2012) have observed, the results of PDC in hyperscanning studies have not replicated well, but whether this is related to the use of PDC, or to some other cause, is not clear.

The final class of measures of brain-to-brain coupling all involve measures of phase synchrony (Lindenberger et al., 2009; Dumas et al., 2010, 2012a; Sanger et al., 2012, 2013; Yun et al., 2012). The first use of phase synchronization as a measure of coupling with electrophysiological data was by Tass et al. (1998), who defined synchronization as occurring when $|\varphi_{n,m}| < \text{const}$, where const is some suitably small value, n and m are integers, $\varphi_{n,m}(t)$ is the phase difference, $n\phi_1(t) - m\phi_2(t)$ and $\phi_{1,2}$ are the phases of the two oscillators. The most widely used index of phase locking adopted in hyperscanning studies has been the Phase Locking Value (PLV) (Lachaux et al., 1999) which is a measure that seems well suited for capturing the rapid flow of information between people in social situations. Interestingly, some hyperscanning studies have used PLV to characterize behavioral interactions even when they have used other measures of coupling for the EEG (e.g., Tognoli et al., 2007).

Although both PDC and PLV have been used to measure coupling between cortical oscillations recorded in the EEG from two or more different people, what they actually measure is quite different in each case and, for this reason, it is worth reviewing what is meant by synchronization. The first scientific description of synchronization came in 1665 from Christiaan Huygens who wrote a letter to the Royal Society in which he described “*an odd kind of sympathy*” in which the pendulums of identical clocks mounted on the same support came to swing exactly out of phase

(i.e., anti-phase) regardless of the phase they had been in when they had been set running (Pikovsky et al., 2001; Klarreich, 2002). The explanation of this phenomenon is that the swing of the pendulum in one clock induced small movements in the support from which the clocks were suspended that would slightly alter the swing of the pendulum of the second clock. At the same time, the pendulum of the second clock would induce movements in the support that affected the swing of the pendulum in the first clock. These small mutual nudges would continue to shift the phase of each pendulum until they came to a point where the nudge from one would exactly counterbalance the nudge from the other and this would occur when the pendulums were precisely anti-phase. In modern terms, the two clocks were in a system of reciprocal negative feedback and would continue to change until the system reached the state of minimum energy transfer between the two. Minimum information transfer (in fact, zero energy transfer) occurs in the anti-phase condition. An example of in-phase reciprocal synchronization is shown in **Figure 1A**.

True synchronization then, is of interest in neuroscience because it is a reliable marker of the flow of information between elements of a system. Simply observing a consistent phase relationship between two oscillators (clocks, human brains etc.), however, does not necessarily mean that they are in the



same condition of reciprocal information exchange displayed by Huygens' clocks. Synchronization might also occur if both clocks are driven by some external influence as in **Figure 1B**. In hyperscanning experiments, this might occur if the participants simultaneously experience the same stimuli such as watching a movie together, even though they are not directly interacting (Hasson et al., 2008). Alternatively, the influence between oscillators might be one-way with one oscillator driving another, **Figure 1C**, which is exactly the type of coupling that PDC is designed to identify. Each of these types of synchronization might be of interest, depending upon the context of the study, and it would often be of interest to know which type of synchronization is being observed. In practice, however, these different types of synchronization may be difficult to tell apart.

There is a fourth type of synchrony which is not really synchronization at all: coincidental synchrony, **Figure 1D**. This is a phenomenon which is generally of no interest and, in the context of hyperscanning, has nuisance value only. Unfortunately, it is not a rare phenomenon. Had Huygens's clocks been too far apart to influence each other, they would have remained in the same fixed phase relationship to each other indefinitely. Over time, small differences between the clocks would lead to a gradual shift in phase but, at least over short periods of time, the phase difference would be nearly constant. In general, two oscillators will show a consistent phase relationship whenever they share a common frequency of oscillation. To put this in the context of the brain, consider two adults, each with a dominant alpha rhythm of ~ 10 Hz sitting in isolation in separate rooms. If we were to measure their EEG, we could expect to see a fairly consistent phase relationship between their alpha rhythms, at least over short time scales, even though there is no communication between them. This situation is exactly the same as the example of the identical but unconnected pendulum clocks and stems solely from the fact that they share a common frequency of oscillation. It follows from this that simply observing a consistent phase relationship does not imply synchronization or information exchange or, as Pikovsky et al. (2001) put it, "*synchronous variation of two variables does not necessarily imply synchronization*." The critical feature of synchronization is not that the oscillators are synchronous but that there is "*... adjustment of their rhythms, or appearance of phase locking due to interaction*" (Tass et al., 1998).

To put this more formally, two oscillators can be said to be synchronized if deviations from the regular oscillatory cycle of one oscillator provides information about deviations in the oscillatory cycle of the other. Such a definition suggests that a measure of the co-variation or correlation between oscillators might sometimes be more useful. It is for this reason, that most hyperscanning studies do not simply measure phase coupling in the EEG between individuals but compare the degree of coupling between different experimental conditions. In the best studies, the experimental conditions are identical in every way except that in one case the participants are socially engaged and in the other they are not. In practice, however, this level of experimental control is difficult to achieve.

The aim of this paper is to examine the performance of currently used measures of phase synchronization in hyperconnectivity studies (PDC and PLV) and compare them

with alternative measures including coherence (COH), the circular correlation co-efficient (CCorr) and Kraskov's Mutual Information estimator (KMI) (Kraskov et al., 2004). Good performance, in this context, is defined by three qualities. First, the measure should be unbiased and have a low root mean squared error of estimation (RMSE). Specifically, when the true connectivity, $r = 0$, the estimated connectivity should be zero or very close to it. Second, the estimate of connectivity should increase monotonically as r increases and third, the estimate of coupling strength between two channels should be independent of the distribution of the signal in either of the constituent channels. In particular, the estimate of coupling strength should be insensitive to changes in the variance of the marginal distributions of deviations from the expected phase in either channel.

The first comparison included simulated time series where the degree of connectivity could be systematically varied. The second comparison compared EEG from individuals independently recorded but analyzed as though they had been recorded as part of a hyperscanning study. Because these EEG recordings were completely independent and there was no social contract between participants, a good measure of hyperconnectivity should not detect any synchronization between them. The first example of EEG data was from an event-related potential paradigm in which data recorded around the time of the presentation of a visual stimulus was used. This is analogous to induced synchrony (**Figure 1B**) as there may be some apparent connectivity between individuals because they share similar external stimulation. The second example of EEG data was from two independent resting state conditions in which there was no external stimulation to induce synchrony.

MATERIALS AND METHODS

MEASURES

Five different methods for estimating functional hyperconnectivity were used in this study.

Coherence (COH)

COH is the traditional Fourier-based method of connectivity and the Welch estimate of coherence is given by:

$$\text{COH}_{xy} = \frac{\left| \frac{1}{N} \sum_{k=1}^N Y_k(f) X_k^*(f) \right|}{\sqrt{\frac{1}{N} \sum_{k=1}^N X_k(f) X_k^*(f) \cdot \frac{1}{N} \sum_{k=1}^N Y_k(f) Y_k^*(f)}} \quad (1)$$

where $X_i(\omega)$ denotes FFT of the k th segment of the time series $x(t)$ at frequency f and $*$ indicates the transpose and complex conjugate. The analysis was performed using the MatLab function *mscohere.m*. COH values range from 0 to +1.

Partial directed coherence (PDC)

The PDC from y to x is defined as:

$$\text{PDC}_{xy}(f) = \frac{A_{xy}(f)}{\sqrt{a_y^*(f) \cdot a_x(f)}} \quad (2)$$

where $A_{xy}(f)$ is an element in $A(f)$ which is the Fourier Transform of the multivariate autoregressive (MVAR) model coefficients,

$\mathbf{A}(t)$, of the time series ; $a_y(f)$ is y th column of $\mathbf{A}(f)$. MVAR and PDC analysis was performed using the Extended Multivariate Autoregressive Modeling Toolbox for MatLab (Faes and Nollo, 2011). PDC values range from 0 to +1 but as $\text{PDC}_{x,y} \neq \text{PDC}_{y,x}$ both are reported.

Phase locking value (PLV)

There is an unfortunate terminological confusion over the use of the term “PLV” as, not only is it often referred to as the Phase Locking Index (PLI) but, both “PLV” and “PLI” can refer to two quite different measures that have equations of the identical form but quite different meaning. The PLV, as originally defined by Lachaux et al. (1999), is estimated by:

$$\text{PLV}_n = \frac{1}{N} \left| \sum_{k=1}^N e^{i(\phi_{(t,n)} - \psi_{(t,k)})} \right| \quad (3)$$

where N is the number of trials, $\phi_{(t,n)}$, is the phase on trial, n at time t , in channel ϕ and $\psi_{(t,n)}$ in channel ψ . The PLV_n varies between 0 and 1 where 1 indicates perfect phase locking and 0 indicates no phase locking. This form of the PLV_n is a measure of the consistency of the phase difference and is related to the inter-trial variance of the phase difference, $\sigma_{\phi-\psi}^2$, by the relationship $\text{PLV}_n = 1 - \sigma_{\phi-\psi}^2$. Because this form of the PLV_n is based on the phase difference across trials, it is only suitable for event-related paradigms.

However, there is a variant of the Equation (3) that has been frequently used in EEG hyperscanning studies which involves averaging the instantaneous phase differences over time within a single trial:

$$\text{PLV}_t = \frac{1}{T} \left| \sum_{n=1}^T e^{i(\phi_{(t,n)} - \psi_{(t,n)})} \right| \quad (4)$$

where T is the number of time points. This form of the PLV is essentially a measure of the intra-trial consistency of the phase difference between channels. As will become clear, this small difference between Equations (3) and (4) has important implications for the interpretation of EEG hyperscanning methods. In an attempt to remove any ambiguity, we shall refer to the measure defined by Equation (3) as the trial-averaged PLV or PLV_n and that described by Equation (4) as the time-averaged PLV, PLV_t . PLV values range from 0 to +1.

The PLV is a measure of the consistency of the phase-difference but, as noted above, simply observing that there is a consistent phase relationship between two signals does not imply covariance or information exchange or between them. Indeed, the PLV_t cannot distinguish between coincidental phase synchronization and true phase synchronization. To see why phase difference is a poor measure of information exchange, consider the variance of the difference in the case of the bivariate normal distribution¹ which is given by:

$$\sigma_{x-y}^2 = \sigma_x^2 + \sigma_y^2 - 2\sigma_x\sigma_y\rho, \quad (5)$$

¹Unfortunately, the equivalent equation for the bivariate von Mises distribution is not known.

where σ^2 is the variance and ρ is the correlation between the two distributions x and y . Clearly σ_{x-y}^2 can be small, indicating strong association between the two variables, not only when ρ is large but when σ_x^2 and σ_y^2 are small. This means that although σ_{x-y}^2 is related to ρ , it is a rather poor proxy for it and makes no sense to measure correlation this way in such cases. The natural measure of correlation in this case is the Pearson Product Moment Correlation Coefficient which measures the covariance of the deviations from the expected (i.e., mean) values of the two variables.

Circular correlation coefficient (CCorr)

The Pearson Product Moment Correlation Coefficient is not suitable for use with circular distributions like phase but there are several suitable candidates including the Circular Correlation Coefficient (CCorr) (Jammalamadaka and Sengupta, 2001), CCorr is a direct parallel to the Pearson Product Moment Correlation Coefficient for circular data and is given by:

$$\text{CCorr}_{\phi,\psi} = \frac{\sum_{k=1}^N \sin(\phi - \bar{\phi}) \sin(\psi - \bar{\psi})}{\sqrt{\sum_{k=1}^N \sin^2(\phi - \bar{\phi}) \sin^2(\psi - \bar{\psi})}} \quad (6)$$

where $\bar{\phi}$ and $\bar{\psi}$ are the mean directions for channels 1 and 2 respectively. For oscillatory signals, like the EEG, phase is approximately uniformly distributed and the population mean directions are not defined. However, in the case of uniform marginal distributions, any arbitrary direction can be defined as the mean without ill effect although for convenience, the sample mean directions, $\bar{\phi}$ and $\bar{\psi}$ were always used. Unlike PLV_t , the Circular correlation, CCorr, is much more robust to coincidental synchronization. The reason for this is that CCorr measures the circular covariance of differences between the observed phase and the expected (i.e., mean) phase. In the case of a perfect oscillator, the frequency of oscillation will be constant and there will be no variance. In the case of a sinusoidal oscillation, knowing the frequency of oscillation and its phase at any single time point provides a complete description of its behavior. For imperfect oscillators, as all real-world oscillators are, there will be small variations in phase over time. However, knowing the phase of such an oscillator in its recent past makes it possible to predict its phase in the near future. In the case of two related channels, if one channel is slightly in advance of its expected phase at a given time, then the phase in the other channel is also likely to be advanced (for positively correlated signals; the reverse for negatively correlated signals). That is, the phase variance of the oscillators co-varies and this is what CCorr measures. In the case of two unrelated channels, the phase variance will not co-vary and the CCorr will be zero. As the PLV measures the phase difference, which is a poor proxy for phase covariance, it is likely to be poorer at discriminating between related and unrelated signals. CCorr was measured using the CircStat toolbox for MatLab (Berens, 2009). CCorr values range from 0 to +1.

Kraskov mutual information (KMI)

The KMI is a non-parametric estimator of mutual information (Kraskov et al., 2004) based nearest-neighbor method for

estimating entropy proposed by Kozachenko and Leonenko (1987) cited in Beirlant et al. (1997). The KMI, adapted for use with phase data, is given by:

$$I_{\phi\psi} = \Psi(k) + \Psi(N) - \sum_{i=1}^N (\Psi(n_{\phi(i)} + 1) + \Psi(n_{\psi(i)} + 1)) \quad (7)$$

where $\Psi(\cdot)$ is the digamma function, $n_{\phi(i)}$ is the number of points with $\|\phi_i - \phi_j\| \leq \varepsilon(i)/2$ and $n_{\psi(i)}$ is the number of points with $\|\psi_i - \psi_j\| \leq \frac{\varepsilon(i)}{2}$; $\varepsilon(i)$ is the distance from observation i to its j^{th} nearest neighbor and distances are measured with respect to the maximum norm $\varepsilon(i) = \max\{\varepsilon_{\phi}(i), \varepsilon_{\psi}(i)\}$ and N is the total number of independent observations. In the simulations reported here, $j = 5$ and the distances were angular distances.

For convenience, all mutual information values were transformed to the range 0–1 using the relationship $r = \sqrt{1 - e^{-2I_{\phi\psi}}}$ where, $I_{\phi\psi}$, is the mutual information between ϕ and ψ and, r , is the correlation from a bivariate normal distribution with the same mutual information.

SIMULATIONS

The objective of the simulations was to generate time series when the phase-coupling between the two could be systematically varied. Phase distributions can be generated from the von Mises distribution, a circular analog of the Gaussian distribution that ranges from $-\pi$ to $+\pi$. The von Mises distribution is defined by its mean direction, μ , and concentration, κ , which are analogous to the Gaussian mean, μ , and the reciprocal of the variance, $1/\sigma^2$, respectively. Examples of the von Mises distribution for $\mu = 0$ and varying values of κ are shown in Figure 2. The von Mises distribution can be generalized to two dimensions where phase can be represented as a distribution on the surface of a torus (Singh et al., 2002). The covariance between the two dimensions of the bivariate von Mises distribution is controlled by a parameter λ . The joint probability density function is defined by the 5 parameters ($\mu_1, \mu_2, \kappa_1, \kappa_2$, and λ) and from this it is a simple matter of numerical integration to calculate the mutual information between the two distributions (see Appendix). Given the

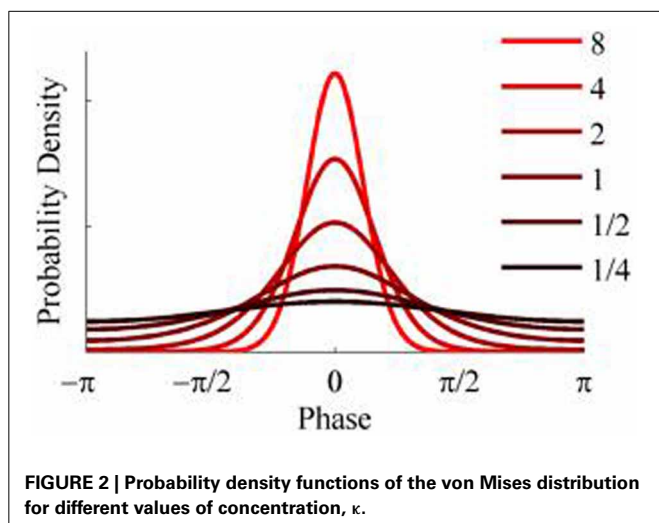


FIGURE 2 | Probability density functions of the von Mises distribution for different values of concentration, κ .

probability density function of a 2-D von Mises distributions it is a simple matter to generate random variables with any different levels of mutual information and concentration (Figure 3) using the acceptance/rejection method (Gentle, 1998).

To generate a time series with randomly varying phase shifts, we first generated an unwrapped and perfectly regular phase series $[0, 2\pi, 3\pi \dots n\pi]$, and generated n independent samples from a von Mises random distribution $[\phi_1; \phi_2; \phi_3; \dots \phi_n]$ and added the two together giving a new phase series $[0 + \phi_1, 2\pi + \phi_2, 3\pi + \phi_3, \dots n\pi + \phi_n]$. The von Mises random variables were added as phase deviations to the expected regular phase series. In this case, the aim was to simulate an alpha rhythm with a mean frequency of $f = 10$ Hz sampled at $= 500$ Hz. The phase series $[0, 2\pi, 3\pi \dots n\pi]$ corresponded to a time series of $[0, 0.1, 0.2, 0.3 \dots n/f]$ s so the phase values for intermediate time points from 0 to n/f seconds in $1/\omega$ second intervals were estimated by spline interpolation. Finally, the pseudo-alpha rhythm was obtained by taking the sine of the interpolated phase series. This created a smoothly frequency-varying oscillation with constant amplitude in which the variance of the frequency was determined by, κ , the concentration parameter of the von Mises distribution. In these simulations, therefore, $1/\kappa$ is a measure of the variance of the marginal distributions of deviations from the expected phase. An example is shown in Figure 4. It is a simple matter to generalize this process to the 2D cases using random variables a 2D-von Mises Distribution and the degree of dependency can be controlled by the parameter λ . For the simulations values of λ were chosen to approximate bivariate correlations of $[0, 0.2, 0.4, 0.6, 0.8]$ and the concentration values of, κ , were $[0.25, 0.5, 1, 2, 4, 8]$. One hundred samples of 100 s epochs of pseudo-alpha were generated for analysis for each value of λ and κ .

In order to generate pseudo-alpha time series in which there was a time-lagged dependency between channels, $n + 1$ independent samples were drawn from a 2D-von Mises distribution $[\phi_1; \phi_2; \phi_3; \dots \phi_{n+1}]$ and added to the phase series giving two new phase series $[0 + f(1, 1), 2\pi + \phi(2, 1), 3\pi + \phi(3, 1) \dots n\pi + \phi(n, 1)]$ and $[0 + \phi(2, 2), 2\pi + \phi(3, 2), 3\pi + \phi(4, 2), \dots n\pi + \phi(n+1, 2)]$. The rest of the procedure was identical to that for the zero-lagged time series but with the result that the two pseudo-alpha time series were maximally correlated with a lag of 100 ms but uncorrelated at lag 0. That is, one time series “caused” the other in the Granger sense.

Hyperconnectivity analysis

COH was estimated for each pair of time series using Welch’s method with non-overlapping Hamming Windows of 1024 ms Equation (1). For PDC, an MVAR model was generated for each 100 s pair of time series using a model order determined by the Akaike Information Criterion. The PDC was estimated from the MVAR coefficients following Equation (2). COH and PDC values were averaged across each of the 100 randomizations.

Estimates of PLV, CCorr, and KMI were derived from the instantaneous phase of the time series. Instantaneous phase at each time point in each time series was estimated from the Hilbert Transform of the pseudo-alpha data using FFT with a window of 1024 ms and it was these estimates that were used for estimating coupling strength. The Hilbert Transform produces a “real” and

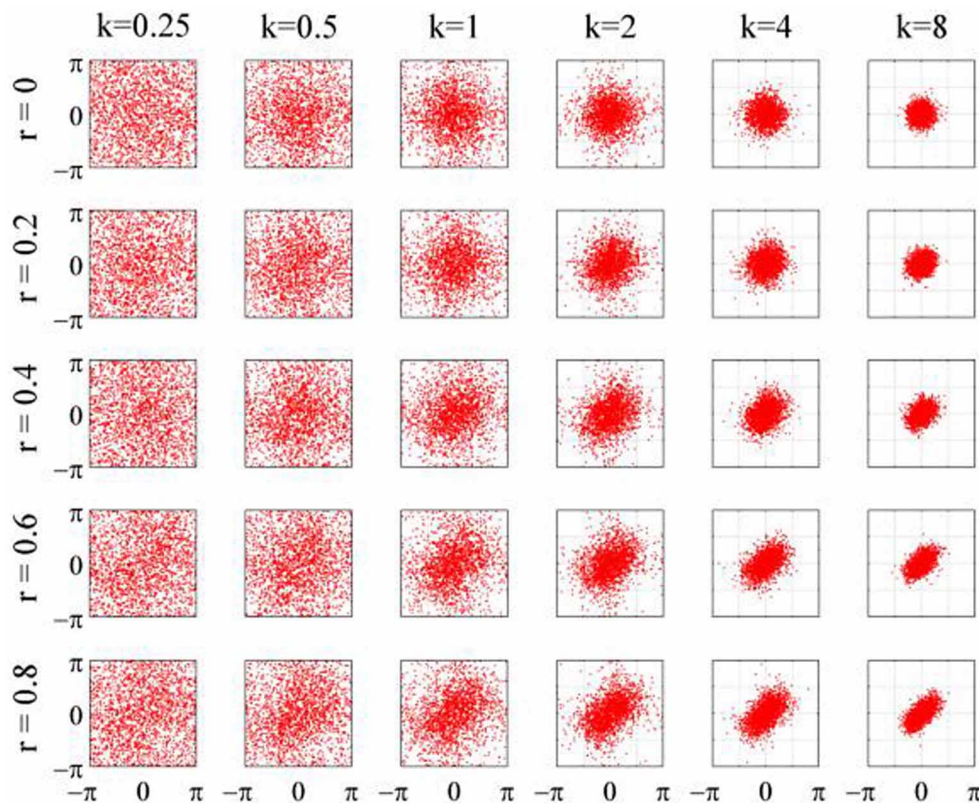


FIGURE 3 | Scatterplots of the 2D-von Mises distribution for different values of concentration, κ , and correlation, r .

“imaginary” time series and the phase was estimated by $\phi(t) = \tan^{-1} \left(\frac{\text{Imag}(t)}{\text{Real}(t)} \right)$. In all cases, the Hilbert-estimated phases were very close to “true” phase values that had been entered into the simulation. The phase-series were divided into epochs of 1024 ms and the PLV_t and $CCorr$ were estimated for each using Equations (4) and (6) respectively. The resulting values were averaged across all epochs and all randomizations. This procedure of estimating hyperconnectivity over short epochs and averaging follows the methods reported in the literature (Lindenberger et al., 2009; Dumas et al., 2010, 2012a; Sanger et al., 2012, 2013; Yun et al., 2012) each of whom used segments of EEG of less than 800 ms.

As estimation of KMI assumes independent observations, the instantaneous phase data was down-sampled to a rate equal to the mean frequency of the signal i.e., 10 Hz. An estimate of KMI was derived for each of the down-sampled segments of pseudo-alpha phase data using Equation (7) and averaged across the 100 random samples.

Statistical analysis

Each of the measures of connectivity was evaluated in terms of their bias and Root Mean Squared Error of Estimation (RMSE) for the case where the true connectivity, r , was zero. Bias and RMSE were defined as: $\text{Bias} = \frac{1}{N} \sum_{k=1}^N (r_i - \hat{r}_i)$ and $\text{RMSE} = \frac{1}{N} \sqrt{\sum_{k=1}^N (r_i - \hat{r}_i)^2}$ where r_i is the true connectivity and \hat{r}_i is the estimate of the true connectivity. Note that for COH, PDC and

PLV_t , where the values are defined to be greater than or equal to zero, the Bias and RMSE are equal. Mutual information, by definition must also be greater than or equal to zero but, the KMI estimator can produce small negative values and for this reason, Bias will not always be equal to RMSE.

HUMAN EEG

PARTICIPANTS

The data used for this study are a subset of a dataset that has previously been reported on and full details of the experiment are reported in Burgess (2012). Participants were 10 healthy young adults (5 women, 5 men) recruited through advertisement with a mean age of 25.4 years ($SD = 5.8$; range 20–40). Written informed consent was obtained from all subjects and the experiment was conducted as approved by the Riverside Research Ethics Committee. All investigations were conducted according to the principles expressed in the Declaration of Helsinki and data were analyzed anonymously.

Procedure

EEG was recorded from participants at rest (60 s Eyes Open Relaxed and 60 s Eyes Closed Relaxed) and as they were presented with a series of faces. There were 90 trials which included the presentation of a fixation cross for 1000 ms followed by a photograph of a face for the same duration. Each photograph was of the head and shoulders of a man or woman with neutral emotional

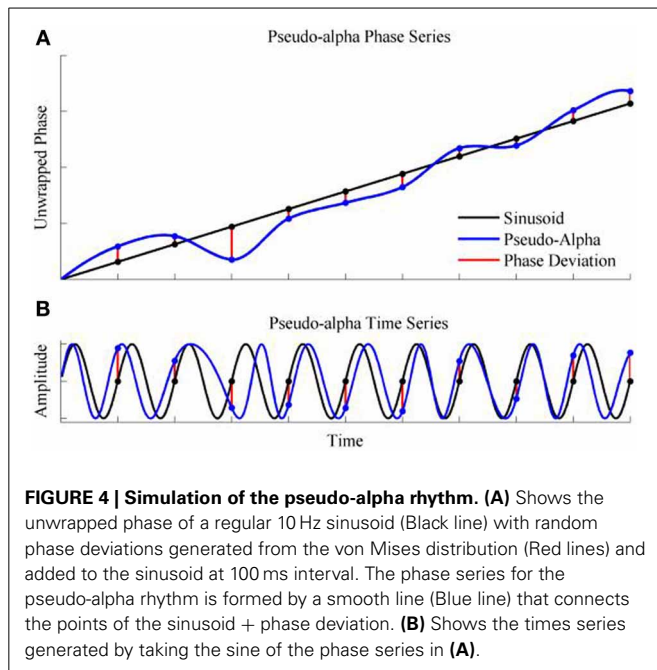


FIGURE 4 | Simulation of the pseudo-alpha rhythm. (A) Shows the unwrapped phase of a regular 10 Hz sinusoid (Black line) with random phase deviations generated from the von Mises distribution (Red lines) and added to the sinusoid at 100 ms interval. The phase series for the pseudo-alpha rhythm is formed by a smooth line (Blue line) that connects the points of the sinusoid + phase deviation. **(B)** Shows the times series generated by taking the sine of the phase series in **(A)**.

expressions, facing directly toward the participant. The inter-trial interval consisted of a blank screen and randomly varied between 1000 and 2000 ms. All data were recorded from participants completely independently and at separate times. There was no social interaction between any of the participants at any time during the recording of these data.

Materials and equipment

Twenty-eight electrodes were positioned on the scalp using an ECI electrode cap with electrodes placed according to the International 10–20 system with an additional nine electrodes: Oz, FC5/6, CP1/2, CP5/6 PO1/2. Horizontal electro-oculogram (EOG) was recorded from the external canthus of each eye, and the vertical EOG was recorded from the supra- to suborbit of the left eye. Electrode impedances were all under 5 k Ω . EEG and EOG were amplified using a 32 channel Neuroscan Synapse-II System. Signal bandpass was 0.1–100 Hz and the digital sampling frequency was 500 Hz. Reference was to the left ear and converted to average reference offline.

Data preparation

For the resting state, data were divided into consecutive epochs of 1024 ms. For the event-related paradigm, EEG was divided into pre-stimulus and post-stimulus epochs each of 1024 ms duration. The pre-stimulus epochs included data from –1024 ms to –1 ms and the post-stimulus epochs contained data from +1 to +1024 ms where zero was defined as the time of stimulus onset.

For both data sets, epochs including values outside the range –100 to +100 μ V range were excluded from the analysis. In order to facilitate the comparison between EEG recorded from different individuals, it was convenient to ensure that each participant contributed the same amount of data. For this reason, only the first 20 epochs for the resting state conditions and the first 50 epochs for the event-related paradigm were included.

Hyperconnectivity analysis

The data from each participant was paired with every other participant and analyzed as if they had been recorded jointly in a hyperscanning experiment. With 10 participants, this gave a total of 45 pseudo-pairings, one of whom was arbitrarily nominated as participant 1 and the other as participant 2. Twenty-eight channels of EEG were recorded for each person meaning that there were 56 channels for each pair of participants giving a total of 1540 possible different channel combinations. Of these, only the 784 hyper-connections that paired data between people were considered further.

For each pairing, EEG data were concatenated across epochs in preparation for the hyperconnectivity analysis. For the resting state data, 20 consecutive epochs of artifact-free EEG were joined together from each condition to form 20.48 s of data for each of the eyes open and eyes closed conditions. For the event-related data, 50 epochs of pre-stimulus and post-stimulus EEG were concatenated separately to give two time series of 51.2 s each.

COH and PDC were estimated from these concatenated data for each participant separately using the method described for simulated data and hyperconnectivity estimates were the highest values obtained in each of the Theta (4–8 Hz), Alpha (8–12), Beta1 (13–19 Hz), Beta2 (20–29 Hz), and Gamma (30–70 Hz) frequency bands. For the phase-based measures, PLV_{*t*}, CCorr and KMI, the concatenated data were filtered into the same frequency bands using Butterworth filters and the instantaneous phase was estimated using the Hilbert transform in the same way as for the simulated data. PLV_{*t*} and CCorr were estimated for each 1024 ms epoch and frequency band separately and averaged. The KMI was estimated from the same data down-sampled to 10 Hz.

Statistical analysis

For the rest conditions, connectivity in the Eyes Open and Eyes Closed conditions were compared and for the event-related data, connectivity in the pre-stimulus period was compared to that in the post-stimulus period. The difference in connectivity between experimental conditions was estimated for each of the 784 electrode pairs and averaged across each of the 45 pseudo-pairs of participants.

In order to determine if the differences were reliable, a randomization testing procedure was used to control the Type-1 error (Holmes et al., 1996; Burgess and Gruzelier, 1997). Consider one electrode pair; under the null hypothesis, there should be no difference between conditions and so randomly swapping the data between them and calculating the difference many times should provide a good estimate of the variability in the connectivity of that electrode pair that is due to chance. If the difference in connectivity observed in the real data set is larger than 95% of the differences observed in the randomized data sets, it is reasonable to say that that difference is greater than might be expected by chance. To extend this idea to multiple electrode pairs, instead of examining the distribution of the connectivity difference at each electrode pair in turn, the distribution of the largest difference in connectivity across all electrode pairs for each randomization was examined. The 95th percentile of the distribution of the maximum difference represents the value that would not be exceeded

at any electrode pair by chance. In this way, the family-wise Type-1 error can be controlled to 5%.

The maximum difference across all 784 electrode pairs was estimated for 1000 randomizations of the data. The 95th percentile of this distribution was used as the upper cut-off for determining statistical significance and controlling the per-condition comparison Type-1 error to 5%. The same process was used to obtain a lower cut-off value.

RESULTS

SIMULATIONS

The results from the simulations showing the effects of varying the concentration, κ , and the zero-lagged correlation, r , on each of the measures of connectivity are shown in **Figure 5**. The first criterion of good performance, that the measures should have low bias and low RMSE can be addressed by examining the mean bias and RMSE of each of the connectivity measures when $r = 0$ and for each value of κ (**Figure 6**). Note that for COH, PDC and PLV, the bias equals the RMSE as all values are positive and greater than 0; only for CCorr and KMI do they differ. COH did not meet the criterion for any value of r and PDC and PLV_t only came close for low values of κ . KMI was close to the criteria for all values of κ but, as the minimum value of KMI is zero, there was a small, consistent bias. Only CCorr met the criteria fully.

The second and third criteria of good performance, that the estimate of connectivity should increase monotonically as r increases and that it should be insensitive to changes in the variance of the marginal distributions of deviations from the expected phase ($1/\kappa$), can be considered together. **Table 1** shows the proportion of variance in each measure of connectivity that can be accounted for by r , κ , the interaction r by κ and error derived from a Two-Way ANOVA of the simulation data. For all of the measures, except PDC, r accounted for a good proportion of the variance but for COH and PLV, this proportion was small

compared to the proportion attributable to κ . The poor performance of PDC in this context was unsurprising as it is designed to identify Granger causality in which one time series leads the other, not instantaneous associations as seen here. Nevertheless, the sensitivity of PDC to κ meant that relatively high values of PDC were obtained even where there was no real association between channels and it was the measure that showed the highest proportion of error variance. The interaction, r by κ , was important only for the PLV_t where it accounted for 7.5% of the variance and was manifest as a relatively greater influence of r , at low values of κ (**Figure 5C**). The two measures that best met the criteria were CCorr and KMI as they were both overwhelmingly influenced by r but not κ and, of the two, CCorr had a much smaller error variance.

The results from the simulations showing the effects of varying the concentration, κ , and the 100 ms-lagged correlation, r , on each of the measures of connectivity are shown in **Figure 7**. This simulation was designed to provide an example of Granger Causality that would be well-suited for analysis by PDC. The first point to note is that COH was largely unaffected by the change (compare **Figures 5A** and **7A**) and performed badly with both sets of data. In contrast, the PLV, CCorr, and KMI were all adversely affected which is unsurprising as these measures are not designed for use in this context. In the case of PLV_t and KMI, less than 1% of the variance was attributable to r . For PLV_t most variance was accounted for by κ whereas for KMI it was error. The poor performance of KMI with this data set occurred because it was estimated from the phase-series down-sampled to 10 Hz, the same rate at which the random phase deviations were added to the phase sequence. This meant that the simultaneous estimates of phase were truly independent. In contrast, because the PLV_t and CCorr were estimated based on intermediate points that were spline estimates of the preceding and subsequent phase deviations, each datum contained some information about the lagged

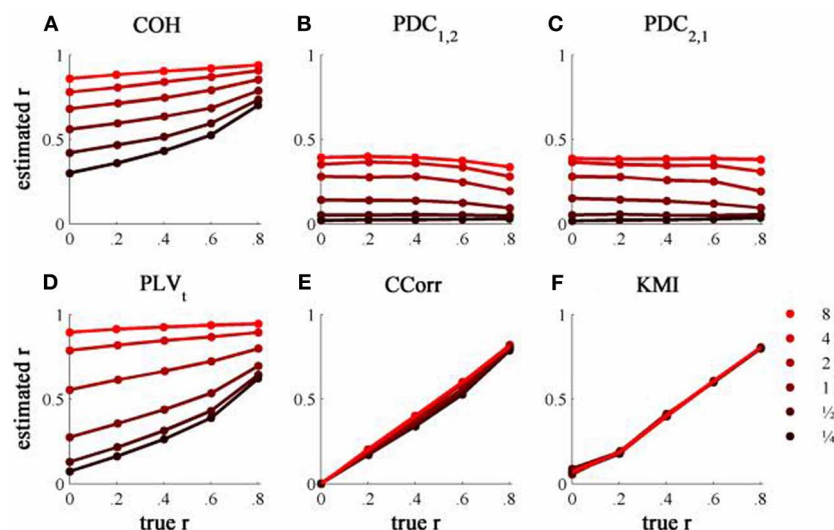


FIGURE 5 | The relationship between the true and estimated coupling for each measure of connectivity for the zero-lagged simulated data at different levels of concentration, κ . (A) Shows coherence, (B,C) partial

directed coherence, (D) time-averaged phase-locking value, (E) circular correlation coefficient and (F) Kraskov mutual information. Concentration values are $\frac{1}{4}$, $\frac{1}{2}$, 1, 2, 4, and 8.

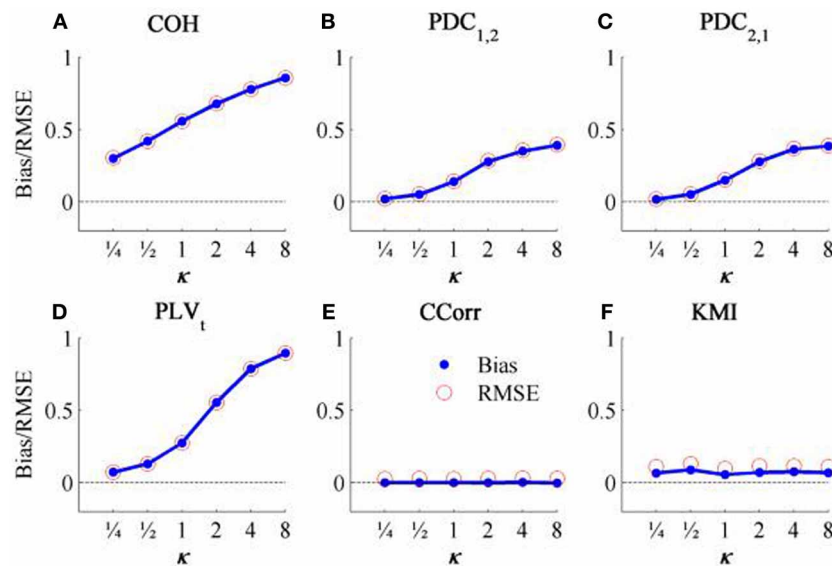


FIGURE 6 | The bias and RMSE for each connectivity measure estimated from the zero-lagged simulated data at different levels of concentration, κ , when the coupling, $r = 0$. Blue dots indicate bias and red circles RMSE. (A) Shows coherence, (B,C) partial directed coherence, (D) time-averaged phase-locking value, (E) circular correlation coefficient and (F) Kraskov mutual information. For COH, PDC and PLV, as all values are >0 , bias = RMSE are equal. For CCorr and KMI, where values may be ≤ 0 , bias \neq RMSE.

(D) time-averaged phase-locking value, (E) circular correlation coefficient and (F) Kraskov mutual information. For COH, PDC and PLV, as all values are >0 , bias = RMSE are equal. For CCorr and KMI, where values may be ≤ 0 , bias \neq RMSE.

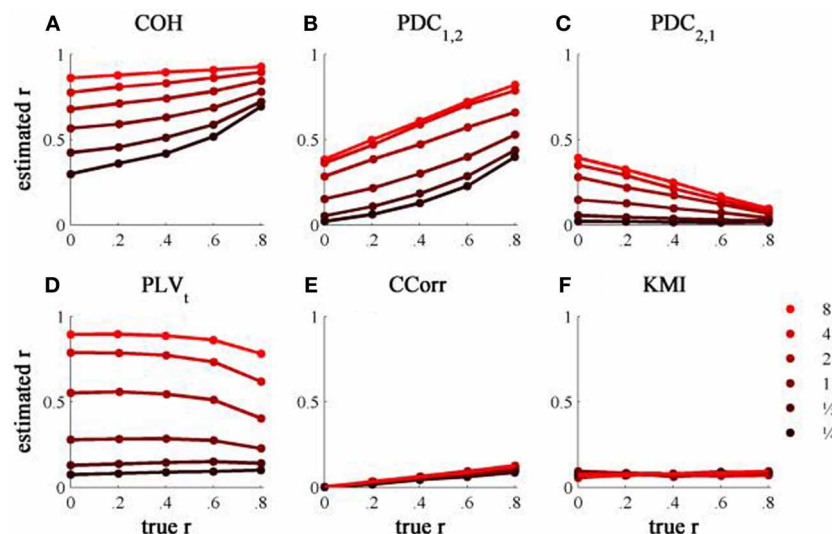


FIGURE 7 | The relationship between the true and estimated coupling for each measure of connectivity for the 100ms-lagged simulated data at different levels of concentration, κ . (A) Shows coherence, (B,C) partial

directed coherence, (D) time-averaged phase-locking value, (E) circular correlation coefficient and (F) Kraskov mutual information. Concentration values were $\frac{1}{4}$, $\frac{1}{2}$, 1, 2, 4, and 8.

relationship between the phase series. This is the reason why CCorr shows some sensitivity to increases in r , although much less than for the zero-lagged data. Of course, each of these measures would perform much better if they had been estimated across a range of time lags.

As expected, PDC performed better on this simulation than with the zero-lagged data. $PDC_{1,2}$ showed a clear monotonic increase with r correctly showing that channel 1 led channel 2. Similarly, $PDC_{2,1}$ showed a monotonic decrease with r , meaning

that the predictability of channel 1 given channel 2 diminished as the predictability of channel 2 increased. However, in both cases, the largest proportion of variance was attributable to κ , not r .

HUMAN STUDIES

Event-related changes in synchrony

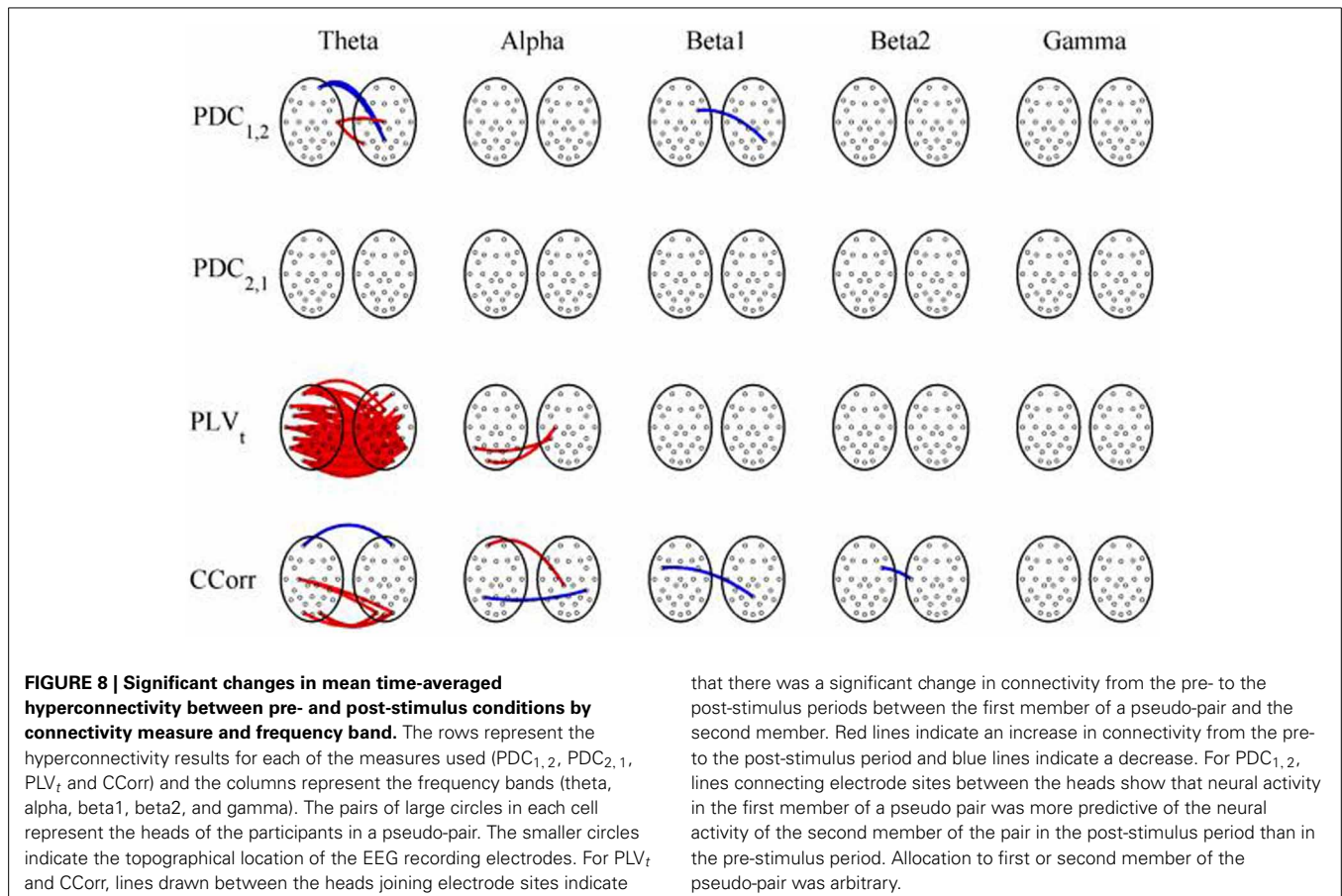
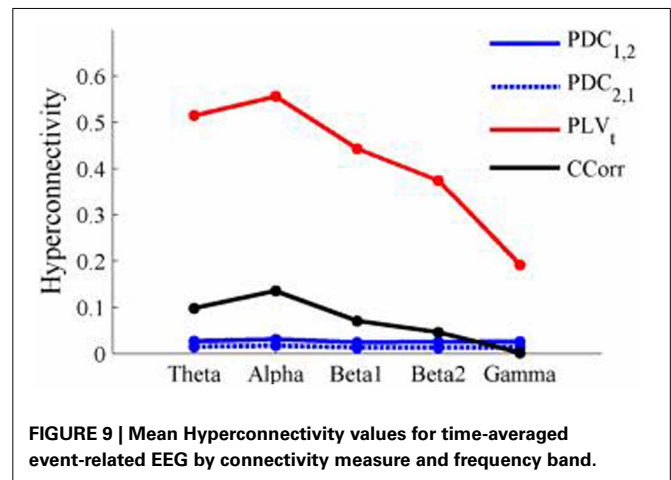
The results of the hyperconnectivity analysis between pre-stimulus and post-stimulus conditions, controlled for multiple comparisons, are shown in **Figure 8**. As all the data were recorded

independently, there can have been no true synchronization between the recordings. Nevertheless, there were a small number of significant changes in synchronization between the pre- and post-stimulus conditions identified by PDC and CCorr and a very large number for the PLV_t . For PDC and CCorr, the changes in synchronizations involved both increases and decreases but for PLV_t , they were exclusively in the direction of increased synchrony in the post-stimulus period. The estimates of mean synchrony averaged across the pre- and post-stimulus periods for each of the connectivity measures are shown in **Figure 9**. For PDC, the estimated levels of synchrony were consistently very low (range 0.01–0.03) and were also low for CCorr but more variable (range 0.001–0.14). In contrast, the mean synchronization was much higher for PLV with values ranging from 0.19 to 0.56.

As these data were from an event-related paradigm, it was also possible to estimate the between-trial synchronization using PLV_n and $CCorr_n$. **Figure 10** shows the significant differences in PLV_n and $CCorr_n$ between the pre- and post-stimulus periods. There were no significant differences in synchronization between conditions using $CCorr_n$ but there were several using PLV_n in the theta and alpha frequency ranges. The estimates of mean synchrony in the pre- and post-stimulus periods for PLV_n and $CCorr_n$ are shown in **Figure 11**. The PLV_n and $CCorr_n$ were rather larger than their time-averaged equivalents and were approximately equal across the frequency bands (PLV_n range 0.12–0.17; $CCorr_n$ range 0.12–0.19).

Resting state

The results of the hyperconnectivity analysis between the eyes open and eyes closed resting states, controlled for multiple comparisons, are shown in **Figure 12**. There were a number of significant differences in hyperconnectivity between eyes open and eyes closed using PDC. Most of these indicated that neural activity at multiple sites in pseudo-pair participant 1 was a significantly stronger predictor of neural activity at electrode



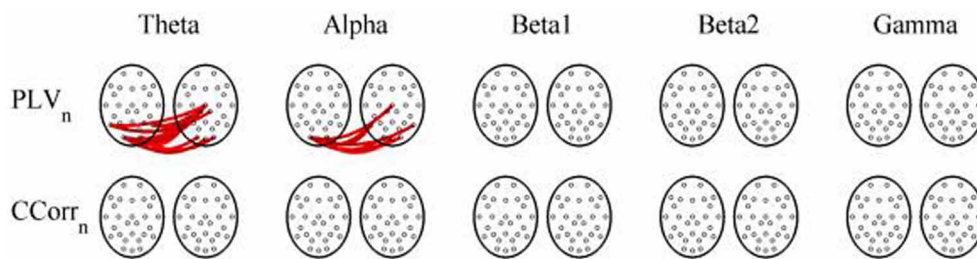


FIGURE 10 | Significant changes in mean trial-averaged hyperconnectivity between pre- and post-stimulus conditions by connectivity measure and frequency band. The rows represent the hyperconnectivity results for each of the measures used (PLV_n and $CCorr_n$) and the columns represent the frequency bands (theta, alpha, beta1, beta2, and gamma). The pairs of large circles in each cell represent the heads of the participants in a pseudo-pair. The smaller

circles indicate the topographical location of the EEG recording electrodes. Lines drawn between the heads joining electrode sites indicate that there was a significant change in connectivity from the pre- to the post-stimulus periods between the first member of a pseudo-pair and the second member. Red lines indicate an increase in connectivity from the pre- to the post-stimulus period and blue lines indicate a decrease.

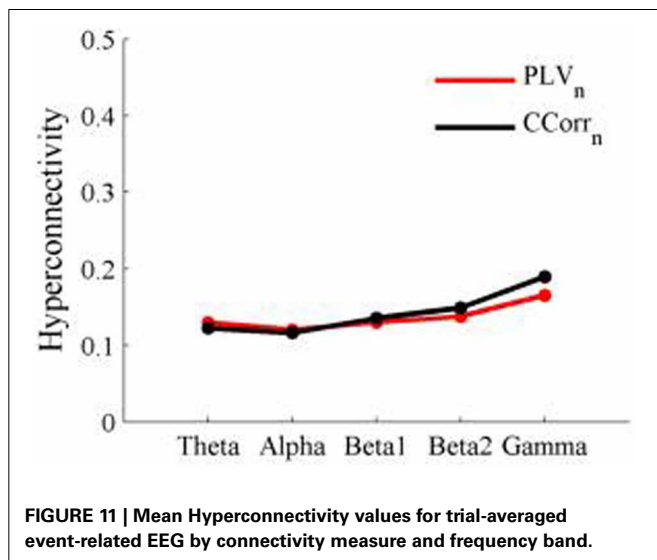


FIGURE 11 | Mean Hyperconnectivity values for trial-averaged event-related EEG by connectivity measure and frequency band.

site FP1 in participant 2 when the eyes were closed than when they were open. There were also two links indicating that neural activity participant 2 drove neural activity in participant 1. There were also a small number of hyper-connections identified by $CCorr$, one showing significantly lower synchronization between the participants in the eyes closed condition in theta frequency range and four showing the reverse in the alpha frequency range. However, by far the largest numbers of significant changes in synchrony were identified by PLV_t . In the theta frequency range, there were multiple hyper-connections that were significantly higher in the eyes open condition than in the eyes closed condition. In the alpha frequency range, there was an even larger number of hyper-connections that were greater in the eyes closed condition. The estimates of mean synchrony in the eyes open and eyes closed conditions for each of the connectivity measures are shown in **Figure 13**. As was the case with the event-related data, mean connectivity was low for PDC (range 0.01–0.11) and $CCorr$ (0.001–0.06) but was very much greater for PLV_t (range 0.13–0.40).

DISCUSSION

The issue of how best to measure hyperconnectivity depends in no small part on what one is trying to measure. Many hyperconnectivity researchers intended to measure synchronization which, in the Huygens sense means that two oscillators (in this case, the EEG of two people) interact in such a way that their cycles become synchronous. However, synchronization, as defined by the PLV, is rather different and simply means there is a consistent phase difference between the two signals but does not necessarily imply covariance between them. By this criterion, any pair of EEG channels with a common dominant frequency would be synchronized, which surely makes this definition too inclusive to be useful. Instead, a more useful definition is that two oscillators can be said to be synchronized if deviations from the regular oscillatory cycle of one oscillator provides information about deviations in the oscillatory cycle of the other.

By this definition, none of the commonly used measures of connectivity fared well in the simulations. COH, PDC, and PLV were biased measures of the co-variation between phase series and, under a broad range of conditions provided inaccurate estimates of the true hyperconnectivity. In particular, they were each prone to detect hyperconnectivity that didn't exist. It is well known that COH is a biased estimator of true coherence (Maris et al., 2007) but using Welch's method limits the extent of the problem. PLV too, is a biased estimator of coupling strength and the bias is greater when small samples of data are used, particularly, as is the case with PLV_t , when non-independent data points are used (Vinck et al., 2012). To put the scale of the problem in context, consider those simulations where the concentration was close to the mean value seen in the human EEG recordings and the true hyperconnectivity was zero ($\kappa = 2$, $r = 0$). Here the estimated coupling strengths were 0.65, 0.19, and 0.58 for COH, PDC, and PLV respectively.

These spurious couplings are not solely due to the familiar bias of the estimators. Rather, the coupling was driven by changes in the variances of the individual phase series (i.e., $1/\kappa$ of the marginal distributions of deviations from the expected phase). As **Table 1** shows, COH, PDC, and PLV_t were more sensitive to changes in the variance of the marginal distributions of deviations

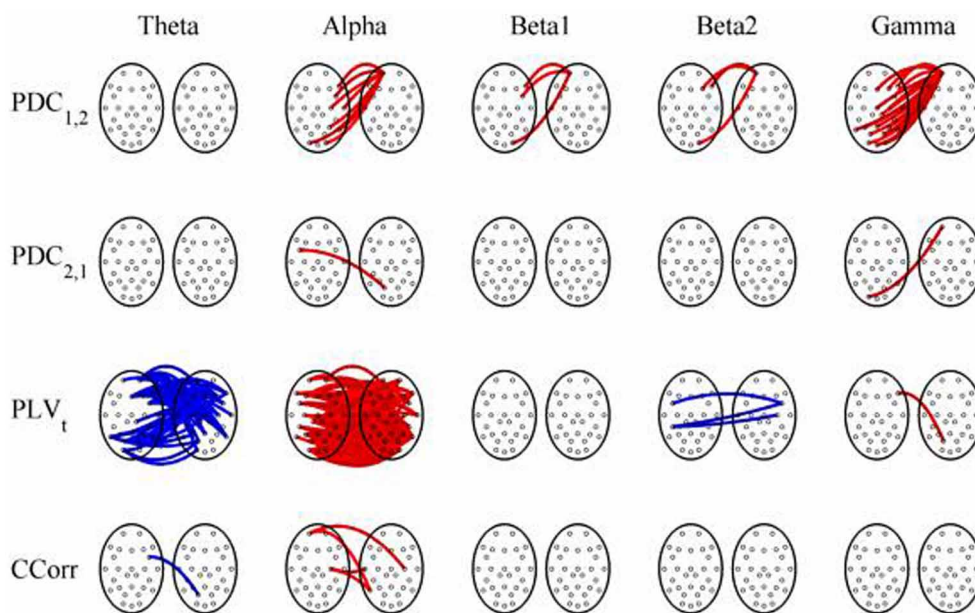


FIGURE 12 | Significant changes in mean time-averaged hyperconnectivity between eyes open and eyes closed resting states by connectivity measure and frequency band. The rows represent the hyperconnectivity results for each of the measures used ($PDC_{1,2}$, $PDC_{2,1}$, PLV_t , and $CCorr$) and the columns represent the frequency bands (theta, alpha, beta1, beta2, and gamma). The pairs of large circles in each cell represent the heads of the participants in a pseudo-pair. The smaller circles indicate the topographical location of the EEG recording electrodes. For PLV_t and $CCorr$, lines drawn between the heads joining electrode sites indicate

that there was a significant change in connectivity from the pre- to the post-stimulus periods between the first member of a pseudo-pair and the second member. Red lines indicate an increase in connectivity from the pre- to the post-stimulus period and blue lines indicate a decrease. For $PDC_{1,2}$, lines connecting electrode sites between the heads show that neural activity in the first member of a pseudo pair was more predictive of the neural activity of the second member of the pair in the post-stimulus period than in the pre-stimulus period. Allocation to first or second member of the pseudo-pair was arbitrary.

from the expected phase than to changes in the covariance of the phases (Table 1). The result is that any change in the variance of the marginal distributions of deviations from the expected phase will be identified as a change in hyperconnectivity whether or not there is any real change in the covariance of the signals. Indeed, using PLV to measure hyperconnectivity is akin to trying to determine the correlation between two continuous variables by measuring the variance of the difference between them; the difference is related to co-variance (see Equation 5), but only indirectly so.

Instead, it may be more appropriate to use a measure that estimates the co-variation of the distributions directly. Both COH and PDC measure the co-variation between the signals (to be precise, the cross-power spectral density) and so should be suitable for this purpose. However, both methods assume that the covariance between signals is stationary throughout an epoch, which in our simulations, it was not. The rapidly changing phase shifts in our simulations are the most likely reason for the poor performance of COH and PDC here. CCorr also estimates the co-variation of the distributions directly but does not assume a constant phase relationship across each epoch and we were able to show in the simulations that it provides an unbiased estimate of hyperconnectivity with a very low RMSE. In addition, we showed that a more general measure of hyperconnectivity, which estimates mutual information rather than phase-covariance, KMI, also performs well, although there was a small positive bias

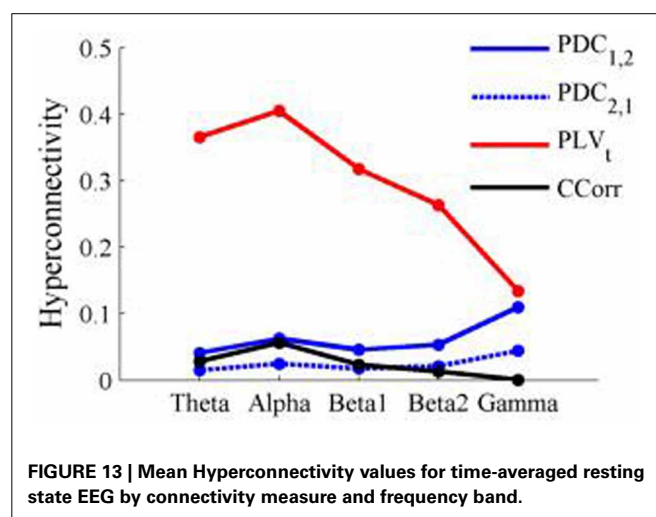


FIGURE 13 | Mean Hyperconnectivity values for time-averaged resting state EEG by connectivity measure and frequency band.

in the estimates and the computational demands were much greater.

The persuasiveness of simulations depends in no small measure on how realistic one perceives them to be, so it is often helpful to supplement them with evidence from real data. By creating pseudo-pairs of participants from EEG data recorded in completely independent sessions, and analyzing them as if their data had been collected during a hyperscanning study, we

Table 1 | Showing the proportion of variance accounted in each connectivity measure by correlation and concentration.

Connectivity measure	Zero-lagged data source of variance (%)				100 ms-lagged data source of variance (%)			
	<i>R</i>	κ	<i>r</i> by κ	Error	<i>R</i>	κ	<i>r</i> by κ	Error
COH	18.2	77.3	2.5	2.0	16.7	78.4	2.8	2.1
PDC _{1,2}	1.2	85.8	1.0	12.0	39.5	56.9	0.9	2.7
PDC _{2,1}	0.4	86.4	0.9	12.3	22.1	55.3	16.1	6.6
PLV _{<i>t</i>}	15.6	76.2	7.9	0.3	0.8	97.8	1.1	0.2
CCorr	99.0	0.3	0.2	0.6	62.7	2.1	1.4	33.8
KMI	95.6	0.0	0.0	4.4	0.0	0.1	0.0	99.9

could be confident that any hyper-connections observed would be spurious. We considered two conditions. The first was an event-related paradigm that might be expected to generate spurious hyper-connections because the participants were subject to similar sensory experiences and this comparison was designed to emulate the case of induced synchrony (Figure 1B). The second was a comparison of two resting states (eyes open and eyes closed) in which there was no exogenous stimulation and this comparison was designed to emulate the case of co-incidental synchrony (Figure 1D).

In both the event-related and resting-state paradigms, PDC and CCorr each identified a small number of spurious hyper-connections that differed between conditions. Most of these connections were weak (<0.1) and some showed an increase in hyperconnectivity whilst others showed a decrease and they can easily be dismissed as Type-1 errors. The only exception to this was the anomalous finding of multiple spurious hyper-connections using PDC_{1,2} focused on a single electrode (FP1).

A very different pattern was seen in the case of PLV_{*t*}, however. In the event-related data, nearly 20% of all possible connections in the theta frequency band ($n = 145$) were erroneously found to be significantly higher in the post-stimulus period. In addition, the strength of connectivity was strong with a mean PLV_{*t*} of 0.51. There were also multiple spurious hyper-connections found using the trial-averaged PLV_{*n*} with 14 (1.8%) and 10 (1.3%) found in the theta and alpha frequency bands although the strength of the connections was weak, 0.13 and 0.12 respectively. In the resting state comparisons, PLV_{*t*} showed a decrease in hyper-connectivity from the eyes open to the eyes closed conditions in 54 cases (7%) whilst in alpha, there was a corresponding increase in 170 (22%) hyper-connections and again, the strengths of the connections were moderately strong with a mean value of 0.37 in theta and 0.41 in alpha.

This strong and systematic pattern of findings using PLV in these very different paradigms is troubling because, in the absence our knowledge that these hyper-connections must be spurious, they might easily have been accepted as real. Such a large number of hyper-connections cannot easily be dismissed as Type-1 errors. The problem of multiple comparisons is well-understood by hyperconnectivity researchers and most recent studies have included appropriate statistical mechanisms to control the family-wise Type-1 errors that would otherwise

ensure. In this case, a robust and well-established method for controlling the family-wise Type-1 error control had been used but the real problem is that spurious connections were found despite these precautions. The clear implication is that statistical control of Type-1 errors is not sufficient to guard against detecting spurious connections.

Far from being a statistical artifact, it is likely that the large numbers of spurious hyper-connections identified by PLV_{*t*} arose from real similarities between the EEG recorded from different participants. In general, any systematic difference between the experimental conditions that affects the variance of the phase difference of the EEG recorded, will affect the PLV. This might occur in a number of ways but would include, for example, a systematic difference in rhythmicity between conditions. Any strong oscillatory component in the EEG means that the phase at any time point is much more predictable (i.e., the phase variance is lower). If the phase variance in one or both EEG channels is reduced, the variance of the phase difference will also be reduced and this means that PLV_{*t*} will be higher.

For this to happen, it is necessary that the change in rhythmicity is one that reliably occurs in most individuals but this is not difficult to achieve. The remarkably consistent, yet reliably predictable responses of the EEG to challenges attest to this (e.g., event-related potentials and event-related desynchronization). Given the same stimulation and cognitive and motor demands, any arbitrarily chosen group of neurotypical participants will produce event-related changes in their EEG that look very much like those produced by any other neurotypical group. Change the stimuli or the demands, and the topography and time-frequency characteristics of the responses will change in predictable ways. In short, different people presented with the same conditions will produce similar EEG responses.

Most of our spurious hyper-connections can be explained through this mechanism. Consider the resting state comparisons. The difference between the eyes open and eyes closed resting states is typically characterized in terms of the Berger effect in which opening the eyes severely attenuates the alpha rhythm. That is, the rhythmicity in alpha is greater when the eyes are closed than when they are open. We should expect, therefore, that in the alpha frequency band, PLV_{*t*} would be higher when the eyes were closed and this is what we observed. In addition, there is a stronger theta rhythm in the eyes open condition than in the eyes closed condition so we should expect to find higher PLV_{*t*} with eyes open, and this too was seen (Figure 12).

The same phenomenon can account for the spurious hyper-connections seen with the event-related data. The presentation of a visual stimulus, like a face, will induce a power increase in the theta frequency range in the post stimulus period (i.e., theta synchronization) (Burgess and Gruzelier, 1997). The presence of a stronger oscillatory component in the post-stimulus period meant that phase variance was lower than in the pre-stimulus period giving higher PLV_{*t*} values (Figure 8). One might also have expected a reduction in PLV_{*t*} in alpha because the presentation of a visual stimulus is invariably followed by a power reduction in that frequency range (alpha desynchronization) but this was not seen in this case.

A similar mechanism can account for the spurious synchronizations detected by the trial-averaged PLV_n . The presentation of a visual stimulus induces a phase-re-organization of the ongoing EEG (Burgess, 2012). In the pre-stimulus period, a cross-section across trials at any given time point, would show that the phases were randomly distributed. In the post-stimulus period, although the EEG is not strictly phase-locked, the phase-variance is much reduced and this reduction of phase-variance within each channel means that the phase difference between channels will also be reduced. The result is the increase in PLV_n that we observed (Figure 10).

The important point to note is that the statistically significant but spurious differences in PLV observed derived not from any connection between the participants involved but from the fact that our experimental conditions were associated with systematic differences in the rhythmicity of the EEG. This has two important implications for the field of hyperscanning. First, it means that spurious hyper-connections are likely to be found under a broad range of experimental conditions as any systematic difference between conditions in terms of movement, stimulus presentation or mentation could have this effect. Second, these spurious connections are not Type-1 errors that can be overcome using a statistical control for multiple comparisons.

There are two obvious ways to tackle this problem: improved experimental control and the use of a different measure of phase synchronization. There is certainly no substitute for good experimental design and if the conditions to be compared can be matched in terms of stimulus presentation and movement, and if appropriate control conditions are used, then much of this problem would be resolved. Indeed, this is already the case with the better designed studies in the field. However, although it might be possible to obtain this level of experimental control in restricted social situations, one of the key attractions of hyperscanning is that it has the potential to open a window on the neural co-ordination of people socially interacting in the real world. Not for the first time, strict experimental control and ecological validity stand in opposition to one another.

The other approach to tackle this problem is to adopt an alternative measure of phase synchronization. Any measure that is sensitive to changes in the marginal distributions of deviations from the expected phase is also likely to be sensitive to changes in the rhythmicity of the EEG. Although PLV was the most problematic measure in this context, at least in terms of detecting spurious hyper-connections in human EEG, the simulations showed that PDC and COH were also vulnerable in this respect, at least under certain circumstances. The real problem is that, although the PLV is widely used as a measure of phase synchronization, a high value of PLV does not necessarily mean there is any true phase synchronization at all. If we wish to claim that two time series, or, in this case, two phase series, are related to each other, we need to show that deviations from the dominant frequency in one oscillator co-vary with deviations in the other. Had the pendulums on Huygens's clocks simply shown a consistent phase relationship to each other, he would never have discovered the phenomenon of phase synchronization. What surprised him was not that the pendulums remained in the same fixed phase relationship to each other where they'd started, but that they progressively shifted

phase until their swings became aligned. As Pikovsky et al. (2001) put it, "*This adjustment of rhythms due to interaction is the essence of synchronization.*"

This emphasis on synchronization has been unfortunate because what most EEG hyperscanning researchers wish to show is that cortical oscillations from different people are systematically related to each other in a way that depends upon their social interactions. This means that we need to show that there is covariance (or more generally, mutual information) between the EEG of the people concerned. Synchronization is one way of doing this but, as this study has shown, there may be advantages from using a measure of correlation instead. Fortunately, we have at least two candidate measures that might serve: CCorr and KMI. CCorr is insensitive to changes in the marginal distributions of deviations from the expected phase and, hence, resistant to changes in the rhythmicity of the EEG because it measures the co-variation between phase series. Adopting this measure, or some suitable alternative such as KMI, may not solve the problem completely, but it may go a long way to reducing the risk of detecting spurious hyper-connections in future.

To conclude, existing measures of hyper-connectivity are biased and prone to detect coupling where none exists. In particular, spurious hyper-connections are likely to be found whenever any difference between experimental conditions induces systematic changes in the rhythmicity of the EEG. These spurious hyper-connections are not Type-1 errors and cannot be controlled statistically. Measures of the co-variance or mutual information between phases-series provide more robust evidence of true hyperconnectivity and are to be preferred in this context.

AUTHOR CONTRIBUTIONS

Adrian P. Burgess designed the study, supervised the data collection, performed all the analysis and simulations and wrote the paper and sang the theme tune.

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APPENDIX: THE 2 DIMENSIONAL VON MOSES DISTRIBUTION

The probability density function of the von Mises distribution is given by:

$$f(\phi) = \frac{e^{\kappa \cos(\phi - \mu)}}{2\pi I_0(\kappa)} \quad (\text{A1})$$

where ϕ is the phase ($-\pi < \phi < \pi$), μ and $1/\kappa$ are analogous to the mean and variance of the normal distribution respectively and $I_0(\kappa)$ is the zero-order modified Bessel function. In two dimensions, circular variables can be represented as a probability distribution on a torus and a convenient parallel to the bivariate normal distribution is given by the two dimensional von Mises distribution whose probability density function is given by Singh et al. (2002):

$$f(\phi, \psi) = \frac{1}{C} e^{\kappa_\phi \cos[(\phi - \mu_\phi)] + \kappa_\psi \cos[(\psi - \mu_\psi)] + \lambda \sin[(\phi - \mu_\phi)] \sin[(\psi - \mu_\psi)]} \quad (\text{A2})$$

where C is a normalizing constant and λ is a parameter describing the statistical dependency between the two distributions ϕ and ψ . Concentration values of, κ , were defined so that $\kappa_\phi = \kappa_\psi$ and the values used in the simulations were [0.25, 0.5, 1, 2, 4, 8]—see **Figure 2**. The mutual information, $I_{\phi\psi}$, between distributions depended upon λ and κ and could be estimated accurately through numerical integration (Hnizdo et al., 2008). Values of λ were selected for each value of κ , that generated distributions with mutual information values of [0, 0.0204, 0.0872, 0.2231, 0.5108]. For convenience, mutual information values were converted to putative correlation values by the relationship $r = \sqrt{1 - e^{-2I_{\phi\psi}}}$ giving values of [0, 0.2, 0.4, 0.6, 0.8] respectively.



Operationalizing interdisciplinary research—a model of co-production in organizational cognitive neuroscience

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There is a biological turn in order to understand the underlying processes concerning markets and organizations. As part of the biological turn, in 2008, I wrote an article for the *Journal of Consumer Behavior* about neuromarketing and the perceptions of knowledge (Butler, 2008). The argument put forward in the article is that there are inter-related and potentially competing perspectives which combine to make up the biological turn. In order to conceptualize these varied perspectives I introduced a novel Neuromarketing Research Model. This commentary is concerned with updating the Model and using it to reveal some of the current intersections between society, organizations and the brain.

By taking this approach, I want to supplement David Waldman's opinion article in this special issue titled "Interdisciplinary research is the key." Waldman (2013) argues that organizational sciences are rapidly coming together with neuroscience theory and methods to provide new insights into organizational phenomena, especially the larger problems facing organizations. I add to this argument by identifying specific points of how organizations and neuroscientists are coming together, and operationalize interdisciplinary research by proposing a new Model of Co-Production in Organizational Cognitive Neuroscience (OCN). OCN is defined as the application of neuroscientific methods to analyse and understand human behavior within the applied setting of organizations, which may be at the individual, group, organizational, inter-organizational, and societal levels. OCN draws together all the fields of business and management in order to integrate understanding about human behavior in organizations and to more

fully understand social behavior (Butler and Senior, 2007).

I will re-introduce the purpose of the original Neuromarketing Research Model and state why it fits with this collection of papers, then I will briefly describe the Model in more detail. This will be followed by revising the Model to capture developments in OCN since 2008, and by using the updated Model to cohere different and fundamental themes and directions at the frontier of human neuroscience.

HUMAN MODES OF PERCEPTION IN ORGANIZATIONAL COGNITIVE NEUROSCIENCES

The purpose of connecting neuromarketing and the perception of knowledge was to address the perennial concern about the interconnection between research and practice, and the different perceptions about the development and application of knowledge about neuromarketing. This concern is implicit in the theme of society, organizations and the brain. Basic human neuroscience research in the field of management and organizations is likely to be applied to practitioners through knowledge exchange processes.

I used Jacob Bronowski and Kant to connect neuromarketing and the perception of knowledge. In 1967, Bronowski profoundly argued that it is pointless to talk about what the world is like when the modes of perception of the world which are accessible to us have changed so much (Bronowski, 1978). By the role of perception Bronowski (1978) took a Kantian view which argues that our knowledge of the outside world depends on our human modes of perception.

Nearly fifty years on from Bronowski's lecture series, our modes of perception have moved on again—neuroscience as

a field of study has emerged. As a consequence, a Neuromarketing Research Model was proposed. The Model was developed from the work of Stokes (1997) and Tushman et al. (2007; Tushman and O'Reilly, 2007). Tushman et al. (2007; Tushman and O'Reilly, 2007) adapted Stokes' (1997) work to inform the debate about the role of business school research. Tushman et al. (2007; Tushman and O'Reilly, 2007) argue that unlike conventional academic disciplines which focus on basic disciplinary research (economics, psychology, and sociology) and consulting firms which focus on meeting clients' needs, business schools are about rigor and relevance. Whilst agreeing with Tushman et al.'s (2007; Tushman and O'Reilly, 2007) argument, their model is problematic because it compresses the range of business school activity into a narrow set of behaviors concerning research and its application.

In its place, the Neuromarketing Research Model interconnected different perceptions of neuromarketing knowledge. Basic research reporting satisfies the needs of academics and applied research reporting the needs of employers (Doherty, 1994). Media reporting is less definitive because it satisfies the needs of the target audience for the publication, which could be academic or practice-based. Similarly, power processes is less definitive because they satisfy the needs of dominant actors in the networks identified here by knowledge becoming ideological and biased in favor of particular actors through a conflictual process (Clegg and Palmer, 1996; Stiles, 2004). Waldman (2013) dedicates a section in his article to institutional and personal impediments hindering the application of neuroscience

to his own area of expertise, leadership in organizations.

A MODEL OF CO-PRODUCTION IN ORGANIZATIONAL COGNITIVE NEUROSCIENCE

This commentary proposes a new Model of Co-Production in OCN because our modes of perception have moved on still further (Figure 1). The components of the original Model remain in place (in bold text). There are, however, four substantial changes. First, this commentary emphasizes the rigorous quest for understanding OCN rather than those which are less rigorous, in other words, the presentation of OCN work which reassures readers that appropriate methods and approaches have been adopted. Second, the new Model has additional elements to capture the emergent complexities at the intersection between society, organizations, and the brain. The new cells have dotted line divisions to indicate that they are sub-divisions of the four main quadrants described in the previous section: Basic Research Reporting, Applied Research Reporting, Media Reporting, and Power Processes. Third, because human neuroscience is being applied more widely across management and organizations, going beyond neuromarketing and neuroeconomics, the examples used in the following sections reflect this expansion of application. Fourth, the term “co-production” is used to describe the model.

Co-production is derived from a mode 2 approach to researching management and organizations (Gibbons et al., 1994).

Knowledge is produced in the context of a real-world problem and the theoretical development is co-negotiated with practitioners. The Model of Co-Production in OCN reflects this intersection, highlighting both rigor and relevance, or the quest for fundamental understanding and the conditions of use. Indeed, university-organization relationships provide a productive setting for knowledge exchange research (Perkmann and Walsh, 2007). Waldman (2013) expresses this approach in his article stating he has had much more success at connecting with neuroscientists who combine the scientist-practitioner model, including establishing their own firms to produce applications to such maladies as attention deficit disorder and sleep apnea.

Waldman’s (2013) point fits within the Applied Research Reporting quadrant of Figure 1, the university spinout cell. The quadrant as a whole emphasizes that practitioners are mindful of the need for scientific rigor and ethical considerations in human neuroscience work. Commercial success, whether a university spinout or another type of commercial enterprise, depends on clients having confidence in the results they are presented with and confidence comes from rigor and ethical practice (Brammer, 2004).

My focus is the intersection between Basic Research Reporting and Power Processes. In my original article, I noted that most attention is being given to basic research reporting because foundational research is currently being undertaken. The debates have become much more

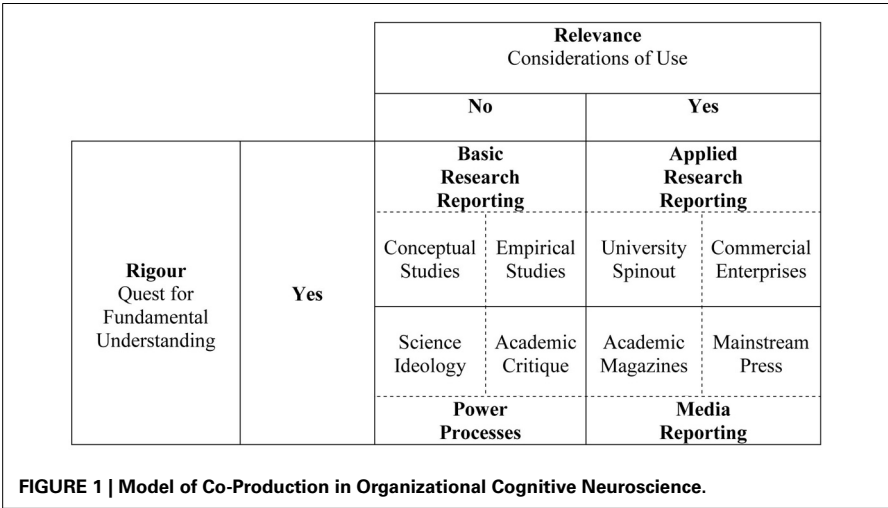
nuanced over the last 5 years and the new Model of Co-Production in OCN divides Basic Research Reporting into two further cells to take account of the wealth of conceptual articles and the growing empirical research. Conceptual debates are now appearing in established management and organization journals like the Journal of Management, and the journal web site has dedicated space to emphasize the emerging conversation about human neuroscience in the context of management (see Becker et al., 2011; Lee et al., 2012a).

In addition, special issues of highly regarded academic journals like the Leadership Quarterly capture specific themes at the intersection between organizations and the brain. Crucially, this allows conversations about OCN and leadership to involve both conceptual and empirical studies which include rigorous data collection and analysis (see Lee et al., 2012b). An illustrative empirical piece is Boyatzis et al. (2012), which examines the neural substrates activated in memories of experiences with resonant and dissonant leaders.

The intersection between the Basic Research Reporting and the Power Processes quadrants is crucial to the development of frontier research. As the number of published conceptual and empirical studies in the field of OCN grows, so does the academic critique of the OCN perspective. Rigorous and relevant debate advances OCN. This avoids knowledge, including emerging science theories like OCN, becoming ideological and biased in favor of particular actors through a conflictual process (Callon et al., 1986; Clegg and Palmer, 1996; Stiles, 2004).

Edwards (2013) introduces a realist critique of OCN. The argument being that it is important to consider how mental processes interact with “context” to produce social behavior. The Model of Co-Production in OCN is one manifestation of the interaction between the micro and macro levels. More generally, in the field of strategy implementation, my work explicitly acknowledges that different levels of change are co-evolving and dynamic (Butler, 2003; Butler and Allen, 2008).

Lindebaum and Zundel (2013a) rightly maintain that without explicit consideration of, and solutions to, the challenges of



reductionism, the possibilities to advance leadership studies theoretically and empirically are limited. By reductionism they mean that neuroscientific approaches identify and analyze basic mechanisms that are assumed to give rise to higher order organizational phenomena, for instance, the way that inspirational leaders are identified and developed. In a lively exchange, Lindebaum (2012) and Cropanzano and Becker (2013) discuss the relative merits of neuro-feedback processes for the purpose of leader development and the ethical implications.

In terms of the Model of Co-Production in OCN, the previous discussion has an important implication for Basic Research Reporting—the danger of informing organizational practice inadequately and perhaps dangerously. As Edwards (2013) indicates, OCN can lend itself to over-interpretation, especially where scholars wish to find a simple and unique truth.

There is a similar implication for Media Reporting. The mainstream press can popularize ideas related to OCN and in doing so over-simplify complex research. Hannaford (2013), though, includes relevant research from leading institutions like the Max Planck Institute to support the argument in his newspaper article. Lindebaum and Zundel's (2013b) recent article in the academic magazine *Times Higher Education* also helps to re-balance popular perceptions of OCN.

CONCLUDING REMARKS

We are further along the lifecycle of the new field of study of OCN. Fugate (2007) argues that in order for OCN to become legitimized, it would be necessary to construct a behavioral model that would predict which stimuli provide the appropriate brain structure with the material it needs to accomplish its assigned task. We seem some distance from a behavioral model.

Nevertheless, this commentary has captured how research reporting within OCN is advancing, by proposing the Model of Co-Production in OCN. In particular, different themes and directions of research are found at the intersection between Basic Research Reporting and Power Processes. These debates, however, are also migrating into Applied Research Reporting and Media Reporting. This can only advance

OCN. A variety of voices rigorously and relevantly debating OCN will advance this particular frontier in human neuroscience through the critique of emergent ideas.

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Dehumanization in organizational settings: some scientific and ethical considerations

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Dehumanizing attitudes and behaviors frequently occur in organizational settings and are often viewed as an acceptable, and even necessary, strategy for pursuing personal and organizational goals. Here I examine a number of commonly held beliefs about dehumanization and argue that there is relatively little support for them in light of the evidence emerging from social psychological and neuroscientific research. Contrary to the commonly held belief that everyday forms of dehumanization are innocent and inconsequential, the evidence shows profoundly negative consequences for both victims and perpetrators. As well, the belief that suppressing empathy automatically leads to improved problem solving is not supported by the evidence. The more general belief that empathy interferes with problem solving receives partial support, but only in the case of mechanistic problem solving. Overall, I question the usefulness of dehumanization in organizational settings and argue that it can be replaced by superior strategies that are ethically more acceptable and do not entail the severely negative consequences associated with dehumanization.

Keywords: dehumanization, empathy, problem solving, reasoning, beliefs, ethics, medicine, decision making

INTRODUCTION

Dehumanizing attitudes and behaviors frequently occur in organizational settings and are often viewed as an acceptable, and even necessary, strategy for pursuing personal and organizational goals. Behind this view, there lie a number of commonly held beliefs about dehumanization. These beliefs are culturally determined, rather than based on scientific observation. One such belief is that subtle forms of dehumanization, such as disrespect, condescension, and neglect, are innocent and inconsequential. It is also commonly believed that empathy interferes with problem solving and that therefore, suppressing our naturally occurring empathy, and the dehumanization this suppression entails, are necessary to help us make better decisions and improve our problem solving capacity.

Are those beliefs supported by the scientific evidence? Here I review social psychological and neuroscientific advances on dehumanization and show that a number of our beliefs about dehumanization are not supported by the evidence. Although the belief that empathy interferes with problem solving is partially supported, the scientific evidence on this is very new and still contentious. Overall, I question the usefulness of dehumanization in organizational settings and argue that it can be replaced by superior strategies that are ethically more acceptable and do not entail the severely negative consequences that are often associated with dehumanization.

DEHUMANIZATION AS AN EVERYDAY PHENOMENON

Early psychological theories viewed dehumanization as an extreme phenomenon, occurring primarily in the context of

ethnic or racial intergroup conflict (Kelman, 1976; Staub, 1989; Opatow, 1990). More recently, however, an expanded view of dehumanization has emerged. This expanded view recognizes that dehumanization can occur in interpersonal as well as intergroup contexts, and is not limited to conditions of overt conflict (for review see, Haslam and Loughnan, 2014). Instead, dehumanization appears to be an everyday social phenomenon, rooted in ordinary social-cognitive processes (Haslam, 2006).

How do people dehumanize others? When someone is dehumanized, they are implicitly or explicitly perceived as lacking qualities that are considered to be characteristically human. According to Haslam's (2006) dual model of dehumanization, there are two forms of dehumanization corresponding to two different forms of humanness being denied. One is an "animalistic" form of dehumanization in which humans are denied qualities that are considered to distinguish them from animals—qualities such as refinement, self-control, intelligence, and rationality. This form of dehumanization is often discussed in the context of ethnicity, race, and related topics such as immigration and genocide (e.g., Kelman, 1976; Chalk and Jonassohn, 1990).

Dehumanization can also take a "mechanistic" form in which humans are likened to objects or automata and are denied qualities such as warmth, emotion, and individuality (Haslam, 2006). Such "mechanistic" dehumanization is more likely to occur in interpersonal interactions and organizational settings. It is frequently discussed in the contexts of technology (Montague and Matson, 1983), medicine

(Szasz, 1973; Fink, 1982; Barnard, 2001), and other domains such as sexual objectification (Fredrickson and Roberts, 1997; Nussbaum, 1999) in which people are often perceived as inert or instrumental.

Dehumanization can also range from blatant and severe to subtle and relatively mild (Haslam and Loughnan, 2014). Such relatively mild dehumanizing behaviors can manifest themselves in the form of subtle disrespect, condescension, neglect, social ostracism and other relational slights (Bastian and Haslam, 2011), often only evident in looks, gestures, and tones of voices. These subtle, everyday forms of dehumanization are often viewed as innocent and inconsequential (e.g., Sue et al., 2007). How does this view compare to the scientific evidence?

THE NEGATIVE CONSEQUENCES OF EVERYDAY DEHUMANIZATION

There is overwhelming evidence for the wide-reaching negative consequences of relatively mild dehumanizing attitudes and behaviors. Dehumanizing others leads to increased anti-sociality towards them in the form of increased aggressive behaviors such as bullying (Obermann, 2011) and harassment (Rudman and Mescher, 2012), as well as hostile avoidance behaviors such as social rejection (Martinez et al., 2011). This increased hostility and aggression are accompanied by reduced moral worth attributed to those who are dehumanized (Opatow, 1990; Haslam and Loughnan, 2014) and they are therefore judged less worthy of protection from harm (Gray et al., 2007; Bastian and Haslam, 2011). The perpetrators of such interpersonal maltreatments themselves may experience negative emotions such as guilt and shame (Baumeister et al., 1995; Tangney et al., 1996), which may lead to even stronger dehumanizing attitudes towards their targets in an attempt to downplay their suffering and justify their maltreatment. Such dehumanization in response to guilt has been demonstrated in intergroup contexts (Castano and Giner-Sorolla, 2006). A vicious cycle may emerge, whereby dehumanization promotes maltreatment and aggression, which further promotes dehumanization.

The negative consequences for those who are dehumanized are also striking. Everyday interpersonal maltreatments can leave its victims feeling degraded, invalidated, or demoralized (Hinton, 2004; Sue et al., 2007). There is extensive research into the negative consequences of being denied autonomy (Ryan and Deci, 2000), betrayed (Finkel et al., 2002), humiliated (Miller, 1993), socially excluded (Baumeister and Leary, 1995; Twenge et al., 2007), or not recognized as a person (Honneth, 1992)—all situations that are likely to be experienced as dehumanizing (Bastian and Haslam, 2011).

When people are mechanistically dehumanized by being treated as objects, as means to an end, or as lacking the capacity for feeling, they tend to enter into “cognitive deconstructive” states that are characterized by reduced clarity of thought, emotional numbing, cognitive inflexibility, and an absence of meaningful thought (Twenge et al., 2003; Bastian and Haslam, 2011). Experiencing this form of dehumanization leads to pervasive feelings of sadness and anger. Also dehumanizing are status-reducing interpersonal maltreatments such as condescension, degradation, or being treated as embarrassing, incompetent, unintelligent, or

unsophisticated (Vohs et al., 2007), which lead to feelings of guilt and shame (Bastian and Haslam, 2011).

Such dehumanizing maltreatments are likely to have a detrimental effect on psychological wellbeing. According to self-determination theory (Ryan and Deci, 2000), psychological wellbeing requires that the basic psychological needs of autonomy, competence, and relatedness are met. Dehumanizing maltreatments, however subtle, lead to impaired ability to satisfy these needs and may therefore directly contribute to mental illnesses such as depression, anxiety, and stress-related disorders. In short, the scientific evidence does not support the view of everyday dehumanization as an innocent and inconsequential phenomenon; on the contrary, the evidence clearly demonstrates a range of significant negative consequences.

THE RELATIONSHIP BETWEEN EMPATHY AND PROBLEM SOLVING

Another commonly held view about dehumanization concerns the relationship between empathy and problem solving. According to this view, there is a trade-off between empathy and problem solving (e.g., Haque and Waytz, 2012) and the two are mutually incompatible; therefore, suppressing empathy is necessary for effective problem solving. To what extent does psychological and neuroscientific research support this view?

Human thinking and problem solving can be said to occur in two distinct domains: the physical domain, which involves reasoning about the mechanical properties of inanimate objects, and the social domain, which involves thinking about the mental states of others (Jack et al., 2012)—a process also known as “mentalizing” (Frith et al., 1991). Psychological and neuroscientific research shows that empathy—or our capacity to recognize other people’s emotions—is not only compatible with problem solving in the social domain, but that it is also crucial for it (Amodio and Frith, 2006; Harris and Fiske, 2006). On the other hand, is there evidence that empathy is incompatible with problem solving in the physical domain?

A distinction between social and physical problem solving has been suggested at the neural level. Social reasoning about the mental states of others is associated with increased recruitment of the brain’s “default” network and reduced recruitment of the so called “task-positive” network; conversely, “mechanistic” reasoning about physical objects appears to be associated with increased recruitment of the “task-positive” network and reduced recruitment of the “default” network (Jack et al., 2012). Although these two networks are involved in multiple processes and the specificity of their function is still under much debate, they appear to be frequently anti-correlated during conditions of “rest” (Fox et al., 2005) and during many standard cognitive tasks (Shulman et al., 1997).

Anti-correlations between the “default” and the “task-positive” networks were originally interpreted to indicate that the two networks function in opposition to each other and are marked by a negative reciprocal relationship (e.g., Fox et al., 2005). More recently however, neuroscientists have realized that the exact nature of the neural relationship between these two networks is much more complex than a simple obligatory negative reciprocity

(e.g., Spreng et al., 2010; Boyatzis et al., 2014). Positive correlations or lack of anti-correlations between the two networks have been observed during creative thinking (Ellamil et al., 2011), mind-wandering (Christoff et al., 2009), and naturalistic film viewing (Golland et al., 2007). Furthermore, it has become apparent that reduced recruitment in one network does not necessarily lead to increased recruitment in the other. With specific relevance to dehumanization, reductions in “default” network recruitment have been observed in the absence of change in recruitment of “task-positive” regions (Jack et al., 2013). While this field is new and still growing, the neuroscientific evidence so far does not support the notion that reduced empathy (or dehumanization) automatically and necessarily leads to improved mechanistic reasoning at the cognitive level.

There is some evidence, however, that the social and physical domains may become incompatible at higher levels of reasoning complexity. The process of relational integration, or considering multiple relations simultaneously, characterizes complex forms of reasoning (Halford et al., 2010) and is specifically associated with increased recruitment of rostralateral prefrontal cortex (RLPFC) during problem solving in both the physical (e.g., Christoff et al., 2001) and social (Raposo et al., 2011) domains. Problem solving in the two domains may, therefore, become incompatible at higher levels of reasoning complexity due to competition for access to the same neural and cognitive resources.

In short, scientific evidence suggests that the distinction between reasoning in the social and physical domains may be crucial for determining the relationship between empathy and problem solving. In the social domain, empathy is not only compatible with problem solving; it is a crucial component of reasoning about other people’s mental states. In the physical domain, on the other hand, there is some suggestive evidence that empathy and mechanistic problem solving may interfere, especially at higher levels of reasoning complexity (see also Dixon et al., 2014). However, the notion that reductions in empathy automatically lead to improved mechanistic problem solving is not supported by the evidence.

QUESTIONING THE USEFULNESS AND ETHICS OF DEHUMANIZING STRATEGIES

Dehumanization is sometimes presented as both necessary and beneficial. For example, it has been argued that dehumanization and moral disengagement allows physicians to inflict pain on their patients—pain which is sometimes necessary for diagnosis and treatment (Lammers and Stapel, 2011; Haque and Waytz, 2012). This argument has been extended beyond medical contexts, to argue that dehumanization in general helps people in position of power to make “tough” decisions that may cause pain and suffering for others; it helps by allowing such decisions to be made in a more distant, cold, and rational manner (Lammers and Stapel, 2011). It has also been argued that by dehumanizing patients, health care workers can “protect” themselves against “burnout” from the emotional demands of working with suffering patients (Vaes and Muratore, 2013), and that mechanistic dehumanization of patients in the form of “decomposing people and their symptoms into physiological systems and subsystems” is

necessary for “higher level” medical problem solving (Haque and Waytz, 2012).

Whether such “functional” dehumanization is a truly beneficial strategy, however, is highly questionable. It is true that physicians sometimes need to inflict pain on their patients through diagnosis and treatment, but if this pain is necessary for the reduction in the patient’s overall suffering, physicians could mentally focus on this overall improvement as a way of coping. Dehumanizing their patients seems, in comparison, a much more negative and, arguably, much more *dysfunctional* way of coping—especially considering the profoundly negative consequences it can have for the doctor-patient relationship (Benedetti, 2011). Similarly, avoiding burnout in health care workers can be achieved without requiring them to dehumanize their patients; instead, health care workers could be provided with reduced workload and better support. Furthermore, continually having to suppress their naturally occurring empathic response may create an additional form of stress in some health care workers. Alternative forms of emotional regulation (Gross, 1998; Grandey, 2000) may help reduce health care workers’ stress with fewer costs to themselves and their patients. Overall, the argument that dehumanization helps health care workers provide “better care” (Vaes and Muratore, 2013) only makes sense if “care” itself is understood in a dehumanized mechanistic sense.

It is also true that people in position of power sometimes have to make “tough” decisions that may cause pain and suffering for others. The difficulty in such “tough” decisions, however, comes from their moral nature and the ethical dilemmas they present. Moral reasoning and decisions making by definition require that we use our emotions and our experiences of being human—emotional and otherwise. Dehumanizing those about whom we are making a moral decision would of course eliminate the moral elements of the decision making process (and therefore make it “easier” for the decision maker), but it should also raise some serious ethical concerns. A much more constructive and ethically acceptable way to ease the burden of such difficult moral decisions would be to relieve the person in power of the decision making responsibility and to place it where it rightfully belongs: with the person who will bear the greatest consequences of the decision. In medical contexts, this person would be the patient (or the patient’s chosen substitute decision maker). On the rare occasions when a patient is unable to make such decisions and there is no available substitute decision maker, physicians could seek moral support and advice from others and could allow the necessary time and emotional expenditure it takes to respect the moral and ethical nature of medical decision making.

As well, the argument that mechanistic dehumanization, in the sense of reducing patients to their symptoms and body parts, is necessary for medical problem solving rests on an outdated and largely discredited “biomedical” model of disease. The narrow, exclusive focus on anatomical, physiological, and molecular mechanisms within this “biomedical” model has been criticized and rejected in favor of the much broader “biopsychosocial” model of disease and recovery (Engel, 1977; Benedetti, 2011), which requires that psychological and social factors are included alongside biological factors in medical diagnosis

and decision making. Within this newer model, dehumanization would be expected to *impair* medical problem solving by causing the relevance of psychological and social factors to be neglected.

Thus, viewing dehumanization as “functional” and beneficial only makes sense within a very narrow and mechanistic context. What appears “functional” within this narrow context, appears clearly dysfunctional from a broader and more humanized perspective. Far from being necessary, dehumanization in medical contexts can be replaced by superior strategies that are ethically much more acceptable and do not entail the negative consequence that become apparent when dehumanization is viewed from a broader perspective.

CONCLUSIONS

Many of our beliefs about the role of dehumanization are based on implicit empirical claims that can be examined in light of the scientific evidence. Here I examined a number of such beliefs and found relatively little support for them. First, contrary to the commonly held belief that everyday forms of dehumanization are innocent and inconsequential, the evidence shows profoundly negative consequences of such milder forms of dehumanization for both victims and perpetrators. Second, the belief that reductions in empathy automatically lead to improved mechanistic problem solving is not supported by the evidence. Third, the belief that empathy is incompatible with problem solving is partially supported by the evidence, but only if “problem solving” is equated with mechanistic reasoning about inanimate objects in the physical domain. If problem solving is instead equated with mentalizing, or social reasoning about other people’s mental states, this belief is contradicted by the evidence which shows that empathy is a necessary and a crucial element of problem solving in the social domain. Overall, there seems to be a need to reassess our beliefs about the role of dehumanization in organizational settings.

Dehumanization in organizational settings is a highly complex phenomenon with far-reaching implications, from individual, to societal, to global environmental levels. Although scientific evidence can be brought to bear in examining the validity of commonly held beliefs in this area, the present analysis also shows that many of those beliefs carry significant moral and ethical implications. Furthermore, those beliefs may also have implicit normative aspects that have remained unexamined so far.

An interesting case of a complex mixture of an empirical claim and an implicit normative statement may be presented by the argument that suppressing empathy is necessary for problem solving in organizational settings. There is empirical evidence in support of this argument, but only if “problem solving” is reduced to problem solving in the physical domain (i.e., mechanistic problem solving about inanimate objects). Therefore, this argument privileges the value of mechanistic problem solving over the value of problem solving in the social domain, thus making an implicit normative statement. In other words, when employees are encouraged to suppress empathy and focus on “getting the job done”, they are also given the message that mechanistic problem solving is more efficient at getting the job done than empathy or mentalizing. Such implicit normative statements may sometimes

lie at the basis of what may appear to be empirically-based arguments.

Recognizing the co-existence of empirical and normative bases of our beliefs about dehumanization can help us develop a more effective approach to their critical examination. While the empirical basis of our beliefs, when identified, can be examined in light of findings from scientific research, the normative aspects of our beliefs are beyond the scope of scientific evidence. Instead, they need to be assessed from ethical, philosophical, and legalistic perspectives. Only an integrated approach that brings together these multiple levels of analysis can help us achieve what seems to be an insurmountable and yet a vitally important task: the humanization of our organizations and, ultimately, the re-humanization of our society.

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Cognitive requirements of competing neuro-behavioral decision systems: some implications of temporal horizon for managerial behavior in organizations

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Interpretation of managerial activity in terms of neuroscience is typically concerned with extreme behaviors such as corporate fraud or reckless investment (Peterson, 2007; Wargo et al., 2010a). This paper is concerned to map out the neurophysiological and cognitive mechanisms at work across the spectrum of managerial behaviors encountered in more day-to-day contexts. It proposes that the *competing neuro-behavioral decisions systems (CNBDS) hypothesis* (Bickel et al., 2012b) captures well the range of managerial behaviors that can be characterized as hyper- or hypo-activity in either the limbically-based impulsive system or the frontal-cortically based executive system with the corresponding level of activity encountered in the alternative brain region. This pattern of neurophysiological responding also features in the Somatic Marker Hypothesis (Damasio, 1994) and in Reinforcement Sensitivity Theory (RST; Gray and McNaughton, 2000; McNaughton and Corr, 2004), which usefully extend the thesis, for example in the direction of personality. In discussing these theories, the paper has three purposes: to clarify the role of cognitive explanation in neuro-behavioral decision theory, to propose picoeconomics (Ainslie, 1992) as the cognitive component of competing neuro-behavioral decision systems theory and to suggest solutions to the problems of imbalanced neurophysiological activity in managerial behavior. The first is accomplished through discussion of the role of picoeconomics in neuro-behavioral decision theory; the second, by consideration of adaptive-innovative cognitive styles (Kirton, 2003) in the construction of managerial teams, a theme that can now be investigated by a dedicated research program that incorporates psychometric analysis of personality types and cognitive styles involved in managerial decision-making and the underlying neurophysiological bases of such decision-making.

Keywords: organizational management, decision-making, neuro-behavioral decisions systems, cognitive style, adaption-innovation, picoeconomics

INTRODUCTION

Organizational dysfunction has numerous outcomes, from the lack of an appropriate fit between the organization and its environment, through the inappropriate composition of task-based management teams, to the incompatible predispositions and behavioral styles of individual managers. This paper is concerned with the neurophysiological underpinnings of managerial behaviors, in particular with the implications these have for the styles of decision-making and problem-solving managers adopt and their appropriateness for the tasks in hand. Although the neurophysiological basis of behavior in organizations has attracted considerable research attention of late (e.g., Butler and Senior, 2007a,b; Lee et al., 2007; Lee and Chamberlain, 2007), there has been some tendency to address particular aspects of managerial behavior such as trust, cooperation and conflict, reward processing and social interaction rather than to seek a broader framework of conceptualization and analysis for this central aspect of organizational functioning. Worthy as these themes are, this

paper proposes that the competing neuro-behavioral decision systems hypothesis (Bickel and Yi, 2008) captures the neurological bases of forms of managerial excess that engender a pathological tendency to avoid risk on one hand and a more reckless tendency to discount the future consequences of current actions on the other.

Theories of managerial behavior and, in particular, prescriptions that derive from them, require a cognitive understanding of the nature of decision-making. The competing neuro-behavioral decisions systems (CNBDS), in common with other neurophysiological accounts of behavior, tend not to have a well-developed cognitive level of exposition. The paper, therefore, examines picoeconomics (Ainslie, 1992), which is similarly couched in terms of temporal discounting, as a candidate for the cognitive component of neuro-behavioral decision theory. Although there is a strong fit, however, picoeconomics provides prescriptions for dealing with the excesses of managerial behavior which befit clinical interventions but are not easily

implementable in the context of organizational functioning. In order to overcome this problem, two complementary areas of cognitive-behavioral interaction are examined with a view to increasing understanding of the cognitive component of behavior and suggesting managerial prescriptions, especially for team-building. These are RST (Corr, 2008a) and Adaption-Innovation Theory of cognitive style (Kirton, 1976, 2003), both of which rest on neurophysiological bases that overlap with those on which neuro-behavioral decision theory rests and contribute to the cognitive articulation of the CNBDS hypothesis and the suggestion of meliorating action.

Section Management, Decisions and Cognition discusses the different kinds of management decision and relates them to their possible underlying neurophysiological bases. It also raises the need for clarification of the cognitive dimension of existing theories of neuro-behavioral decision systems and the necessity for managerial application. Section Competing Decision Systems describes the CNBDS hypothesis in detail and relates it to RST and the relevance to managerial decision-making of managers' temporal horizons. Section The Cognitive Dimension introduces in detail the necessity of a cognitive component of the CNBDS hypothesis and the philosophical implications of speaking of cognition. It lays out criteria for a suitable cognitive component including the necessity of a cognitive theory that proceeds at the personal level of exposition, an intentional account, and potential integration with the economic bases of CNBDS theory, and a close relationship to the basic disciplines in terms of which the theory is couched. Section The Cognitive Dimension also proposes picoeconomics (Ainslie, 1992) as a suitable basis for the cognitive component of neuro-behavioral decision theory and evaluates it in terms of these criteria.

The question of appropriate prescriptions for organizational management is raised in Section Organization-Level Strategies for Changing Managerial Behavior. Although picoeconomics provides insight into the nature of dysfunctional decision-making, its prescriptions are couched in clinical terms and are directed towards the amelioration of addictive behavior. The paper turns, therefore, to the conceptualization of managerial behavior in terms of adaptive-innovative cognitive style (Kirton, 2003) which has broadly similar neurophysiological foundations but which comes equipped with clearer implications for organizational team-building and management. The theory also has implications which are discussed for the understanding of commonplace terms such as strategy, innovation and structure. Overall, the integration of neuro-behavioral decision systems with picoeconomics, RST and adaptive-innovative cognitive style suggests a theory of managerial behavior in organizations which comprehends and proposes means of overcoming problems of dysfunction due to inappropriate temporal horizons (Foxall, 2010).

MANAGEMENT, DECISIONS AND COGNITION

KINDS OF MANAGEMENT DECISION

Some managerial behaviors patently fail to achieve the goals of the organization in which they are performed, leading often to the downfall of the managers who are responsible for them and sometimes to the failure of the entire organization in which the

arise. The hasty shredding of documents of forensic significance, for instance, which has recently figured in more than one dramatic wind-up of a corporation is maladaptive not only for the stakeholders but for the firm itself as a continuing legal entity. For the managers employed by the organization, whether or not they were involved in the termination with extreme prejudice of the documents involved, the maladaptive actions of a few may mean at the very least the interruption of careers. The apparent greed and excessive seeking of immediate reward that accompanied and partially caused the financial crisis of 2008 provides another graphic illustration of the catastrophic effects of maladaptive managerial behavior (Wargo et al., 2010a). This extreme form of maladaptive managerial behavior illustrates vividly the immediacy that motivates some actions within organizations (Peterson, 2007). The informed planning of long-term business operations, in the absence of intrusions caused by short-term concerns, and the timely implementation of strategic intentions, represent the opposite extreme.

It is most probable that neither of these scenarios will figure in the careers of most managers but temporal horizons nevertheless are the hallmark of most managerial activities. Some are most accurately characterized as impulsive; others as planned. This categorization does not correspond exactly to the idea of functional decisions on the one hand, those that meet the goals of the organization and its members, versus dysfunction decisions on the other, those that have outcomes that are contrary to such goals. But it seems reasonable to argue that the majority of impulsive decisions have some dysfunctional consequences, while the majority of planned decisions are functional in the sense defined. It is not helpful to write off the dysfunctional behavior as simply "irrational": it has its own logic and we should seek its causes just as we seek those of its antithesis. A unified neuroscientific framework within which to pursue these ends is required. First, however, it is necessary to define more closely the range of decisions with which we are concerned.

Two classifications of decisions have proved remarkably resilient and are particularly relevant to the present discussion because they are closely related to temporal horizons: administrative, operating and strategic decisions (Ansoff, 1965) and Simon's (1965) distinction between programmed and non-programmed decisions. Administrative decisions tend to be routine and to have short time frames. Strategic decisions are, by contrast, long-term and concern the product-market scope of the enterprise, which involves such considerations as diversification policy, the definition of the business, the nature of customer behavior now and in the future, and the integration of the key business areas, namely marketing and innovation (Drucker, 2007). Operating decisions are derived from strategic decisions that have been taken and entail the implementation not only of current interfaces with the business environment, such as the management of marketing mixes, but also the implementation and management of appropriate administrative practices. Programmed decisions are those that are sufficiently routine to have attracted tried and tested, rule-of-thumb decisions systems; so predictable and delegable are these matters that some authorities question whether they entail decision-making at all. Non-programmed decisions are those that arise *de novo* in

the wake of required responses to unstructured situations: new governmental regulations, novel market requirements, radical changes in a competitor's behavior, and so on. These are generally top-management responsibilities.

Although it is true that most administrative decisions are well-programmed, most strategic decisions non-programmed, and operating decisions a mixture of the two, there are programmed and non-programmed aspects of all three types of decision identified by Ansoff. The key question is what level of management is likely to be involved in each decision type. By and large, administrative decisions can be delegated and taken therefore by relatively junior managers. The repetitiveness that characterizes them suggests that they entail a limited temporal purview which recurs each time they are taken. Indeed, given the extent to which they can be programmed, it is arguable that they are not decisions at all. Strategic decisions are almost by definition unprogrammable and are the domain of senior managers responsible for the overall policy, strategic scope and strategic direction of the enterprise. These decisions, which entail very long-term perspectives on how the firm will develop are almost by definition made in a context of uncertainty. They of course have implications for the administrative and operating decisions that flow from them. Operating decisions are typically the province of middle managers. Although they refer to a time period when relatively accurate assumptions can be made about the product and factor markets in which the firm operates, they are subject to unpredictable fluctuations, e.g., in the behavior of competitors, which necessitate one-off tactical decisions. The temporal horizons of such decisions may vary from the immediate future to short market cycles.

Another way of looking at these decisions is that administrative and to a large extent operating decisions have a pre-existing framework of conceptualization and analysis within which they can be resolved as they arise; in the case of genuinely strategic decisions, it is necessary to construct such a framework coterminously with the initial decision process. It also has to be recognized that once strategic decisions have been made and a suitable decision framework established, the managerial work involved in such decisions takes on an increasingly routine aspect. It is a myth to think that strategic decision-making involves a root and branch analysis of opportunities and capabilities with each planning cycle: many strategic decisions are made recurrently with only small changes in managerial outlook involved on each occasion. This is of course, given the changing market, technological and competitive environments that are the context of such decisions, a source of danger if the firm fails to monitor its strategic space.

From the point of view of the organization, the overall object with respect to decision-making will be to reach an acceptable balance among administrative, operating, and strategic decision-making so that each kind of decision is made in a timely manner and coordinated with the taking of the other kinds of decision. This state of affairs will ensure that conflict between short-term and long-term organizational goals is minimized. Most analyses of managerial decision-making take this purview. But the social cognitive neuroscience approach to organizational behavior makes it possible to discuss the tensions arising within individual managers' behavior patterns that makes them more or less suited

to undertake the decision tasks we have identified. This does not of course mean anything so simplistic as that there are some managers who are predisposed by their limbic systems to make programmed decisions while others have a propensity to make strategic decisions because of their advanced executive functions (EFs). But what the explanation of managerial behavior in terms of the CNBDS hypothesis (Bickel et al., 2012b) has in common with work on extreme behaviors like addiction, etc., is a willingness to embrace the idea that managers' activities reflect the degree of balance shown by their impulsive and executive systems especially when hypoactivity of the latter permits hyperactivity of the former. It is to this hypothesis that we now turn.

COMPETING NEURO-BEHAVORIAL DECISION SYSTEMS

The neuroscientific and especially the neuroeconomic account of managerial behavior in organizations has often concentrated on such matters as trust (Zak, 2004, 2007; Zak and Nadler, 2010), cooperation and conflict (Levine, 2007; Tabibnia and Lieberman, 2007), reward processing (Wargo et al., 2010b); and social interaction (Caldú and Dreher, 2007). All of these have some bearing on the kinds of functional and dysfunctional behavior with which we are concerned.

However, this paper seeks an additional explanation for these behaviors in the competing impulsive and executive decision systems associated with the operations of separate, though related, brain regions in the context of corporate problem solving. These neural areas are also associated with differences of temporal horizon, emotional response to circumstances and the cognitive control of behavior. Much of the work inspired by the CNBDS hypothesis involves addictive behavior, influenced by activity located at the impulsive end of the neural spectrum, in contrast to the more calculated behavior that is associated with the EFs, located towards the other pole, which manifest in planning, foresight and evaluation (Bickel et al., 2006, 2012b). Each neural decision system generates its own rewards, relatively immediate and strongly-emotional in the case of the impulsive system, relatively long-term, considered and cognitive in the case of the executive system (Moll and Grafman, 2011). Could it be that the explanation of maladaptive and adaptive organizational decision-making is to be found in the operation of these systems too?

The suspicion that CNBDS might be implicated in managers' maladaptive behaviors is especially significant in the case of small entrepreneurial businesses which rely largely on the endeavors of a single prime-mover. That person's tendency towards either impulsiveness or self-control is likely to be a dominant influence on the effectiveness of the enterprise. A tendency towards impulsiveness is likely to manifest in unplanned responses to momentarily appearing opportunities which are implemented without consideration of the long-term consequences for the firm. Unless such instant reactions are constrained by the exercise of EFs which engender planning, foresight, weighing of the relevant consequences, the balance required to build and maintain a successful organization is unlikely to be forthcoming. Conversely, an exaggerated emphasis on strategic thinking and planning which does not express itself in action to launch business ventures will stymie enterprise. The possibility of imbalance arises in a different manner in the large-scale organization. Large firms face similar

imperatives requiring the coordination of strategic planning and operational decision-making but the coordination is considerably more complex since different managers are responsible for these tasks. Complications arise because managers charged with making administrative and operational decisions may show cognitive and managerial styles that are incompatible with those of managers charged with strategic planning.

The clearest operational measure of balance/imbalance between the neural systems is the extent of temporal discounting apparent in the manager's behavior (Bickel and Yi, 2008; see also Baumesiter and Tierney, 2011). The organization-level goal of achieving and maintaining balance among administrative decisions which are predominantly programmed in Simon's sense, strategic decisions which are relatively unprogrammed, and operating decisions which are predominantly programmed, but sometimes contain unprogrammed elements, has to be accomplished through managers who are typically responsible for a single kind of decision but who bring a particular personal time horizon to it. While the avoidance of conflict between short-term and long-term objectives is an organizational goal, it is not necessarily within the competence or interests of individual managers.

THE NEED FOR CONCEPTUAL CLARIFICATION

The CNBDS hypothesis *per se* has not previously been applied to managerial concerns. However, the distinction it makes between the functioning of an impulsive system based on the limbic and paralimbic systems and an executive system based on the prefrontal cortex (PFC), together with the possibility that an imbalance between the operations of the two systems may lead to dysfunctional behavior, is strongly represented in the emerging literature of the neuroeconomics of organizations (e.g., Senior and Butler, 2007a,b; Stanton et al., 2010). What we may refer to as *neuro-behavioral decision theory*, which includes the CNBDS hypothesis, other models such as the somatic marker hypothesis (Damasio, 1994), and the application of similar thinking in management (e.g., Wargo et al., 2010a), appears to be emerging as a research paradigm within which to understand dysfunctional behavior (Klein and D'Esposito, 2007; Michl and Taing, 2010).

The first purpose of this paper is to examine and suggest a solution to a conceptual problem that arises in these analyses, a solution which may have a bearing on the kinds of problem of dysfunctional management mentioned above. Like the CNBDS model itself, the discussion of competing neural systems in the context of organizational management tends to conflate events taking place at the neurophysiological level with the cognitive processes ascribed in order to explain and interpret behavior. We are often assured, for instance, that this part of the brain "evaluates", "plans", or "decides". These terms all describe cognitive operations that belong at a level of exposition that refers to the person as a whole rather than the sub-personal level of neurobiology. Each level is properly described in its own language that obeys particular rules and which points to a separate kind of explanation. To draw this distinction between levels of exposition is not to make ontological distinctions or to invite a dualistic approach: it is simply to make clear that we must speak in quite different ways of the rate of firing of neurons from those we employ in speaking of the way in which a consumer evaluates

alternative brands. The argument is that while ontologically we have nothing to work with but material events, in accounting for behavior we need to maintain the distinction between what is happening at the sub-personal level of exposition and how we account for behavior at the personal level.

Part of the difficulty arises from a failure to delineate a cognitive component of neuro-behavioral decision theory and to show how it is related to the sub-personal level of neurophysiological events and the super-personal level of behavioral reinforcement. This paper proposes that Picoeconomics (Ainslie, 1992), which analyses the interaction of motivational states that refer to competing temporal horizons, provides the necessary cognitive level of exposition. If this incorporation of picoeconomics as a cognitive level of exposition for neuro-behavioral decision theory is successful, it suggests a means of overcoming problems of dysfunctional managerial behavior that are due to hyperactivity of the impulsive system aided and abetted by hypoactivity of the executive system.

THE NEED FOR MANAGERIAL APPLICATION

The kind of extreme decision-making involved in corporate fraud or the reckless investing that brings whole economic systems low is comparatively rare. In any case, while neuro-physiological processes can explain the behavior of individual participants in such dramas, the opportunity so to act and the far-reaching consequences of such decision-making are likely to be determined by structural factors and special events that lie perhaps beyond the immediate purview, and certainly beyond the control, of the decision-makers themselves (Bailey, 2007; Yeats and Yeats, 2007). An important focus of this paper is on understanding better the nature of decision-making by managers who are, by comparison, involved in more day-to-day corporate management.

The decisions that managers are required to make vary in terms of the cognitive level they demand, including level of intelligence and capacity to cope with complexity. They differ also in terms of their paradigmatic context: at the extremes, some decisions are solvable within the framework of assumption, behavioral norms and market structure that has prevailed hitherto while others require that assumption, behaviors, structures and other variables be reconceptualized and perhaps even recreated. We cannot take all of these factors into consideration but we can speak in terms of the decision styles of managers which have a bearing on their likelihood of success in tackling the various kinds of decision with which they are confronted. Our task is to understand better the causal fabric of the environment within which managers operate (the "super-personal level of exposition") and the influence of neurophysiology on their behaviors (the "sub-personal level").

The paper next examines the CNBDS thesis in greater depth, relating it as appropriate to managerial behavior and concerns (Section Competing Decision Systems). This is a prelude to its discussing the cognitive requirements of the model and evaluate picoeconomics as its cognitive component (Section The Cognitive Dimension). Once that is achieved, it is possible to consider the application of the insights of picoeconomics and adaption—innovation theory in addressing problems of

managerial dysfunction and the research agenda that emerge from these approaches (Section Organization-Level Strategies for Changing Managerial Behavior).

COMPETING DECISION SYSTEMS

OVERVIEW OF THE HYPOTHESIS

The CNBDS hypothesis rests on the somewhat simplifying assumption that a “limbic system” can be coherently identified which is differentially implicated in emotional responding and that a cortical area, differentially implicated in judgment, planning and other cognitive activities, can also be identified. Although the reality is undoubtedly more complicated than this—neural activations are seldom exclusive to one part of the brain—the dichotomy is retained here for ease of exposition with regard to the CNBDS hypothesis and for the sake of continuity with a wider literature (cf. however Lawrence and Calder (2004) with Ross (2012)). Bickel’s hypothesis suggests that the degree of addictiveness exhibited in behavior reflects the balance of activity in these two broadly defined brain regions, the first of which, based on the amygdala and ventral striatum, involves the distribution of dopamine (DA) during reinforcement learning, while the second, residing in the PFC, is implicated in the evaluation of rewards and their outcomes (Walton et al., 2011; see also Dayan, 2012; Symmonds and Dolan, 2012).

The *impulsive system* inheres in the amygdala and ventral striatum, a midbrain region concerned with the valence of immediate results of action, and is liable to become hyperactive as a result of “exaggerated processing of the incentive value of substance-related cues” (Bechara, 2005, p. 1459; see also Delgado and Tricomi, 2011). Drug-induced behaviors correlate with enhanced response in this region when the amygdala displays increased sensitization to reward (London et al., 2000; Bickel and Yi, 2008). The *executive system*, located in the PFC is normally associated with planning and foresight but is hypothesized to become hypoactive in the event of addiction; the absence of its moderating function is responsible for the exacerbation of the effects of the hyperactive dopaminergic reward pathway; this imbalance is then viewed as the cause of dysfunctional behavior (Bickel et al., 2011b, 2013). In summary, the CNBDS hypothesis posits that drug seeking results from “amplified incentive value bestowed on drugs and drug-related cues (via reward processing by the amygdala) and impaired ability to inhibit behavior (due to frontal cortical dysfunction)” (Bickel and Yi, 2010, p. 2; see also Jentsch and Taylor, 1999; Rolls, 2009).

THE IMPULSIVE SYSTEM

Before considering the CNBDS hypothesis, it is useful to note Damasio’s (1994) *somatic marker hypothesis* which bases a model of decision-making systems on similar neurophysiological foundations but emphasizes the role of emotion and feelings, downplaying economic considerations. Decision-making reflects the marker signals laid down in bioregulatory systems by conscious and non-conscious emotion and feeling; hence, Bechara and Damasio (2005; see also Bechara et al., 2000) argue that in dealing with decision-making economic theory ignores emotion. Economics is exclusively concerned with “rational Bayesian maximization of expected utility, as if humans were equipped with

unlimited knowledge, time, and information processing power”. They point, by contrast, to neural evidence which shows that “sound and rational” decision-making requires antecedent accurate emotional processing (Bechara and Damasio, 2005, p. 336; see also Phelps and Sokol-Hessner, 2012).

Damasio’s (1994) hypothesis is the outcome of brain lesion studies in which damage to the ventromedial prefrontal cortex (vmPFC) was found to be associated with behaving in ways that were personally harmful, especially insofar as they contributed to injury to the social and financial status of the individual and to their social relationships. Although many aspects of these patients’ intellectual functioning such as long-term memory were unimpaired, they were notably disadvantaged with respect to learning from experience and responding appropriately to emotional situations. Moreover, their general emotional level was described as “flat”. Damasio’s observation on these findings was that “the primary dysfunction of patients with vmPFC damage was an inability to use emotions in decision making, particularly decision making in the personal, financial and moral realms” (Naqvi et al., 2006, p. 261). Thus was born the central assumption of the somatic marker hypothesis that “emotions play a role in guiding decisions, especially in situations in which the outcomes of one’s choices, in terms of reward and punishment, are uncertain” (ib.; see also Bechara, 2011). Of relevance here is the finding that the vmPFC may be implicated in activity of the parasympathetic nervous system (PNS), which in contrast to the sympathetic nervous system (SNS) is involved in the explorative monitoring of the environment and the discovery of novelty (Eisenberger and Cole, 2012). This is corroborative of both Damasio’s view and the nature and behavior of the innovative manager discussed below.

Inherent in the somatic marker hypothesis is the attempt to describe not only the separate functions of the brain regions involved in emotional processing but also the interconnections between them (Haber, 2009). The starting point is operant behavior, particularly the mechanisms of reinforcement learning (Daw, 2013; Daw and Tobler, 2013). Specific behaviors eventuate in rewards as a result of which the amygdala triggers emotional/bodily states. These states are then associated via a learning process to the behaviors that brought them about by means of mental representations. As each behavioral alternative is subsequently deliberated upon in the course of decision-making, the somatic state corresponding to it is re-enacted by the vmPFC. After being brought to mind in the course of decision-making the somatic states are represented in the brain by sensory processes in two ways. First, emotional states are related to cortical activation (e.g., insular cortex) in the form of *conscious* “gut feelings” of desire or aversion that are mentally attributed to the behavioral options as they are considered. Secondly, there is an *unconscious* mapping of the somatic states at the subcortical level—e.g., in the mesolimbic dopaminergic system; in this case, individuals choose the more beneficial option without knowingly feeling the desire for it or the aversiveness of a less beneficial alternative (Ross et al., 2008; see also Di Chiara, 2002; Robbins and Everitt, 2002; Tobler and Kobayashi, 2009).

The rapidity with which the impulsive system acts in propelling behavior is underlined by Rolls’s (2005) theory of emotion in which the reinforcing stimuli consequent on a behavioral act as

conditioned stimuli that elicit emotion feelings. The automaticity of this interaction of operant and Pavlovian conditioning may account for behavior in two ways. The emotion feeling may function as an internal discriminative stimulus to increase the probability of the behavior that produced it being reprised; it is equally likely that the emotion feeling is the ultimate reward of the behavior in question and that, by definition, it performs a reinforcing role (Foxall, 2011). Either way, the effects of basic emotions on subsequent responding is immediate and uninfluenced by reflection at the cognitive level. While the criticism of economics shown by the authors of the somatic marker hypothesis appears to rule an economic orientation out of their purview, the CNBDS approach actively builds on insights from operant behavioral economics (Bickel et al., 1999, 2010, 2011a,b; Bickel and Vuchinich, 2000; Bickel and Marsch, 2001; Bickel and Johnson, 2003).

While the somatic marker hypothesis relied in its inaugural stages on lesion studies, the central research technique of cognitive neuropsychology, the work of Rolls (2005) offers confirmation of the role of operant behavior in the emerging paradigm. Recording single neurons' activity levels, Rolls (2005, 2008) reports that vmPFC neurons respond to the receipt of primary reinforcers such as pleasant-tasting foods. The integrity of the conditioning paradigm is evinced by the finding that devaluation of the reinforcer, for example through satiety, reduced the responses of such areas to these primary reinforcers. fMRI studies also offer corroboration. Gottfried et al. (2003) report that when a predicted primary reinforcer is devalued then vmPFC activity engendered by that reinforcer is reduced. Hence, the vmPFC contributes to the prediction of the reward values of alternative behaviors by reference to their capacity to generate rewarding consequences in prior occasions. Schoenbaum et al. (2003) used lesion and physiological studies to show that this capacity to encode *predictive reward value* depends on an intact amygdala.

The CNBDS model differs in emphasis from Damasio's somatic marker hypothesis. Their underlying similarity inheres in an acknowledgement that separate functions are performed within the overall impulsive-executive system. But Bickel draws attention to the interconnected operations of the impulsive system and the executive system in the production of behavior (Bickel et al., 2007). The CNBDS hypothesis is open, moreover, to the incorporation of economic analysis in the form of behavioral economics and neuroeconomics (Bickel et al., 2011a). Impulsive action, defined as the choice of a smaller but sooner reward (SSR) over a larger but later reward (LLR), is certainly associated with the over-activation of the older limbic and paralimbic areas, while the valuation and planning of future events and outcomes engages the relatively new (in evolutionary terms) PFC. However, it is the interaction of these areas, which are densely inter-meshed, that generates overt behaviors. The CNBDS hypothesis thus stresses the continuity of the components of the neurophysiologically-based decision system and Bickel's conception is therefore one of a continuum on which the impulsive and executive systems are arrayed theoretically as polar opponents (Porcelli and Delgado, 2009).

Specifically, Bickel et al. (2012a) identify, in addition to trait impulsivity, four kinds of state impulsivity: behavioral

disinhibition, attentional deficit impulsivity, reflection impulsivity and impulsive choice. Trait impulsivity is associated with mesolimbic OFC and correlates with medial PFC, pregenual anterior cingulate cortex (ACC) and ventrolateral PFC; venturesomeness (sensation-seeking) correlates with right lateral orbitofrontal cortex, subgenual anterior cingulate cortex, and left caudate nucleus activations. The concept of trait impulsivity recognizes behavioral regularities that are cross-situationally resilient. Within this broad construct, sensation-seeking or venturesomeness is widely known to be related to a need to reach an optimum stimulation level. Bickel et al. (2012a) associate it with sensitivity to reinforcement, the theory of which has been extensively developed by Corr (2008b) and is discussed in greater detail below. Of the four state impulsivities discussed by Bickel et al. (2012a), behavioral disinhibition is associated with deficiencies in the anterior cingulate and prefrontal cortices, attentional deficit impulsivity with impairments of caudate nuclei, ACC, and parietal cortical structures, and with strong activity in insular cortex; reflection impulsivity with impaired frontal lobe function; and impulsive choice with increased activation in limbic and paralimbic regions in the course of the selection of immediate rewards.

This latter is again strongly predicted by RST (McNaughton and Corr, 2008). It is debatable whether the state impulsivities mentioned here are anything other than the behavioral manifestations of trait impulsivity in particular contexts. The four state impulsivities that Bickel et al. (2012a) note are probably outcomes of a general tendency to act impulsively from which they are predictable. Behavioral disinhibition is the inability to arrest a pattern of behavior once it has started; it is also evinced in acting prematurely with deleterious outcomes. Attentional deficit impulsivity is failure to concentrate, to persevere with salient stimuli. Again, the outcome is the adoption of risky behavioral modes with poor consequences. Reflection impulsivity is failure to gather sufficient information before deciding and acting; inability to get an adequate measure of the situation leads to unrewarding behaviors. Impulsive choice is a behavioral preference for a SSR over a LLR for which the individual must wait. All of these state impulsivities are actually behaviors, the outcomes of trait impulsivity. More relevant to the present discussion is *preference reversal* in which a longer-term, more advantageous goal is preferred (e.g., verbally) at the outset only to decline dramatically in relative value as the delivery of the earlier less advantageous reward becomes imminent.

THE EXECUTIVE SYSTEM

Bickel et al. (2012a) define EFs as "behavior that is self-directed toward altering future outcomes" (p. 363; see also Barkley, 2012) and point out that EFs are consensually associated with activity in the PFC. PFC is generally recognized as implicated in the integration of motivational information and subsequent decision-making (Wantanabe, 2009), exerting a supervisory function that governs the regulation of behavior (Bickel et al., 2012a); hence, Bickel et al. (2012a) point out, its designation as a supervisory attentional system (SAS; Shallice and Cooper, 2011).

While some authors emphasize a single element of EFs such as the attentional control of behavior or working memory or

inhibition, others stress groups of elements: planning, working memory, attentional shifting or valuing future events, emotional aspects of decision-making. Addiction can then be viewed as a breakdown in the operations of the EFs or as impaired response inhibition leading to the increased salience of addiction-orientated cues. Bickel et al. (2012a) concentrate on Attention, Behavioral flexibility, Planning, Working memory, Emotional activation and self regulation (EASR) which they group into three major categories: (1) *the cross-temporal organization of behavior* (CTOB) which is concerned with the awareness of the future consequences of current or contemplated behavior and therefore with planning for events that will occur later; (2) EASR which involves the processing of emotion-related information and “initiating and maintaining goal-related responding”; and (3) *metacognition* which includes social cognition and insight, empathy, and theory of mind (ToM).

The CTOB comprises *attention* (closely related to dorsolateral prefrontal cortex (DLPFC), *behavioral flexibility* (frontal gyrus activity; lesioning of PFC is well-known to be associated with the diminution of behavioral flexibility (Damasio, 1994; Bechara, 2011), *behavioral inhibition* (right inferior frontal cortex and insula are activated during behavioral inhibition which is also associated with reduced activity in left DLPFC, the right frontal gyrus, right medial gyrus, left cingulate, left putamen, medial temporal, and inferior parietal cortex), *planning* (in which DLPFC the VMPFC, parietal cortex, and striatum are implicated), *valuing future events* (in the case of previewing and selecting immediate rewards: limbic and paralimbic regions; in the case of long-term decisions: prefrontal regions; see McClure et al., 2004); and *working memory* (DLPFC, VMPFC, dorsal cingulate, frontal poles, medial inferior parietal cortex, frontal gyrus, medial frontal gyrus, and precentral gyrus; Bickel et al., 2012a, pp. 363–367).

EASR concerned with the management of emotional responses is implemented in Medial PFC, lateral PFC, ACC, OFC. *Metacognitive processes* (MP) involve recognition of one's own motivation and that of others which is implemented in the case of *insight* or self-awareness by the insula and ACC, and in the case of *social cognition* by medial PFC, right superior temporal gyrus, left temporal parietal junction, left somatosensory cortex, right DLPFC; moreover, *impaired social cognition* follows lesions to VMPFC (Damasio, 1994; Bechara, 2005; Bickel et al., 2012a, pp. 367–368).

REINFORCEMENT SENSITIVITY AND PERSONALITY

RST (Gray, 1982; Corr, 2008b; Smillie, 2008) includes the excitatory (impulsivity) and inhibition (executive) components of the CNBDS model but also permits us to make extensions relating to the expected behavior patterns that follow from each and the way in which individual differences can be summed up in terms of an ascription of personality types.¹ RST proposes that the basic behavioral processes of approach and avoidance are differentially associated with reinforcement and punishment

and that individuals show variations in their sensitivity to these stimuli.²

Approach is behavior under the control of positively reinforcing or appetitive stimuli and is mediated by neurophysiological reward circuitry that the theory categorizes as a Behavioral Approach System or BAS. The BAS consists in the basal ganglia, especially in the mesolimbic dopaminergic system that projects from the ventral tegmental area (VTA) to the ventral striatum (notably the nucleus accumbens) and mesocortical DA PFC (Smillie, 2008; cf. Pickering and Smillie, 2008). For recent discussion of the role of the striatum in decision-making and the processing of rewards, see Delgado and Tricomi (2011). Recent research demonstrating the role of this dopaminergic system in formulating “reward prediction errors” is consonant with this understanding. Unpredicted reward is followed by increase in phasic dopaminergic activity whereas unpredicted non-reward is followed by a decrease and unchanged when reward is entirely predicted (Schultz, 2000, 2002; Schultz and Dickinson, 2000; Schultz et al., 2008). Unpredicted reward instantiates the activity of the BAS, therefore, and predicted reward maintains its operation. Moreover, BAS activity increases positive reward (pleasure) and motivates approach to reinforcing stimuli and stimuli that predict reinforcement. Such approach is characteristic of the extraverted personality; Corr (2008b, p. 10) sums up the personality type as “optimism, reward-orientation and impulsivity” and notes that it maps clinically on to addictive behaviors.

These emotional and motivational outcomes represent one pole of a continuum of individual differences that manifest differential BAS and Behavioral Inhibition System (BIS) reactions to stimuli. There is a corresponding though antithetical explanation of avoidance in RST. Avoidance is shaped by sensitivity to stimuli of punishment and threat and mediated by two bio-behaviorally based systems of emotion and motivation. The first of these, the Fight-Flight-Freeze system (FFFS), is triggered by aversive stimuli and the resulting feeling of fear, what Corr (2008b, p. 10) refers to as the “get me out of here emotion”; the FFFS's motivational output is a behavior pattern characterized as “defensive avoidance”. However, if the consequential stimuli involved are mixed in terms of their emotional valence then the BIS, which is involved generally in the resolution of goal-conflict is activated; in this case, the emotional output is anxiety, the “watch out for danger” emotion Corr (2008b, p. 11) and the behavioral outputs are risk evaluation and cautiousness which are described as manifesting defensive approach. Hence, in summary, reward sensitivity leads to positive emotion and approach and a response pattern that is characterized as “extraversion” via behavioral observation or psychometric testing; by contrast, punishment sensitivity leads to

¹There are several versions of RST. The present paper makes use of the fundamental elements of the version of the theory developed by Gray and McNaughton (2000), McNaughton and Corr (2004) and Corr (2008a).

²RST uses the term “reinforcement” to include both rewarding and punishing stimuli. This usage can be confusing in view of the confinement of “reinforcement” to instances in which consequential stimuli strengthen (i.e., increase) the rate at which a response is emitted and “punishment” to instances in which consequential stimuli reduce that rate, a usage common in behavior analysis in terms of which the CNBDS hypothesis is generally formulated. I have therefore tried to use “reinforcement” and “punishment” consistently in their behavior analytical definitions. However, it is not always possible to do justice to RST by adhering to this rule and on occasion I have used “reward” rather than “reinforcement” where this is clearer.

negative emotion and avoidance and a personality characterized in terms of neuroticism (Smillie, 2008).

RST also relates the FFFS and BIS to specific neurophysiological systems. In the case of the FFFS this is the periaqueductal gray, which is implicated in acute or proximal threat, and the medial hypothalamus, amygdala and anterior cingulate cortex, implicated in distal threats. The BIS comprises the septo-hippocampal system and the amygdala. The emotional output of the FFFS is fearfulness while that of the BIS is anxiety. In either case, the emotional outputs are negative and most forms of RST relate this to neuroticism. The value of employing explanatory constructs referring to personality types such as extraversion and neuroticism is that they summarize individual differences in reinforcement sensitivity, adding both to the interpretation of behavior and to its prediction in novel environments.

MANAGERIAL BEHAVIOR RECONSIDERED: THE INFLUENCE OF TEMPORAL HORIZON

Dysfunctional behaviors are those *dominated* by either the impulsive system or the executive system. The impulsive system evolved because it was evolutionarily-adaptive as far as inclusive fitness was concerned. Its preoccupation with short-term goals and its immediate response to opportunities ensured its contribution to survival of the individual and thereby to its biological fitness. It is closely related to the kinds of modular functioning posited by Fodor (1983) which allows rapid responses to environmental concerns. It is closely related also to the emotion-feelings associated with such response capacity, pleasure in particular but also arousal and dominance. These are the ultimate rewards of instrumentally conditioned behavior (Rolls, 2008; Foxall, 2011).

When we speak of the dysfunctional consequences of a hyperactive impulsive system in seeking to understand and explain a manager's behavioral repertoire we are referring to hyperactivity in these emotional-reward systems which leads, for instance, to preoccupation with short-term goals at the expense of undertaking longer-term planning, the reckless taking of investment decisions promising rapid high returns and a consequent over-cautiousness, and an unwillingness to invest in future. Another manifestation is rigidity in the pursuit of a previously selected goal even though the environment has changed and flexibility is called for. We are also suggesting that it is unlikely that this impulsive-hyperactivity occurs in isolation from hypoactivity of the executive system. Hence, imbalance occurs because managers place disproportionate importance on the emotional highs resulting from activities that result in immediate or near-immediate reinforcement at the expense of the pursuit of considered action that would be under the control of the executive system. Moreover, both utilitarian reinforcement and informational reinforcement are engendered which brings about high levels of pleasure and arousal, and in a context that permits the emotion-feeling of high dominance (Kringelbach, 2010; Foxall, 2011). This is probably the strongest combinations of interacting reinforcement for the maintenance of managerial behavior. From the organization's point of view, if this behavioral style becomes characteristic of a function, department or even of the firm as a whole, the outcome will be an overconcentration on administrative and operational activities at the expense of a strategic perspective which embraces

and anticipates the opportunities and threats of the changing market-competitive environment.

However, dysfunctional behavior may also result from hypoactivity of the impulsive system and hyperactivity of the executive system (Mojzisch and Schultz-Hardt, 2007). The intellectual rewards of a preoccupation with long-term planning, obtaining and analyzing information, mulling over strategic possibilities, may lead to a lack of strategic implementation so that the short-term decisions necessary for the day-to-day operations of the firm are neglected, working capital is lacking, the firm cannot continue. The pleasures and arousal resulting from cognitive activity and the feeling of dominance that this provides can manifest in organizational sclerosis which over-values intellectual engagement with marker structures, competition and, especially, the strategic scope of the organization. From the organization's viewpoint, if this behavioral style becomes widespread, there will be an imbalance in favor of strategic planning and decision-making at the expense of the day-to-day imperatives of the firm's response to the tactical behavior of competitors and the vagaries of consumer choice. The executive system also evolved because it favored biological fitness. Its operation is much like that of the central cognitive function posited by Fodor (1983).

In view of the importance of avoiding a general tendency towards either kind of imbalance in the behavior of the firm, it might be argued that our unit of analysis should be the organization as a whole since it is presumably structural elements in the organization's culture that require attention if the problem is to be overcome. This is undeniably correct but our present objective is less to overcome problems of imbalance, which are anyway the subject of innumerable management texts, and more to understand how individual managers may be prone to one or other behavioral style. The central factor involved in diagnosing either extreme at the individual level is the temporal horizon of the manager since this correlates highly with the influence of the impulsive and/or executive systems. This is best considered, however, after the way in which cognitive language is used in neuro-behavioral decision theory, which brings further understanding of the role of temporal horizon in decision-making. It also suggests a means of overcoming problems of impulsive-hyperactivity and executive-hypoactivity at the individual level which must be evaluated before an organization-level solution can be proposed and appraised.

THE COGNITIVE DIMENSION

SPEAKING OF COGNITION

Neuroscience and behavioral science employ extensional language, the third-personal mode which is taken as the hallmark of science (Dennett, 1969). The truth value of extensional sentences is preserved when co-designative terms are substituted for one another. The phrase, "the fourth from the sun" can be substituted for "Mars" in the sentence "That planet is Mars" without surrendering the truth value of the sentence. However, the truth value of a sentence containing intentional language, such as "believes", "desires" or "feels", is not maintained when co-designatives are substituted. Given the sentence, "John believes that that planet is Mars", we are not at liberty to say, "John believes that planet is the fourth from the sun", since John may not know that Mars

is the fourth planet. Intentional sentences have another unique property: the *intensional inexistence* of their subjects. The truth-value of my saying “I am driving to Edinburgh this weekend”, an extensionally-expressed statement, is established by there being a place called Edinburgh to which I can travel. But if I say that I am seeking the golden mountain, looking for the fountain of youth or yearning for absolute truth, none of the entities named in these intentional expressions need actually exist for the truth value of the sentences to be upheld. Finally, it is not possible to translate intentional sentences into extensional ones without altering their meaning. Intentional sentences usually take the form of an “attitude” or verb such as *believes*, *desires* or *wants* followed by a proposition such as “that today is Tuesday” or “that eggs are too expensive”; hence, such sentences are known as “propositional attitudes” (Chisholm, 1957).

The proposed development of the CNBDS hypothesis involves more than terminological clarification. The principles just described govern not only linguistic usage but also the kinds of theories we invoke in order to explain our subject matter and care must be taken to ensure that each is confined to the level of explanation or interpretation to which it is appropriate. Cognitive terminology is intentional and belongs only at the level of the person (Bennett and Hacker, 2003).

LEVELS OF EXPOSITION

Dennett (1969) distinguishes the *sub-personal level of explanation*, that of “brains and neuronal functioning” from the *personal level of explanation*, that of “people and minds”. The sub-personal level thus entails a separate kind of scientific purview and approach to explanation: by encompassing neuronal activity it is the domain of the neuroscientist and leads to an extensional account. The personal level which is the domain of mental phenomena is that of the psychologist; it requires an intentional account. A third level of explanation is required, however, in order to cover the whole range of phenomena and sciences that deal with them in a comprehensive approach to the explanation of behavior (Foxall, 2004). This is the *super-personal level of explanation* which encompasses operancy,³ the respect in which the rate of behavior is contingent upon its reinforcing and punishing consequences; this is the field of extensional behavioral science.

Care is necessary to maintain the separation of these three levels since the mode of explanation which each entails is unique and cannot be combined with the others in a simple fashion. The fundamental difference in mode of explanation which must be constantly recognized is as follows. The sub- and super-personal levels, which are based on the neuro- and behavioral-sciences respectively, require the use of extensional language and explanation. Both of which are in principle amenable to experimental (“causal”) analysis, or failing this to the quasi-causal analysis made possible by statistical inference. They differ from one another in terms of the kind of stimuli and responses (independent and dependent variables) that must be taken into

consideration in empirical testing of the hypotheses to which they give rise. They differ more fundamentally from the personal level of explanation, which attracts a wholly different mode of analysis, namely that of intentional psychology; the approach to explanation in this case relies on the ascription of beliefs, desires and feelings on the basis of non-causal criteria.

The proposed development of the CNBDS hypothesis involves more than terminological clarification. The principles just described govern not only linguistic usage but also the kinds of theories we invoke in order to explain our subject matter and care must be taken to ensure that each is confined to the level of explanation or interpretation to which it is appropriate. Cognitive terminology is intentional and belongs only at the level of the person (Bennett and Hacker, 2003).

The critique of the CNBDS hypothesis takes the form therefore of conceptual development. The CNBDS hypothesis is described by Bickel and colleagues in neuroscientific, cognitive and behavioral terms without regard to the domains of explanation to which each of these categories belongs. For example, although they offer what purports to be a behavioral definition of EF, they define several of its component parts in terms that are cognitive. Following Barkley (1997a,b), they define EF as “as behavior that is self-directed toward altering future outcomes” (Bickel et al., 2012a, p. 363), but they list among those of its elements which suggest “CTOB”: *attention, planning, valuing future events and working memory*. These clearly are or involve cognitive events. Similarly, among the elements that make up “emotional and activation self-regulation”, they list: “the processing of emotional information” and “initiating and maintaining goal-related responding”. Finally, as elements of “MP” they list: “social cognition” or “ToM” and “insight”. Bickel et al. (2012a) define impulsivity behaviorally in terms of actions prematurely performed that eventuate in disadvantageous outcomes. They go on, however, to describe impulsivity as consisting in the trait of impulsiveness, a structural personality variable that incorporates sensation-seeking, deficits in attention and reflection impulsivity which is an inability to collect and evaluate information prior to taking a decision. All of these are intensional.

COGNITIVE REQUIREMENTS OF NEURO-BEHAVIORAL DECISION SYSTEMS

So far we have advocated that behavioral and neuroscientists maintain the appropriate syntax in speaking of intentional concepts such as beliefs and desires as opposed to extensional objects such as neurons and behavior patterns. This means understanding and maintaining the sub-personal, personal and super-personal levels of exposition and employing only the appropriate language at each level. A more satisfying outcome for neuro-behavioral decision theory would be to incorporate a level of cognitive exposition the content of which complemented the extensional sciences we have discussed. This section sets out the criteria that such an account should fulfill; the following section evaluates pieoeconomics (Ainslie, 1992) as that cognitive component.

There are four requirements of any candidate for the cognitive component of neuro-behavioral decision theory. It must first be capable of filling the need for a personal level account of the causes of behavior. Second, it must provide an intentional explanation.

³This neologism refers to the effect on behavior of environmental contingencies of reinforcement and punishment. “Operancy”, which refers specifically to the process of reinforcement and punishment of behavior, avoids the theoretical notion of “conditioning” and is therefore more consistent with an extensional portrayal.

Third, it should be capable of linking to the behavioral economics and neuroeconomics analyses that are found in the hypothesis. And, finally, it must relate philosophically to broader disciplinary concerns including neurophysiology and operancy.

A personal level theory

A cognitive account is required to provide understanding of the ways in which individuals subjectively respond to the circumstances which influence their behavior towards rewards that may have short-term benefits but which entail longer-term deleterious consequences. Being able to characterize what individuals desire and believe in these situations, what they perceive and how they feel, provides an indication of their underlying disposition to respond in a particular way to rewards and punishments occurring at different times. This is of course a highly theoretical enterprise; in order to avoid undue speculation and conjecture, therefore, it is important that the cognitive requirements of neuro-behavioral decision theory are provided by a coherent body of knowledge relating personal level factors to situations that promote consumption.

An intentional account

The required personal level exposition must indicate the particular intentional terms that are applicable to the explanation of normal and addictive behaviors within the framework of an overall theory that can systematically relate the two antipodal behavior patterns. It must also be capable of explaining how intentional entities like beliefs and desires, perceptions and emotions would act upon the impulsion towards fulfillment of immediate wants, such as consumption of an addictive substance, in order to bring about a more advantageous long-term result. This calls for a well-worked out theory of human behavior over the continuum of normal to addictive behaviors rather than an ad hoc application of intentional language on the basis of rapid observation of an individual's behavior.

An integrative economic account

The CNBDS hypothesis relies heavily on operant behavioral economics and neuroeconomics in order to explain the reinforcer pathologies that underlie addictive patterns of behavior. It would be advantageous, therefore, for the cognitive component of the model to link to the basic exposition in economic terms. The usefulness of the cognitive account might be questioned because of its inherently theoretical nature; this objection can be overcome if its explanation of behavior can be specified in language that is consonant with the provisions of consumption in the face of extremely high elasticity of demand and temporal discounting of the consequences of behavior.

Relationship to basic disciplines

A broader relationship between the cognitive account of behavior and the underlying neuroscience and behavioral science that comprise the CNBDS hypothesis is necessary that goes beyond economic integration. Although a major point of the present argument is that cognitive accounts differ fundamentally from those provided by the extensional sciences, the intentional component must be consistent with what is known of the

neurophysiological basis of addiction and also with its relationship to the reinforcers and punishers that follow behavior.

PICOECONOMICS: PREFERENCE REVERSAL AND INTERTEMPORAL CONFLICT

Herrnstein's (1997) matching law suggests that the value of a reinforcer is inversely proportional to its delay, i.e., as the delay becomes shorter, the value increases dramatically. This is the essence of hyperbolic discounting. The key difference between exponential and hyperbolic discounting is that in the former the LLR is always preferable to the SSR, regardless of time elapsed, whereas in the latter there is a period during which the SSR is so highly valued (because the time remaining to its possible realization is so short) that it is preferred to the LLR (Ainslie, 1992; Ainslie and Monterosso, 2003). This is clearly not because of its objective value which is by definition less than that which can be obtained through patience, but because the time remaining to its possible realization is now so short, that it is preferred to the later but larger reward. Ainslie notes that these findings harmonize with Freud's observations that an infant behaves as if expecting immediate gratification but becomes, with experience, willing to wait for the longer-term alternative. In other words, still paraphrasing Freud, if the pleasure principle is resisted, the outcome will be the exercise of the reality principle. In the terminology of behavioral psychology, the operants relevant to each of these principles are shaped by their respective outcomes. Ainslie argues that the two principles can be represented as two *interests*, each of which seems to employ devices that undermine the other.

In discussing what these devices are, Ainslie (1992) gives a clue as to how we may speak of the operations of mental mechanisms and also how they are organized to produce phenomena in a cognitive account, i.e., one that conforms to the use of cognitive logic as we have defined it and to the strictures of grounded modularity as they were developed above. His first device, for instance, is *precommitment*, in which for instance one joins a slimming club in order to be able to call upon social pressures in order to reach long term goals. The very language of this account indicates the relevance of the models of cognition we have developed. The processes are unobservable, adopted in order to make behavior intelligible once the extensional accounts of behavioral and neuro-science have been exhausted. Secondly, the interests may hide information from one another, e.g., about the imminence of rewards. Thirdly, the emotions that control short-term responding may be incapable of suppression once they are in train or they may be foreshortened by long-term interests. Finally, current choices may be used as predictors of the whole pattern of behavior, consisting in a sequence of multiple behaviors belonging to the same operant class, that the individual will engage in future. An individual may, that is, see her present choice of a chocolate éclair as indicative that she will make this selection repeatedly and often in the future. Individual choices are thus perceived as precedents. The resulting strategy is what Ainslie later described as *bundling*, in which the outcomes of a series of future events are seen cumulatively as giving rise to a single value. When this value, rather than that of a single future event, is brought into collision with the value of the single immediate choice, the long-term

interest is thereby strengthened (see also Baumeister and Vohs, 2003).

Subsequent behavior that serves the longer rather than the shorter term interest is apparently rule governed rather than contingency shaped (Skinner, 1969). However, the “rules” exist only in the mind of the individual who may not have encountered the contingencies. It is intellectually dishonest to refer to them as rules in the sense proffered by radical behaviorists which require empirical confirmation that the individual has previously encountered similar contingencies or whose rule following behavior from others of similar kind to the present has been reinforced. Since we have no empirical, in particular, experimental indication of this nature, we would more accurately refer to them as beliefs. Our use of intentional language indicates the nature of our explanation or, better perhaps, interpretation. Ainslie himself refers to bundling as the basis of “personal rules” but we can have no this- personal evidence of even the existence of such, let alone their efficacy. Better to characterize our account as interpretation and make this explicit by using intentional language.

In sum, Ainslie’s picoeconomics portrays the conflict between a smaller reward that is available sooner and a larger reward available later in terms of clashing intrapersonal interests. We can now proceed to evaluate picoeconomics in terms of the criteria set out above.

PICOECONOMICS AS THE REQUIRED COGNITIVE COMPONENT

A personal level account

Ainslie’s picoeconomics portrays the conflict between a smaller reward that is available sooner and a larger reward available later in terms of clashing intrapersonal interests. These are personal level events because their purpose is to render intelligible the behavior of an individual when it is no longer obvious how the contingencies of reinforcement/punishment and his neurophysiology are affecting his behavior. The behavior we are attempting to understand is often a single instance of activity (we are taking a molecular perspective) but the behavior which we employ to generate and justify the intentional interpretation we have to make is a *pattern of behavior*: here we are taking a molar standpoint. There must also be a pattern of neurophysiological activity which supports the strategic assumptions we are making about the individual. In addition, the *pattern of reinforcement* (Foxall, 2013) is of crucial importance in interpreting his behavior. We are ascribing *interests* and their effects in determining behavior but we employ constructs in order to accomplish this that are unobservable posits: they cannot enter into an experimental analysis. We use the molar behavior pattern, the pattern of reinforcement and neurophysiology to underpin these strategic assumptions and to justify our interpretation. The language of picoeconomics consists therefore in strategic assumptions that derive from an interpretation of the behavior and neurophysiology of the individual. The strategic assumptions we make and the way we use them must be consistent with the evolution of the species by natural selection, the ontogenetic development of the individual’s behavior through operancy, and the evolutionary psychology of the prevalent behavior of the species. We need to show how the behavioral sensitivity to patterns of reinforcement (which are the subject of our studies of operancy and evolutionary psychology)

are in turn related to evolution by natural selection via synaptic plasticity.

An intentional exposition

Picoeconomics accounts for behavior using intentional language, specifically the cognitive language of decision-making and problem-solving. In particular, as a theory of “the strategic interaction of successive motivational states within the person” (Ainslie, 1992), it is dynamically concerned with the internal weighing of information about the outcomes of alternative courses of action and the motivational states they engender.

An economic account

Can the actions of the interests themselves be economically modeled at the intentional level? Is Ainslie’s picoeconomics entirely a cognitive theory or does it lend itself to microeconomic analysis? In fact, Ross (2012) puts forward an array of economic models of the strategic interactions proposed by picoeconomics among competing preferences. Analysis of behavior in terms of the pattern of reinforcement it has previously resulted in draws upon *operant behavioral economics* which is central to the CNBDS: specifically, the analysis of discounting relates behavior to its consequences, but operant behavioral economics also establishes that individuals maximize utility and the particular combinations of reinforcement that constitute utility.

Related to a broader disciplinary base

It is particularly important from the point of view of the research program within which the current investigation is being performed (see Foxall, 2007a) that the cognitive interpretation of behavior, here picoeconomics, can be defended philosophically in terms of the underlying behavioral and neuroscience (Foxall, 2004). This is clearly the case with picoeconomics (Foxall, 2007b).

Now that picoeconomics has been established as a cognitive component for neuro-behavioral decision theory, its usefulness as a means of overcoming managerial dysfunction with respect to temporal horizon can be evaluated. As Section Organization-Level Strategies for Changing Managerial Behavior indicates, the general thrust of picoeconomics is towards clinical application that may not fit most managerial situations. In that case, alternative approaches to management are discussed, notably adaption-innovation theory, which are founded on similar neurophysiological bases but which suggest more practicable solutions.

ORGANIZATION-LEVEL STRATEGIES FOR CHANGING MANAGERIAL BEHAVIOR

STRATEGIES OF CHANGE BASED ON PICOECONOMICS

An advantage of picoeconomics in the current context is that it suggests means of overcoming the managerial problems likely to arise when individual managers are strongly motivated by the goals and behavioral patterns that reflect hyperactivity in the impulsive system and hypoactivity in the executive system. Ainslie (1992) proposes a number of strategies through which the individual might overcome the temporal discounting that is the hallmark of this tendency. It is here that RST underpins the current analysis by providing neurophysiological systems that

underlie not only the more extreme impulsive—approach tendency (BAS) the fear—engendered escape—avoidance tendency (FFFS), but the goal-resolving tendency that seeks to reconcile the alternative courses of action (BIS). The strategies of self-control suggested by Ainslie can be seen as attempts to aid the BIS in its attempts at conflict-resolution.

Ainslie (1992) proposes four personal strategies, allusion to some of which was made above, by which the individual might make a larger, albeit longer-term, outcome more probable: precommitment, control of attention, preparation of emotion and reward bundling. *Precommitment* involves using external commitments to preclude the irrational choice. The individual seeks to manipulate the external environment in order to make behavior leading to the LLR more likely. Ulysses lashed himself to the mast before temptations arose. But precommitment need not be so dramatic. An addict may imbibe a substance that induces nausea when alcohol is drunk. A student might arrange for friends to take her to the library before a favorite TV program begins. *Control of attention* restricts information processing with respect to the SSR. For example, taking a route home from the office that avoids bars or fast-food restaurants; thinking about the car one can buy if you eliminate cigarette smoking. *Preparation of emotion* may take the form of inhibiting emotions that are customarily connected with the SSR or of increasing incompatible emotions. Hence, graphically recalling the health risks of over-eating, smoking or excessive alcohol consumption, thinking of the displeasure others will show, engage cognitive reasoning in order to eliminate the emotional anticipation that customarily lead to consumption.

Perhaps the principal strategy, *reward bundling* requires the individual to make personal rules about the perception of the smaller-sooner and larger-later choices available. Instead of imagining the present choice and its exciting outcomes (drinking alcohol to excess) as opposed to a single somewhat amorphous outcome of sobriety (“longer life”), reward bundling involves bring a whole sequence of larger- later rewards to oppose rewards of the immediately-available behavior. In the absence of such bundling, the individual is likely to undergo repeated preference reversals but viewing the choice as between two streams of behaviors and outcomes makes self-control more possible. Self-control results from perceiving a single choice between an aggregation of LLRs and a competing aggregation of SSRs. The sum of the LLRs is always greater than that of the SSRs. Decision making is then a matter of imaginatively bringing the LLRs forward in time to the present. The personal rules necessary to ensure this self-control take the form of private “side-bets” in which the current choice predicts future choices. The important point in viewing the reward sequences in this way is that the LLR is *at all times* superior to the SSR even when an SSR is immediately available: preference reversal is therefore not predictable. The rule is a side bet that the current choice will predict future choices. If the SSR is resisted, the bet is won: the expectation of future reward is thus enhanced and the individual’s probability of success in resisting temptation is increased. Selection of the SSR indicates that the individual has lost the bet, however: the individual’s self-image is weakened, along with his or her expectation of resisting the temptation in the future.

The relevance of these strategies to managerial decision-making of the kind we have been discussing is evident though it is unclear whether a manager would be able to recognize and change his or her behavior in the absence of detailed one-on-one counseling. While this methodology obviously has applications in therapeutic contexts, and Ainslie’s prescriptions fit well the needs of substance and behavioral addicts, an application that is more attuned to the social-structural demands of organizational management is called for in the context with which we are here concerned.

ADAPTION-INNOVATION THEORY

There exists an alternative approach to managerial application of the neuropsychological work that has been reviewed in this paper, though the following comments are indicative and call for a dedicated research program. Adaption-innovation theory (Kirton, 2003) suggests a means of structuring decision-making groups that reflects competing neuro-behavioral systems and so avoids reliance on an individual-level prescription for managerial behavior. “Cognitive style” refers to a person’s persistent preferred manner of making decisions, the characteristic way in which they approach problems, information gathering and processing, and the kinds of solution they are likely to work towards and attempt to implement. As such, it is orthogonal to cognitive level, that is intelligence or capacity. Kirton (2003) proposes that individuals’ cognitive styles can be arrayed on a continuum from those that predispose “doing better” (the adaptive pole) to those that predispose “doing differently” (the innovative pole). Adaption-innovation is measured by the Kirton Adaption-Innovation Inventory (KAI) which evinces high levels of reliability and validity and scores correlate with a number of personality variables including extraversion and impulsivity. General population samples indicate that trait adaption-innovation is approximately normally distributed and general population scores, including of course those of managers, are arrayed over a limited continuum which falls within the theoretical spectrum of scores posited by adaption-innovation theory. In line with the purview of this paper, therefore, the managers of whom we speak are not extreme in their behaviors, though they some of them may exhibit scores towards the extremes of the bipolar construct of adaption-innovation. The behavior of the extreme adaptor is generally characterized by a tendency towards caution in decision-making and problem-solving, use of tried-and-tested methods, efficiency, rule-conformity and limited quantitative creativity manifesting in the generation of relatively few, workable solutions. The extreme innovator is, in contrast, more outlandish in selecting decisions, more likely to propose novel solutions to problems (many of which are impracticable), less efficient and more likely to modify or even break the rules. Although extraversion (measured, for example, by Eysenck’s E scale) emerges as more highly correlated with adaption-innovation (measured in the direction of the innovativeness pole), little is known about the underlying personality profiles of adaptive and innovative decision-makers in relation to the contingencies of reinforcement that shape and maintain their preferred behavioral styles. RST (Gray and McNaughton, 2000; McNaughton and Corr, 2004; Corr, 2008a) offers a means of investigating the personality

profiles of decision-makers and the role of reward and punishment in their development and maintenance. This all suggests that a psychometric research program concerned with the integration of a number of fields could provide indicators for the prescription to the problems of extreme managerial style. The program would need to encompass the neurophysiology of cognition together with the psychometric measurement of personality dimensions that underlie cognitive style. Enough has been said to indicate that we understand these fields and their interactions sufficiently to embark on such a program. In the meantime, the following remarks are indicative of the work that needs to be undertaken.

RECOGNIZING INDIVIDUAL DIFFERENCES IN TEAM-BUILDING

In contradistinction to innovators, adapters are typically prudent, using tried and tested methods, cautious, apparently impervious to boredom and unwilling to bend, let alone break, the rules. They seek the kind of efficiency that manifests in accomplishing known tasks more effectively. An extremely adaptive cognitive style suggests hyperactivity of the executive system coupled with hypoactivity of the impulsive system. Moreover, those aspects of the executive system that involve ToM, the observation of social conventions, meta-cognition, and some facets of behavioral flexibility might be adaptor characteristics that would confirm this categorization. The tentative conclusion is that adaptors would cope well and perform advantageously when involved in the intellectual, long-term, detailed thinking that strategic planning requires. The downside to their over-involvement in this kind of decision-making derives from the demands that strategic planning and commitment sometimes exert upon the ability to undertake “outside-the-paradigm” thinking. Such demands are likely to be, relatively, occasional but they are equally likely to arise at times of crisis in the market and competitive environments of firms and to benefit most from the kind of thinking which characterizes a more innovative cognitive style. In contradistinction to adaptors, innovators typically proliferate ideas that require the relatively radical change that can modify strategic direction, the product-market scope of the firm, and possibly diversification. At its extreme however, this cognitive style, suggests hypoactivity of the executive system, hyperactivity of the impulsive system. The impulsive system is geared to the rapid identification and evaluation of opportunities and threats, the capacity to envisage far-reaching, possibly disruptive, change which, in refocusing the entire strategic scope of the enterprise carries with it upheaval in working practices and both the working and non-working lives of managers and other employees. To the extent that these are innovator-traits, it is clear that decision groups need to be balanced by adaptors who can supply the capacity for sounder decision-making and the facilitators who can explain to innovators the rationale behind the behavior of adaptors, who are otherwise likely to be seen as too slow-moving to respond appropriately to the crisis, and to adaptors that which underpins the behavior of innovators who would otherwise be perceived as too outlandish to preserve the values of the organization. Innovators supply strengths in organizational decision-making: they are more likely to think outside the paradigm within which a problem has arisen, unconfined by the tried and tested methods currently in place, and to take risks. These are all relevant when

the organization faces grave uncertainties and requires radical strategic reorganization. But innovators may be unsuited to more short-term decision-making which requires the skills of prudence and caution which are the hallmark of the adapter.

Normally, strategic thinking and planning require the adventurous outlook of the innovator, tempered by the prudence of the adapter. But, without top management vigilance and the planning of the teams that participate in decision-making, it might well attract a preponderance of extreme adapters. If this cognitive style dominates the strategic function, there is likely to be a dysfunctional emphasis on the planning of strategy at the expense of the taking of strategic decisions and the implementation of appropriate policies at the operational and administrative levels. Insofar as strategic decisions are unprogrammed, they therefore require the inputs of innovators. So a prolonged predominance of adapters in this role will lead to organizational imbalance. Normally, operational (and administrative) functions require the efficient involvement of the adapter, tempered by the more outward-looking tendency of the innovator. But, again without top management vigilance, they might attract the extreme innovator who seeks to take risks for short-term benefits. This will interfere with the strategic management of the enterprise and could jeopardize the overall operation of the firm.

LEVEL, STYLE AND STRUCTURE

“Strategic” decisions do not necessarily arise at a managerial level that is automatically higher than that of any other kind of decision, nor do strategic decisions inherently involve the breaking of paradigms, and innovativeness. Just because strategy involves long-range planning does not preclude its occurring within a paradigm, albeit of grand scope, that is nevertheless known and generally-accepted; equally, the innovativeness of eroding boundaries between small-scale organizational systems should not be automatically diminished (Jablokow, 2005). Adaptive and innovative styles of cognition and creativity are constantly required, alongside one another, in the solving of problems. That which predominates appropriately in any given situation depends entirely on the specific context. Organizational problems arise when current strategies no longer fit the demands of the organizational environment: when markets, reflecting demand and competition, are no longer adequately served by the norms of organizational behavior (Jablokow and Kirton, 2009). Such changing circumstances have two vital components. The first is the changing environment must be perceived as involving precipitating events, i.e., the need for change by the organization’s leaders; it is adaptors rather than innovators who are more adept at detecting unforeseen developments that require managerial action. The second is the exploitation of the opportunities such external change is prompting, or the defensive action needed to avoid the threats that the environment contains; these tasks of advancing the required action are more likely taken effectively by the more innovative (Tubbs et al., 2012). This is a matter of cognitive style, not of cognitive or decision level.

This point is summarized by the “paradox of structure” (Kirton, 2003, pp. 126–134): while people require structure whatever their cognitive style, but that structure is ultimately stultifying as persons, organizations and environments exhibit dynamic

behaviors. All the more reason for founding managerial teams and behavior patterns on the contributions of all cognitive styles.

NEUROPHYSIOLOGICAL BASIS OF ADAPTION—INNOVATION

van der Molen (1994) notes on the basis of evolutionary logic that social animals are motivated by two counterposed tendencies: first, to find satisfaction in the company of conspecifics which requires a degree of cooperation and conformity; secondly, to compete with conspecifics for limited resources, such as food, sexual partners, and territory, on which individual survival and biological fitness rely. The personality characteristics which reflect these motivational forces are, in turn, “strongly intercorrelated” traits such as “self-will, thing-orientation, individualism and innovative creativity on the one pole and compliance, person-orientation, sociability, conformity and creative adaptiveness on the other. Individuals differ from one another as far as the balance between these polarities [is] concerned. This variation between individuals must have genetic components” (van der Molen, 1994, p. 140).

Drawing on the work of Cloninger (1986, 1987), van der Molen (1994, pp. 150–152; see also Skinner and Fox-Francoeur, 2013) makes a strong case for the evolutionary and genetic components of adaption—innovation. Cloninger’s “novelty-seeking” and “reward dependence” dimensions of personality are especially pertinent. The former is driven predominantly by the neurotransmitter DA which manifests in behavior that seeks to alleviate boredom and monotony, to deliver the sense of exhilaration and excitement that is generally termed “sensation-seeking” (Zuckerman, 1994); these individuals demonstrate a tendency to be “impulsive, quick-tempered and disorderly. . . quickly distracted or bored. . . easily provoked to prepare for flight or fight” (van der Molen, 1994, p. 151). “Reward dependent” individuals are, in contrast, highly dependent on “social reward and approval, sentiment and succour”; they are “eager to help and please others, persistent, industrious, warmly sympathetic, sentimental, and sensitive to social cues, praise and personal succour, but also able to delay gratification with the expectation of eventually being socially rewarded” (ibid). These individuals’ behavior is strongly controlled by the monoamine neuromodulator norepinephrine.

Which of these bundles of attributes manifests in behavior that marks out some individuals as leaders depends entirely on the demands of the managerial situation: retail banking, relying for the most part on the implementation of standard operating procedures, may have a natural tendency to encourage and reward those behaviors that reflect an adaptive cognitive style; pharmaceutical companies, whose technological, demand and competitive environments reflect a greater dynamism than is ordinarily the norm for retail banking, requires for a much larger part of its activities the presence of individuals whose cognitive and creative styles are predominantly innovative. Investment banking which is expected to reflect a large adaptively-creative style of operation but which attracts innovators is in danger of becoming the kind of “casino banking” that has been so deleterious to both corporate and general social welfare in the last decade. But the inability of an organization to achieve the right cognitive and creative accommodation to its environment will predictably culminate in catastrophe. For the retail bank whose leaders fail to perceive and

respond appropriately to the changing international competition in high-street banking, the pharmaceutical firm that becomes over-involved in the development and marketing of drugs that are novel in the extreme, and for the investment bank that over-emphasizes innovative creativity to the point where reckless decisions are made, catastrophe is equally probable. Predominant organizational climate, adaptive or innovative, can be disastrous if either of these cognitive styles comes to predominate.

These behavioral styles are remarkably consonant the innovative and adaptive cognitive/creative styles, respectively, described by Kirton (2003). Their prevalence and likely genetic basis is borne out by their consistency with the RST described above (Corr, 2008a; see also Eysenck, 2006), though the terminology may vary. The incorporation of adaption-innovation theory into the framework of conceptualization and analysis also suggests a wider search for the neurophysiological basis of styles of creativity. But these are matters for further research.

SUMMARY AND CONCLUSIONS

Analyses of managerial behavior in neurophysiological terms raise two difficulties. The first is conceptual: such accounts conflate cognitive processes with neurophysiological events; the second relates to practical management: such accounts offer little by way of solution to the personal and organizational problems that result from behavior that is motivated by excess influence of either managers’ impulsive systems or their executive systems. This paper has sought to contribute to the resolution of the conceptual problem, by introducing a cognitive dimension, picoeconomics, into neuro-behavioral decision theory, and the adaption—innovation theory of cognitive styles to that of the practical problem by deriving prescriptions for changing managerial behavior.

The prime conclusion is that the use of neurophysiological theory and research in the conceptualization of managerial decision-making and in approaching the solution of problems that arise therein is entirely justified but needs to be qualified by practical considerations suggested by the nature of managerial work and the ways in which managerial behavior can be modified especially in the context of large-scale organizations. Prior to such activity, however, is the resolution of conceptual problems in the explanation of individual behavior on the basis of neurophysiological events. This paper has pursued a central requirement of neuro-behavioral decision theory’s use of intentional terminology to explain human behavior: the role of cognitive terminology and its implication for the shape of the overall theory. It has argued that picoeconomics provides a valuable means of inculcating a cognitive level of explanation into the theory and that one of its advantages is that it suggests solutions to hyperactivity in one or other of the impulsive and executive systems identified by the theory which is exacerbated by hypoactivity in the alternative system. The solutions proposed by picoeconomics may, however, be most suitable for remedial action in clinical settings rather than in organizational settings. The quest for solutions to managerial problems is more readily achieved through organization-level models of managerial activity that incorporate as fully as possible neurophysiological understandings of behavior that are compatible with those found in neuro-behavioral decision theory. One possibility in the present context

is the application of adaption-innovation theory, dimensions of which are known to map reliably on to the neurophysiological and cognitive/personality factors that underpin impulsive and executive systems. The proposal that managerial teams be built and managed in ways that reflect these considerations suggests the most relevant applications of neuro- and behavioral science, with cognitive psychology, for the remediation of certain managerial excesses. These conclusions lead predictably to a call for further research along the lines indicated.

The advantage of this emphasis on cognitive style is that it differentiates managers on the basis of their susceptibility to hyper- or hypo-activity of either the impulsive or executive systems; and recognizing that the managerial functions with which we are concerned are populated by managers of widely differing cognitive styles should reduce our tendencies to stereotype managers on the basis of their broadly-defined functional roles (Foxall and Hackett, 1994; Foxall and Minkes, 1996). The neurophysiological foundations of adaption-innovation as presented here do not map directly on to those of RST or neuro-behavioral decision theory. But there is sufficient overlap to motivate further investigation.

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The marketing firm and consumer choice: implications of bilateral contingency for levels of analysis in organizational neuroscience

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The emergence of a conception of the marketing firm (Foxall, 1999a) conceived within behavioral psychology and based on a corresponding model of consumer choice, (Foxall, 1990/2004) permits an assessment of the levels of behavioral and organizational analysis amenable to neuroscientific examination. This paper explores the ways in which the bilateral contingencies that link the marketing firm with its consumerate allow appropriate levels of organizational neuroscientific analysis to be specified. Having described the concept of the marketing firm and the model of consumer behavior on which it is based, the paper analyzes bilateral contingencies at the levels of (i) market exchange, (ii) emotional reward, and (iii) neuroeconomics. Market exchange emerges as a level of analysis that lends itself predominantly to the explanation of firm—consumerate interactions in terms of the super-personal level of reinforcing and punishing contingencies: the marketing firm can be treated as a contextual or operant system in its own right. However, the emotional reward and neuroeconomic levels of analysis should be confined to the personal level of analysis represented by individual managers on the one hand and individual consumers on the other. This also entails a level of abstraction but it is one that can be satisfactorily handled in terms of the concept of bilateral contingency.

Keywords: consumer behavior analysis, behavioral perspective model, marketing firm, bilateral contingency, emotion, neuroeconomics, levels of explanation, organizational neuroscience

INTRODUCTION

LEVELS OF ANALYSIS IN ORGANIZATIONAL NEUROSCIENCE

An important issue for the emergent discipline of organizational neuroscience is to determine the levels of analysis at which its explanations of behavior may be properly directed. Four such levels may be proposed as appropriate to the explanation of behavior in terms of neurophysiological and environmental (reinforcing and punishing) events: the *sub-personal* level of exposition refers to neurophysiological events; the *personal* level, to the beliefs, desires and other intentional idioms that are ascribed to the individual to account for his/her behavior; the *super-personal* level to the environmental influences that shape and maintain behavior (i.e., reinforcers and punishers); and the *supra-personal* level to the emergent behavior of an organization such as the firm.

Any explanation of behavior in terms of the sub-personal level of neuronal activity (Dennett, 1969), enjoins methodological individualism as a philosophy of science on its practitioners. After all, the neurophysiology of an individual can enter into the explanation of the behavior of that person alone. However, while the behavioral analysis of individual members of organizations proceeds well enough in neurophysiological terms, it is sometimes necessary to understand and predict the behavior of the organization as a whole. Even explanations of behavior based on radical behaviorist models have recently embraced the idea that an organization might be treated as a contextual or operant system in its

own right, its behavior predictable from those of its outputs that are over and above the joint consequences of the behaviors of its members (Glenn, 1991, 2004; Foxall, 1999a; Glenn and Malott, 2004; Biglan and Glenn, 2013). How far is it feasible to construct such an account of organizational behavior on the basis of neurophysiological knowledge?

This may constitute an abstraction too far for traditional behavior analysts for whom the individual organism is the sole bearer of behavior that is to be environmentally explained; but at least the behavioral outputs of supra-individual entities such as organizations are identifiable by intersubjective agreement. The same cannot be said of sub-personal events which are employed in organizational neuroscience to explain the behavior of individual managers; although the effects of such events may be demonstrated under highly-restrictive laboratory conditions, their application in the interpretation of the complex behaviors that characterize human interactions in organizations requires some ground rules for the explanation of personal level behavior by means of inferred sub-personal occurrences.

Since the marketing firm is conceptualized as an organization whose existence is closely tied up with the satisfaction of consumer wants, the analysis of consumer behavior is a prerequisite of the corporate-level investigation appropriate to the marketing firm. The behavior of consumers is depicted comparatively easily in neuroscientific terms because each consumer can be treated

as an individual; this enables analysis to embrace the personal level of analysis which harmonizes with the possibility that sub-personal (neuronal) events within the organism may play a causal role in explaining the organism's behavior. When we consider the behavior of an individual in terms of the super-personal causal texture provided by the consequences of behavior, that is when we consider the individual to be a contextual or operant system, we can specify once again how the persistence of this behavior is influenced by the reinforcing and punishing outcomes it produces. A recent extension of this idea is that the behavior of organizations can be predicted and explained by considering them in their entirety as "contextual systems." A contextual system is an entity the behavior of which can be predicted and explained by reference to its learning history and its current behavior setting; that is by the consequences that have followed its behaviors in the past as they interact with current opportunities to repeat similar behaviors or to engage in competing activities (Foxall, 1999b). This basic assumption of the concept of the marketing firm (Foxall, 1999a), has also been incorporated into behavior analytic thinking through the analysis of metacontingencies (e.g., Biglan and Glenn, 2013).

A complication arises, however, if we seek to apply neuroscientific thinking to the behavior of a supra-personal entity such as a firm or other organization. There is no analog in the organization of the neuronal firing in terms of which individual behavior can be construed. It is, therefore, necessary to deal not with the organization as a neurological unit but with the individual members of the organization whose behavior may be understood by reference to the behavior of other organizational members or external actors. This paper is concerned, nevertheless, to explore the implications of this in order to assess the contribution of organizational neuroscience to the explanation not only of individual managers and consumers, but to the interactions of the marketing firm and its consumerate¹. The key to this lies in the *bilateral contingencies* that these interactions create and maintain (Foxall, 2014a).

CONSUMER BEHAVIOR AND MARKETING MANAGEMENT

Although marketing management is generally understood as a response to the demands of the marketplace, it is unusual for a theory of managerial marketing to proceed in similar terms to those in which the underlying theory of consumer choice is couched. The research program encompassing the Behavioral Perspective Model of consumer behavior (BPM: Foxall, 1990/2004, 2013) and the Theory of the Marketing Firm (TMF: Foxall, 1999a), which employ interfacing operant models, attempts to address this inconsistency. Both models and the interactions they posit have received empirical support in research that has focused on the behavior of the marketing firm as a whole in relation to other firms in the market².

¹This neologism refers simply to the totality of the firm's actual or potential customer base.

²Models developed in organizational sociology of the interaction of the firm and its environment in terms of strategic management are also of relevance to the market-exchange level of analysis explored below (e.g., Hannan and Freeman, 1989; Pfeffer and Salancik, 2003).

This paper proposes and explores a level of analysis that has not previously featured in studies of the marketing firm, namely the neuropsychological and neuroeconomic implications of the completion of successful exchanges with the firm's consumers. The emerging discipline of organizational neuroscience (e.g., Butler and Senior, 2007a,b; Lee and Chamberlain, 2007; Lee et al., 2007; Becker and Cropanzano, 2010) provides a general framework for this analysis, which is extended by the incorporation of some aspects of neuroeconomics to capture the economic and social exchange relationships that characterize marketer-consumer relationships. While the behavior of consumers has been explicated in terms of its neurophysiological underpinnings (Foxall, 2008, 2011), those of managerial and non-managerial firm members have not yet been characterized in this way. The BPM/TMF framework proceeds in terms of operant psychology and operant behavioral economics and it is within this disciplinary matrix that the present paper is constructed. However, the close relationship between reinforcement learning and the operation of the dopaminergic reward prediction error (RPE) system provides an additional reason for undertaking a neuroeconomic analysis of behavior in operant terms (Stanton et al., 2010; Caplin and Glimcher, 2013; Daw, 2013; Daw and Tobler, 2013). This paper therefore examines the activities of managers conceived in operant terms. Although the paper focuses on managerial rather than non-managerial organizational behavior, motivation of the latter is implicit in its treatment of the former since a central component of managerial behavior involves the management of other members of the firm whose motivation must be taken into account.

The paper describes the BPM and TMF approaches before examining in greater detail than hitherto the nature of the bilateral contingencies that link consumer behavior and marketing management. Three levels of analysis of bilateral contingencies are proposed, referring respectively to market-exchange relationships, emotional rewards, and neuroeconomics interactions. The concluding section discusses the capacity of organizational neuroscience to employ analyses of this kind.

CONSUMER BEHAVIOR ANALYSIS

The BPM (Foxall, 1990/2004) is an elaboration of the "three-term contingency," the basis explanatory device of operant behaviorism. In the three-term contingency, a consequential stimulus influences the rate at which a previously-emitted response is repeated (reinforced); any antecedent stimulus present when reinforcement takes place may come to exert control over the subsequent emission of the response, even in the absence of the reinforcer. In summary,

$$S^D \rightarrow R \rightarrow S^R$$

where S^D is a *discriminative stimulus*, i.e., an element of the environment in the presence of which an organism performs selectively by emitting a response, R , which has previously been reinforced in the presence of the S^D ; and S^R is the reinforcing stimulus³.

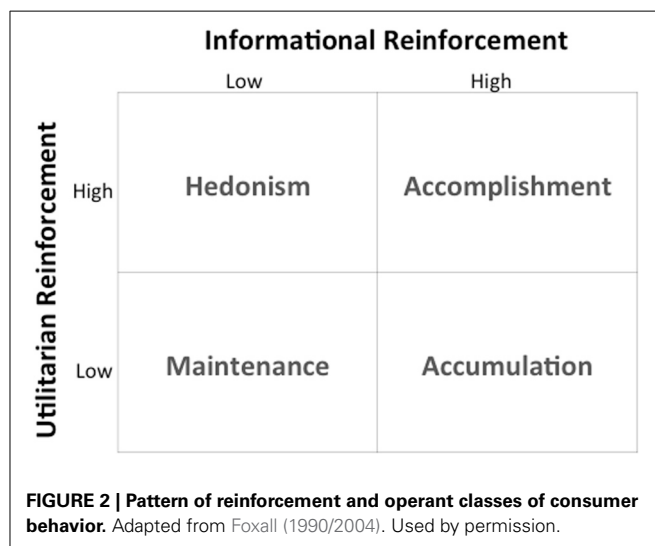
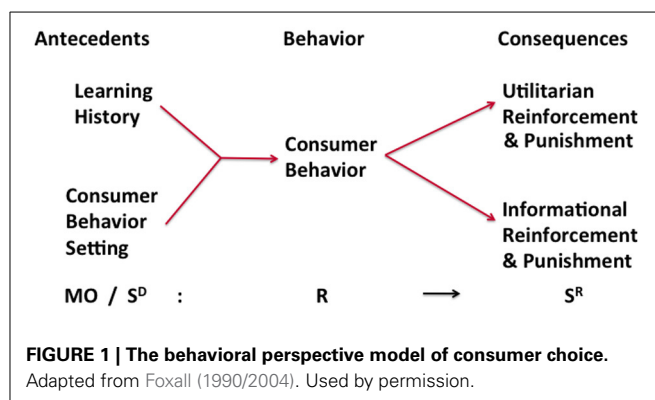
³The paper employs the term *reinforcer* to refer to any environmental stimulus that follows the emission of a response and which has the effect of increasing

The efficacy of a learning history is thus understood as the way in which the outcomes of prior behavior influence current choice. In recent years a 4-term contingency has been proposed in which a motivating operation (MO) is an antecedent event that enhances the relationship between the response and the reinforcer (Michael, 1982; for conceptual and empirical development in the context of consumer behavior analysis, see Fagerström, 2010; Fagerström et al., 2010). An advertisement that promises “This product will stimulate your taste buds like nothing you’ve ever experienced!” is an example of a MO.

This basic paradigm is elaborated in the BPM to bring it into service as a means of predicting and interpreting human economic behavior in naturally-occurring settings. In the BPM, the immediate precursor of consumer behavior is the *consumer situation* which represents the interaction of the consumer’s learning history and the discriminative stimuli and MOs that make up the current behavior setting (Figure 1). In this interaction, the consumer’s experience in similar contexts primes the setting stimuli so that certain behaviors are made more probable while others are inhibited. Consumer behaviors that are encouraged by the consumer situation are those that have met with rewarding or reinforcing consequences on previous consumption occasions while those that are discouraged are those that have been punished. The consequences of consumer behavior, i.e., its reinforcing and aversive outcomes, are of two kinds: *utilitarian reinforcement and punishment* consists in the behavioral consequences that are functionally related to obtaining, owning and using an economic product or service, while *informational reinforcement and punishment* stem from the social and symbolic outcomes of consumption. Consumer behavior is therefore a function of the variables that make up the current consumer behavior setting insofar as these prefigure positive and aversive utilitarian and informational consequences of behaving in particular ways. A more closed consumer behavior setting is one in which one or at most a few behaviors are available to the consumer, while a more open setting is one which presents the consumer with a multiplicity of ways of acting. The topography of consumer behavior is then predictable from the pattern of utilitarian and informational reinforcement which the setting variables signal to be available contingent on the enactment of specific consumer behaviors.

Figure 2 shows the patterns of reinforcement that maintain consumer choice, along with the operant classes of consumer behavior that they define. Figure 3, the BPM Contingency Matrix,

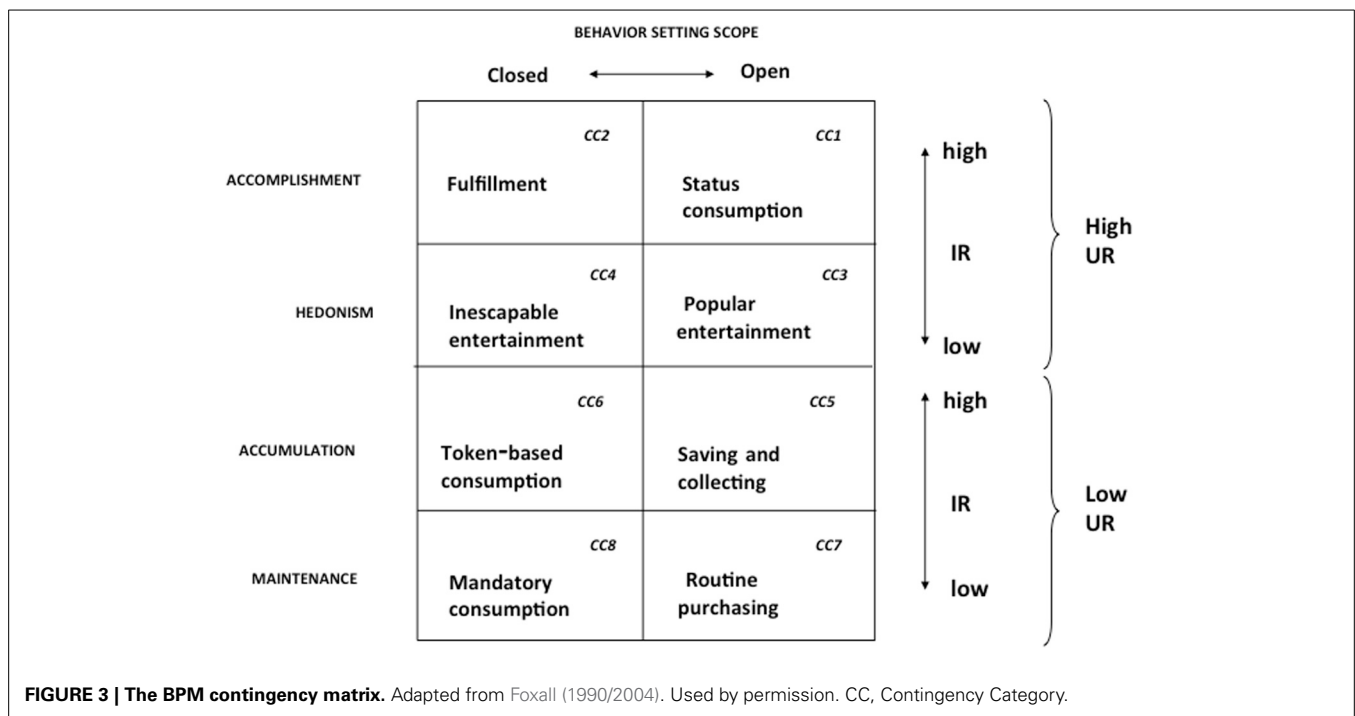
the rate at which that response is performed. This is in line with the usual meaning of a reinforcer as something that strengthens, in this case something that strengthens a response by increasing the probability of its recurrence. This usage is also consonant with the understanding of a reinforcer as something for which an organism will work to achieve. A *punisher* is a consequent stimulus that decreases that rate. Positive reinforcement involves the reception of a reinforcer; negative reinforcement, escape from or avoidance of a punisher. A punisher may also be understood, therefore, as something an organism will work to avoid or escape from. This usage accords with that of Skinner (e.g., 1974) and other radical behaviorists, though it is not followed universally. The term *reward* is employed in this paper to refer to emotional reactions that may affect the rate of behavioral performance and which are elicited by reinforcing stimuli provided by the external environment (Rolls, 1999).



further incorporates the scope of the consumer behavior setting to provide a functional typology of the contingency categories defined by the model. (For a full exposition of the model, see Foxall, 2010). Empirical research demonstrates that changes in consumer behavior, measured as elasticity of demand for fast moving nondurables is a function of the pattern of utilitarian and informational reinforcement (Foxall et al., 2004, 2013; Oliveira-Castro et al., 2011; Yan et al., 2012a,b); moreover, consumers’ utility functions can be estimated to demonstrate that they maximize measurable combinations of these goods: Oliveira-Castro et al. (under review) show that consumers maximize selected combinations of utilitarian reinforcement and informational reinforcement as depicted by the following Cobb-Douglas utility function:

$$U_{(x_1, x_2)} = x_1^a \cdot x_2^b \quad (1)$$

where U is the total amount of utility obtained by consumption of x_1 and x_2 , x_1 is the quantity of utilitarian reinforcement consumed, x_2 is the quantity of informational reinforcement consumed, and a and b are empirically determined parameters such that $a + b = 1$. Furthermore, empirical research suggests that consumers ultimately maximize a combination of emotional responses to consumption situations (Foxall, 2011; Foxall et al.,



2012). In short, we now have a clear picture of the reward structure that shapes and maintains consumer choice, the neuro-physiological processes that govern this structure, and the nature of the emotional utility function which consumers optimize.

THE MARKETING FIRM

The underlying premise of the marketing firm concept (TMF; Foxall, 1999a) is that firms exist in order to market within the competitive structures that compel firms to adopt customer-oriented marketing as a general managerial philosophy is they are to survive (avoid loss) and prosper (innovate in ways that encourage a satisfactory level of sales). The concept reflects elements of the thought of Coase (1937), Simon (1976), and Drucker (2007). The structural conditions that compel such marketing-orientation are marked by the ability to productive capacity to generate supply that exceeds demand, the existence of large levels of discretionary income on the part of consumers engendering inter-industrial competition among firms, and a sophisticated consumerate, i.e., buyers who are knowledgeable with respect to the products they purchase and the alternative offerings available in the marketplace (Foxall, 1981).

The resulting framework of conceptualization and analysis understands corporate institutions as organized patterns of behavior maintained by their consequences, namely the rewards and sanctions that follow them (or, more accurately and avoiding teleology, that have followed them in the past). The behavior of the marketing firm eventuates in the introduction of marketing mixes that offer product, price, promotion, and place utilities to consumers (Foxall, 1999a). The success of the firm, hence its future behavior, depends on the reception these marketing mixes receive in the marketplace. This perspective, based on selection by consequences (Skinner, 1981), permits continuity with evolutionary theories of the firm (Hodgson and Knudsen, 2010) by

embracing the same explanatory principles of selection by consequences that underlies Darwinian natural selection but extending it to events in the ontogenetic development of individuals and organizations. Van Parijs (1981) refers to these explanation as N-evolution and R-evolution respectively, noting the role of natural selection (N) in the former and of reinforcement (R) in the latter.

More specifically, the concept of the marketing firm portrays corporate behavior in marketing-oriented enterprises as the management of the scope of the consumer behavior setting and the pattern of reinforcement available to the consumer. The relationship of the firm and its consumers is depicted in terms of bilateral contingencies in which the behavior of marketers is reinforced and punished by consumer behaviors while consumer behavior is reinforced and punished by managerial actions. This paper concentrates on these *marketing relationships* that are characterized by tangible exchanges of property rights between the firm and its consumers. Its purpose is to complete the picture of *bilateral contingency* between the firm and its consumers by probing (i) what are the reward structures of managers within the marketing firm? (ii) how are these underpinned by neurophysiological processes? (iii) the nature of managers' utility functions. The TMF framework also draws a distinction between two kinds of relationship. The first, between the firm and its customers, between principal and agent within the organization, between the firm and its suppliers, all of which entail literal exchange of legal rights are known as "marketing relationships." Other relationships that do not proceed on this basis even though they may be essential to forming and maintaining marketing relationships, such as social and trade association contacts among firms and broader non-contractual relationships between managers and other employees, are known as "mutuality relationships" (Foxall, 1999a; Vella and Foxall, 2011). This paper is concerned primarily with the former.

The behavior of managers within the marketing firm exhibits many similarities with intra-firm managerial behavior generally. These managerial behaviors have been a central concern of organizational neuroscience. There is a need for cooperation with other managers and other employees, for instance. Work which examines the neurophysiological basis of trust (Zak, 2004, 2007; Zak and Nadler, 2010), cooperation and conflict (Levine, 2007; Tabibnia and Lieberman, 2007), and social interaction (Caldú and Dreher, 2007) are of special interest in the analysis of both mutuality and exchange/marketing relationships. This is especially pertinent to the management of mutuality relationships within the firm as well as outwith the organization, say between the firm and its suppliers. The neurophysiological basis of behavior is not likely to differ among managers but the sources of the rewards they undertake will uniquely follow the pattern of responsibilities their separate job descriptions entail. The various types of decision, from the most administrative or programmed to the most strategic and unprogrammed, that each of these responsibilities requires will have implications for the kind of neurophysiological functioning we can infer (Foxall, 2014b). It is to the strategic sphere, management of bilateral relationships, those that span the connections between the firm and its various publics, that this paper pays special attention, for the very nature of marketing management and the activities of the marketing firm are defined and oriented toward such interactions.

The present analysis is concerned principally with the neurophysiological implications of managerial behavior insofar as it is influenced by the bilateral relationships between the firm and its consumers. Specifically, it traces the sources of reward that sustain these relationships for individual managers. Bilateral contingency implies that the behavior of managers is reinforced by the outcomes of consumer behavior just as consumer behavior is reinforced by the outputs of the marketing firm in the form of products and services. The emphasis is therefore on the *marketing relationships*, those that entail literal exchange, between an executive engaged in marketing management within a supplier organization and its consumers.

BILATERAL CONTINGENCY

THE NATURE OF BILATERAL CONTINGENCY

Behavior analysts have traditionally adopted the individual organism as their unit of analysis. However, by treating the organization that is the marketing firm as a contextual or operant system in its own right, and by assuming that the function of such a firm is to pursue marketing- or customer-oriented marketing, it becomes feasible to interpret the behavior of its managers in terms of the context provided by its customers.

The relationships between the marketing firm and its customers can be conceptualized in terms of bilateral contingencies (Foxall, 1999a). The essence of this approach is that the behavior of an organization is greater than/different from that of the combined repertoires of its members. This conception, which has always been integral to the concept of the marketing firm, is supported by recent thinking in organizational behavior analysis which envisions the behaviors of organizational members as enmeshed in *interlocking behavioral contingencies* (Glenn, 2004; Biglan and Glenn, 2013). In both systems of thought, the behavior

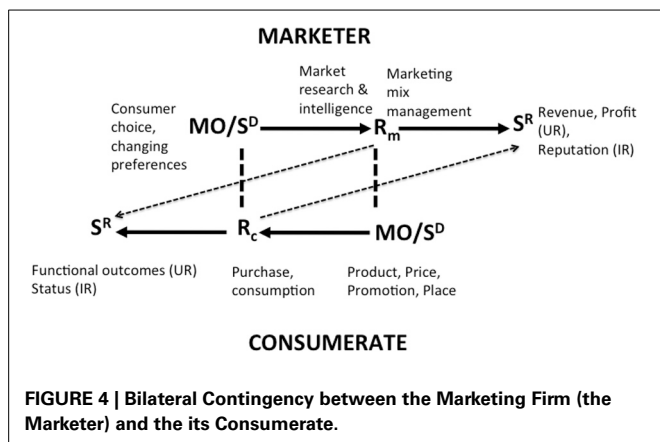
of the system is inferred from the outputs it produces. Hence, each element of the marketing mix—product, price, the promotional communications and distribution systems—affects consumer behavior in such a way as to make the behavior of the organization predictable and explicable. To adopt this kind of analysis is to consider the behavior of an organization or other collectivity of individuals in operant terms, to understand it as a contextual system.

Consideration of the marketing firm as a contextual system has hitherto been confined to the behavioral analysis, in terms of utilitarian and informational reinforcement, of the relationship between its behavioral outputs and their reception by the market and to the scope of the behavior settings of the firm and its customers (Vella and Foxall, 2011, 2013). This has entailed the description and explanation of the firm's behavior in terms of operational measures of behavioral consequences and behavior setting. This is "Market-Exchange Analysis" which is briefly described below. It is feasible, however, to extend the analysis of the marketing firm as a contextual system by comprehending marketer and customer behaviors in neurophysiological terms. This is pursued below in terms of two further analyses: that of the emotional rewards received by consumers and firms as a result of their mutual interactions ("Affective-Reward Analysis"), and that of the capacity of the signals each party to the transaction receives from the other as RPEs that influence its own behavior ("Neuroeconomic Analysis.")

MARKET-EXCHANGE ANALYSIS

Market-exchange analysis concerns the overt relationships between the marketing firm and its customer base (**Figure 4**). The task of marketing management is to plan, devise and implement marketing mixes that deliver satisfactions for the firm's customer base that are profitable for the firm. The components of the marketing mix (product, price, promotion, and place utilities) appear in the market place initially as MOs and discriminative stimuli for the consumer behaviors of browsing, purchasing, and consuming. Purchasing includes the exchange of money for the ownership of the legal right to a product or service and this pecuniary exchange acts as a source of both utilitarian reinforcement (in the form of resources that can be paid out or reinvested) and informational reinforcement (in the form of feedback on corporate performance) for the marketing firm. The efficacy of Rm (managerial behavior) in fulfilling the professional requirements of marketing management, namely the creation of a customer who purchases the product at a price level sufficient to meet the goals of the firm, is determined by the generation of profit and reputation for the firm (depicted by the dotted diagonal line in **Figure 4**). This consumer behavior (Rc) also acts as MOs and discriminative stimuli for further marketing intelligence activities, marketing planning and the devising and implementation of marketing mixes that respond to the stabilities and/or dynamic nature of the behavior of the customer base (Vella and Foxall, 2011, 2013; Foxall, 2014a).

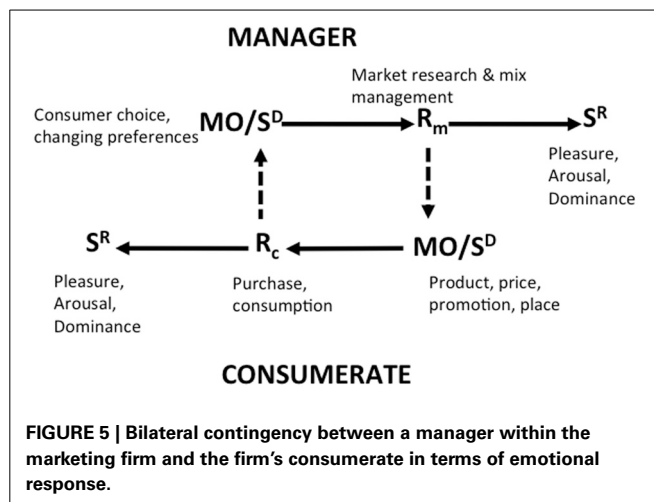
At this level of market interaction between the enterprise and its customer base, managerial behavior can be viewed as maximizing a utility function of the form shown for the individual consumer in Equation (1), comprising a combination of utilitarian reinforcement and informational reinforcement.



AFFECT-REWARD ANALYSIS

The second analysis of bilateral contingency is that which exists between individual managers in the marketing firm pursuing marketing-oriented management, as a strategy of the entire enterprise, via marketing management, the responsibility of the marketing function, and their consumers (Figure 5). The relationships between manager and consumer are maintained at this level of analysis by the reciprocal generation of emotional rewards or satisfactions, particularly *pleasure*, *arousal*, and *dominance* (Mehrabian and Russell, 1974; see also Foxall, 2005).

This hypothesis is supported by the theoretical demonstration of relationships between felt emotion and operant learning as well as by empirical work, albeit with consumers, that shows patterns of emotion to vary consistently and predictably with patterns of reinforcement as defined by the BPM. At the theoretical level, Rolls (1999) suggests a link between learning and emotional reward by proposing that the stimuli that act as reinforcers for behavior also function as elicitors of emotional responses. At the empirical level, there is extensive evidence that consumers respond to retail and consumption environments rich in utilitarian reinforcement with pleasure; to those rich in informational reinforcement with arousal; and to more open settings in terms of dominance. Moreover, consumer behaviors for a wide range of such environments (including the time and money consumers spend within them) has been shown to be determined by these three emotional responses (Foxall, 2011; Foxall et al., 2012; Yani-de-Soriano et al., 2013). Figure 6 summarizes the results of research that indicates a unique pattern of emotional reaction is found for each of the eight BPM-defined contingency categories. We may reasonably conjecture that the responses of individual managers to the reward environments they encounter as members of marketing firms can also be construed in terms of pleasure (derived from utilitarian reinforcement), arousal (informational reinforcement) and dominance (open settings). Although we cannot base this assumption on direct empirical research as is the case for consumer behavior, Mehrabian's theory of emotional responses to environmental cues (Mehrabian, 1980) provides a general warrant for drawing the general conclusion that individual managers' emotional reactions to their reward environments are emotionally reinforced.



		BEHAVIOR SETTING SCOPE	
		Closed	Open
ACCOMPLISHMENT		CC2 PLEASURE AROUSAL dominance	CC1 PLEASURE AROUSAL DOMINANCE
	HEDONISM	CC4 PLEASURE arousal dominance	CC3 PLEASURE arousal DOMINANCE
ACCUMULATION		CC6 pleasure AROUSAL dominance	CC5 pleasure AROUSAL DOMINANCE
	MAINTENANCE	CC8 pleasure arousal dominance	CC7 pleasure arousal DOMINANCE

FIGURE 6 | The BPM emotion-contingency matrix. Source: Foxall (2011). Used by permission. The figure summarizes the research hypotheses and findings. Studies show that: (i) pleasure scores for contingency categories (CCs) 1, 2, 3, and 4 each exceed those of CCs 5, 6, 7, and 8; (ii) arousal scores for CCs 1, 2, 5, and 6 each exceed those of CCs 3, 4, 7, and 8; (iii) dominance scores for CCs 1, 3, 5, and 7 each exceed those for CCs 2, 4, 6, and 8. Moreover, (iv) approach-avoidance (aminusa) scores for CCs 1, 2, 3, and 4 each exceed those for CCs 5, 6, 7, and 8; and (v) approach-avoidance scores for CCs 1 and 3 each exceed those for CCs 2, 4, 5, 6, 7, and 8. (For explication, see text and Foxall et al., 2012).

Regarding pleasure, arousal, and dominance as primary adaptations, it should be possible to identify their neural substrates, their evolutionary significance and their implication in adaptive behaviors (Mehrabian, 1980). Barrett et al. (2007) confirm Mehrabian and Russell's (1974) judgment that pleasure, arousal, and dominance are fundamental to the mental representation of emotion and relate them to reinforcement and punishment (see also Russell and Barrett, 1999; Barrett, 2005; Kober et al., 2008; Lindquist et al., 2012). Moreover, Panksepp's (1998,

2005, 2007) seven core emotional systems – SEEKING, RAGE, FEAR, LUST, CARE, PANIC, PLAY—correspond at a general level to pleasure, arousal and dominance (Foxall, 2008). **Figure 7** proposes a broader classification which incorporates PLEASURE and POWER/DOMINANCE following the suggestion of Toronchuk and Ellis (2010).

Neurophysiological bases of pleasure, arousal, and dominance

Feelings of *pleasure* are closely related to the evolutionarily-based outcomes of biological fitness; moreover, utilitarian or functional reward promotes the restoration and maintenance of homeostasis (Panksepp, 1998). Expectation of pleasure also facilitates goal-orientation by contributing to the setting of objectives (Politzer, 2008). The association of the core emotion of pleasure-displeasure is associated with the utility/disutility of behavioral consequences (Barrett et al., 2007) resulting from approach/avoidance of specific stimuli. This accords with Rolls's (1999) argument that the stimuli that reinforce/punish behavior evoke emotional feeling. Genetic endowment specifies not particular behaviors but the goals of classes of behavior by selecting the stimuli that will reinforce or punish approach and avoidance (Rolls, 2005).

The allocation of localized brain regions to the production of emotions is dangerous since the neuronal basis of any particular source of affect may be distributed (Uttal, 2001; Legrenzi and Umità, 2011; Lindquist et al., 2012). However, there is evidence that self-reports of pleasure coincide with increased activity in the amygdala, orbito-frontal cortex (OFC), and ventromedial pre-frontal cortex (vmPFC) (Cardinal et al., 2002; Rolls et al., 2009). Increases in the activation of the ventral tegmental area (VTA), the subcortical telencephalon areas nucleus accumbens (NAC), and parts of the ventral striatum (vStr), all well-endowed with

dopaminergic neurons, are associated with pleasant experiences; these correlate too with hypothalamus (Hy), vmPFC, and right OFC activation (Wager et al., 2008). The NAC is closely related to reinforcement and pleasure. Winkielman et al. (2005 p. 346) note that “The nucleus accumbens, which lies at the front of the subcortical forebrain and is rich in dopamine and opioid neurotransmitters, is as famous for positive affective states as the amygdala is for fearful ones.” While defending the role of NAC in positive affect, Berridge and Robinson (1998) maintain that the NAC is implicated in “wanting” a stimulus (known as its incentive salience) rather than “pleasure” in obtaining or consuming it.

Moreover, brain areas closely associated with pleasure-displeasure comprise a region “that is involved in establishing the threat or reward value of a stimulus” (Barrett et al., 2007, p. 382). Continuing this theme, Lindquist et al. (2012 p. 124) employ *core affect* to refer to “the mental representations of bodily changes that are sometimes experienced as pleasure and displeasure with some degree of arousal,” and argue that it is related to the identification of and response to motivationally salient environmental stimuli. Representations of bodily states relies on previous experience which we may presume to rely, at least in part, on the outcome of the consequences of operant responding. Lindquist et al. (2012) concur with Panksepp (1998) that emotions fulfill a homeostatic function that indicates the value of approach/avoidance with respect to environmental stimuli.

The neurophysiological bases of *arousal* are distributed, though cortical areas and the thalamic regions whose neurons innervate cortical areas are sensitized in the course of arousing experience (LeDoux, 1998, 2000, 2003). LeDoux (1998 pp. 287–291) notes that four systems found in the brain stem are involved in arousal, each of which generates a different neurotransmitter: acetylcholine (ACh), noradrenaline, dopamine, and serotonin. The amygdala, which is implicated in the production of danger signals, and the nucleus basalis, the latter a repository of ACh, are particularly relevant. Lesioning of either reduces the capacity of fear stimuli to engender arousal; stimulation of either generates cortical arousal (LeDoux, 1998, p. 289). In response to arousing stimuli, the amygdala induces the nucleus basalis to release ACh throughout the cortex. Emotional stimuli in particular produces substantial arousal (as compared with the limited arousal engendered by any novel stimulus), an observation that LeDoux ascribes to the involvement of the amygdala.

The hormones, oxytocin, and testosterone, also play a part in regulating fear and aggression as well as nurturance and affiliation. The neurotransmitter, serotonin contributes to the reduction of anxiety, so that the reduction of CNS serotonin impairs impulse control and is implicated in violence, impatience, and the assumption of risks of punishment or injury (Higley et al., 1996). The administration of serotonin by means of selective serotonin reuptake inhibitor (SSRI) medication modulates antisocial tendencies (Knutson et al., 1998). While dopamine has a general role in the anticipation of rewarded behavior, it may have a particular affinity with behavior that eventuates in (reported) arousal since it is associated with excitement, engagement, and the involved pursuit of primary reinforcers. It is, moreover, involved in energizing higher motor cortex areas on which SEEKING relies (Panksepp, 1998).

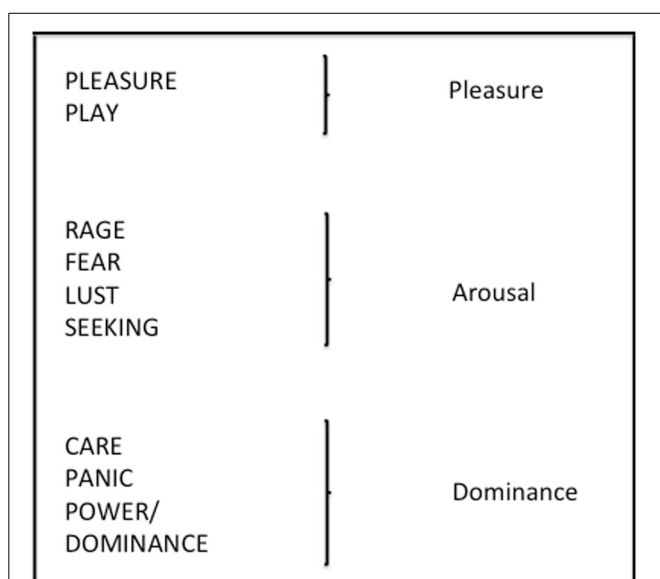


FIGURE 7 | Panksepp's (1998) seven core emotional systems, augmented by Pleasure and Power Dominance (after Toronchuk and Ellis, 2010) and related to Mehrabian and Russell's (1974) tripartite classification of emotions.

In their analyses of the role of dopamine release in learning, Berridge and Robinson (1998, 2003) refer to both a hedonic or affective outcome (denoting “liking” or pleasure) and a motivational element (suggestive of “wanting” or incentive salience). Liking is associated with opioid transmission on to GABAergic neurons in the nucleus accumbens (Winkielman et al., 2005). Wanting or incentive salience is a separate process, more likely associated with dopamine release and retention. Hence, far from being the “pleasure chemical” it has often been identified as, dopamine is neither necessary nor sufficient for “liking.” Manipulation of the dopamine system does, however, change motivated behavior by increasing instrumental responses and the consumption of rewards; incentive salience is a motivational rather than an affective component of reward that transforms neutral stimuli into compelling incentives (Robinson and Berridge, 2003; Berridge, 2004). In line with Berridge’s (2000) argument that liking and wanting should be separated, Toronchuk and Ellis (2010) contrast PLEASURE which is relevant to consummatory behaviors and associated with opioid and GABA release, and Panksepp’s (1998) SEEKING which is associated with dopamine release and which marks appetitive responses. This dichotomy is well-accommodated to the distinction drawn here since the wanting which is inherent in SEEKING is indicated by arousal rather than pleasure.

Dominance is an emotional response that varies as the consumer or managerial behavior setting permits a degree of autonomy or induces conformity by the number of behavioral alternatives it offers. It relates to autonomy and agency, and contrasts with submissiveness and harmoniousness (Barrett et al., 2007). Prosocial behavior and affiliation are associated with dopamine; opioids, with sociability; while the neuropeptide oxytocin increases feelings of trust (Panksepp, 2007). Both serotonin and testosterone are associated with feelings of dominance (Buss, 2004, 2005; Cummins, 2005). The relationship between dominance and the BPM resides in a tendency of consumers to report high levels of this emotional response as well as higher levels of pleasure in relation to more open settings. These are settings which offer a larger number of behavioral outcomes, and which are usually under the control of the consumer rather than an external agent like a marketer or government office. In the case of managerial behavior, dominance is also likely to be felt to an increased extent in situations that permit autonomous and multifaceted activity.

In a paper that positively reviews the evidence for a model of emotionality that includes dominance as well as pleasure and arousal, Demaree et al. (2005 p. 3) propose that “relative left- and right-frontal activation (may be) associated with feelings of dominance and submissiveness, respectively.”

Barrett et al. (2007) make a strong contribution to understanding the inter-relationships among pleasure, arousal, and dominance by proposing that arousal and dominance signify the *content* of core emotion or valence. The first of Barrett et al.’s sources of the content of valence, arousal-based content, denotes *activeness* and is revealed in self-reports of feeling active, attentive or wound-up, while unarousal, denoting *stillness*, is revealed in self-reports of feeling still, quiet and sleepy. Linking to Mehrabian and Russell’s concept of arousal this active—still emotionality is

an affective response to the presentation informational reinforcement. Barrett et al.’s second source of valence-content, relational content, concerns the extent of domination or submissiveness experienced in the presence of others: this social dimension of emotional reaction is redolent of the scope of the consumer’s or manager’s behavior setting. Finally, Barrett et al.’s situational source of content indicates the degree of novelty or unexpectedness of a situation, its contribution to or hindrance of an objective, and its consonance with norms and values. This too is suggestive of setting scope.

Emotional utility function

The manager, like the consumer, is assume⁴ to maximize the combined consumption of pleasure, arousal and dominance so that his/her utility function is

$$U_{(P,A,D)} = P^a, A^b, D^c \quad (2)$$

where U is the total amount of utility obtained by consumption of pleasure, arousal and dominance, P is the quantity of pleasure consumed, A is the quantity of arousal consumed, D is the quantity of dominance consumed, and a, b and c are empirically determined parameters such that $a + b + c = 1$.

Bilateral contingency and emotion

We assume that managers experience pleasure, arousal, and dominance as a result very largely of inputs of informational reinforcement which relate to symbolic representations of the success of market mix implementation in the market place. Sales figures and profitability manifest in pleasure insofar as they relate to the enhancement of the resource base of the enterprise; in arousal insofar as they refer to the achievement of a higher corporate reputation; and dominance insofar as they reflect greater autonomy of the firm in the capacity to meet its goals, raise capital. Over and above the specific rewards provided to managers, such as higher salaries and promotions, these corporate-level enhancements may result in managerial emotional responses. By comparison with salary and promotion, they derive relatively directly from the relationships of the firm with its customer base.

The chief medium through which managers directly receive emotional reward as a result of profitably fulfilling consumers’ requirements is necessarily in the form of informational reinforcement (though if they are recompensed by bonus payments or commissions that are based on levels of sales, they also receive utilitarian reinforcement as a direct result of responding to consumer demand, and in a rationally functioning firm, they will presumably so benefit through salary adjustments and promotions in a somewhat indirect fashion). How is it possible for informational reinforcement, which we have previously identified with arousal, to give rise to all three emotions considered by Mehrabian and Russell (1974)? The version of the BPM that

⁴Whether managers’ utility functions can be represented in this way remains an issue for empirical research, of course, though work in progress by the Consumer Behavior Analysis Research Group at Cardiff University and Consuma at the University of Brasilia is seeking to establish the fact of the matter for both consumers and managers. In the meantime, Equation (2) remains an assumption.

has thus far been the subject of this paper presents its variables in extensional terms; but there are also versions of the model that employ intentional and cognitive variables in order to continue explanation beyond that possible for the extensional portrayal of consumer choice (Foxall, 2007a).

Informational reinforcement, as it is conceptualized in the purely extensional depiction of the BPM, consists in the auditory, visual, and other sensory elements that act as reinforcers for operant behavior. In the cognitive depiction of the BPM, without making any ontological adjustments about the nature of informational reinforcement, we understand it in terms of symbolic reinforcement which has its effect on behavior by virtue of its cognitive and affective functions. It is because we are considering, at the cognitive and affective level, informational reinforcement to be a source of symbolic reinforcement that we can conceptualize the manager's utility function in terms of utilitarian reinforcement and informational reinforcement as represented symbolically (Foxall, 2013).

NEUROECONOMIC ANALYSIS

The third level of bilateral contingency is that obtaining between individual marketing managers and the firm's consumerate depicted as reciprocally generating reward predictions which engender behaviors that reinforce one another's conduct (Figure 8). The ways in which the imminence of rewards is signaled to managers by the behaviors of the consumerate and vice versa may be depicted in terms of "RPEs" between the expected rewards and the actual rewards achieved (Schultz et al., 1997). These signals, which form a strong core of neuroeconomic analysis (Glimcher, 2011) are discussed in detail below after a distinction is made between two styles of neuroeconomics and their relative relevance to the analysis of bilateral contingency.

Modes of neuroeconomic analysis

The role of neuroeconomics in explanation requires elaboration. Ross (2008) distinguishes two styles of neuroeconomics, which he terms *behavioral economics in the scanner* and *neurocellular economics*. Behavioral economics in the scanner (BES) is depicted by Ross as stemming from the dissatisfaction of some behavioral economists with neoclassical microeconomics who, he argues,

attempt to substitute psychological findings and reasoning for standard economic analysis. He argues that BES is "naively reductionist" and denies economics the right to model its subject matter abstractly, something permitted of other sciences. BES simply performs repetitions of standard behavioral-economic experiments such as the ultimatum game, the Prisoner's Dilemma, and intertemporal choice protocols used to access consumers' discounting of future outcomes during the observation of participants' brain functions via fMRI procedures. It is *neurocellular economics* that is of relevance to the current project. We can depict BES as a form of biology in the service of economics.

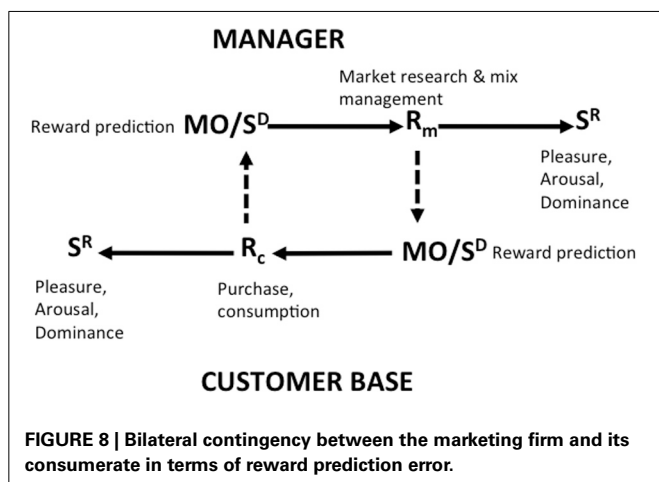
Neurocellular economics (NE), by contrast, is economics in the service of biology. It employs the models derived by mathematical economics, especially those of constrained maximization and equilibrium analysis, to represent brain structures and functions. The underlying assumption is that brains, like markets, are "massively distributed information-processing networks over which executive systems can exert only limited and imperfect governance." NE is an approach to neuroeconomics that uses economic analysis to understand the neurobiology underpinning economic behavior (Glimcher, 2011). It is NE that is of primary relevance to the analysis of bilateral contingency since we are attempting here to establish the ways in which the behavior of other actors in the economic system impinge on the neuronal activity of consumers and managers respectively and prime them for the receipt of reinforcing or punishing outcomes of their own behaviors.

Reward prediction error

It has long been suspected, on the basis of experiments in which monkeys receive food rewards while the activity of dopaminergic neurons in the VTA is recorded (Schultz, 1992), that dopaminergic neurons code reinforcement (Robbins and Everitt, 2002). The responding of these cells to food rewards which takes place in phasic bouts is transferred, after the establishment of predictive stimuli, to those stimuli: the dopaminergic neurons respond to the CS rather than to the reward. Moreover, should the reward not appear, the activity of the dopaminergic neuron (which is recorded at the level of the individual cell) is depressed precisely when the reward was predicted to occur. As Robbins and Everitt (2002, p. 174) point out, this is indicative that the dopaminergic activity is implicated in the establishment of an internal representation of the reward (Montague et al., 1996).

RPE is the difference between a reward actually obtained and that which was predicted or expected. A negative RPE results when the reward is predicted but not obtained; a positive RPE, when a reward is not expected but is nevertheless obtained (Schultz et al., 1997). The reason why this subject has assumed such prominence in neuroeconomics is the possibility that RPEs may be reflected in dopaminergic neurons' firing rates. If so, the mechanism suggests an obvious linkage between neoclassical economics and neuroscience that is fundamental to the emerging discipline of neuroeconomics. In the present context, it adds to the explanatory power of operant psychology by proposing an underlying causal connexion (Glimcher, 2011).

While, in Pavlovian learning, the predictive significance of a signal (CS) for the arrival of a reinforcer is paramount, in



operant learning, which is the principal paradigm we are using to interpret the behaviors of the marketing firm and its consumers, signals (S^D s or MOs) influence the rate of repetition of a response that has previously led reliably to gaining the reinforcer (Schultz and Dickinson, 2000; Daw, 2013; Daw and Tobler, 2013). Associationism, which embraces both of these learning paradigms, argues that both involve the establishment of an association between the representations of either a signal (Pavlovian conditioning) or a response (operant conditioning) and the reinforcer. The procedure in which the association is formed requires that the reinforcer follow closely and reliably on the presentation of either the signal or the response, such that each repetition of the signal or response leading to the reinforcer strengthens the association (Schultz and Dickinson, 2000; see also Schultz, 2010).

The key determinant of whether a signal engenders learning, however, is not its simple presentation but its being unpredicted, novel or surprising (Di Chiara, 2002). The extent to which a stimulus is unpredicted is shown by means of a *prediction error* term, $(\lambda - \Sigma V)$, where λ is the strength of association with the reinforcer that predicts fully the occurrence of the reinforcer, and ΣV is the combined associative strength of all signals present on the learning episode in question. The prediction error $(\lambda - \Sigma V)$ indicates the extent to which the appearance of the reinforcer is novel, surprising, unpredicted or unexpected.

Schultz and Dickinson (2000) draw two conclusions from this which are relevant to the present discussion of bilateral contingency. The first concerns the evocation of emotions by the reinforcers and punishers resulting from operant learning, as posited by Rolls's (1999) theory of emotion. Schultz and Dickinson (2000) define learning as acquiring predictions of outcomes whether these take the form of "reward, punishment, behavioral reactions, external stimuli, internal states" (p. 476). Internal states include emotions; hence, the reinforcing stimuli that evoke emotion-feelings may also predict those feelings.

The second is Schultz and Dickinson's proposal of a sort of homeostatic principle by which behavioral outcomes that produce a mismatch (prediction error) between expected and actual reward alter subsequent behavior so as to reduce the gap between outcome and prediction. By explaining how behavior is modified in light of experience, this appears to be a mechanism for reinforcement. It explains how behavior is modified in light of experience. The process of behavior modification continues until the prediction error is zero at which point the discrepancy between expected/predicted reinforcement and actual reinforcement is eliminated. The outcome occurs exactly as predicted. This process, in line with blocking, confines learning to stimuli that predict unexpected/surprising/novel events, and eliminates learning with respect to redundant stimuli. This reasoning is very much in line with behavioral/operant learning and provides a neurophysiological explanation of learning. In instrumental or operant learning, the response manifests an expectation of reward; when the prediction is falsified by the occurrence of an unpredicted or not-fully-predicted reward (or a punisher), there is a RPE which influences future predictions and behaviors. This, of course, is the essence of operant learning. RPEs thus influence reinforcers, punishers, external signals such as attention-inducing stimuli, and behavioral goals/targets.

The import of RPEs in the current analysis is that they link consumer and managerial behaviors by showing how each relies on signals from the other as to the impending consequences of behavior; these signals may function as discriminative stimuli or MOs for further response.

LEVELS OF ANALYSIS REVISITED

FEASIBLE AND INFEASIBLE LEVELS OF ANALYSIS

The grounds on which both organizations and their separate members may be understood as contextual systems are as follows. Each manager's behavior is constrained by the behavior setting in which he/she works and by the pattern of reinforcement available to him/her. The manager's behavior setting scope/dominance is determined to some extent by his/her ability to manage the structure of this pattern of reinforcement and the scope of the behavior setting, and by his/her ability to influence other managers' setting scope and pattern of reinforcement. But we can also speak of the corporate behavior setting and of the pattern of reinforcement that follows from the delivery of corporate outputs (in terms of marketing mixes) to the marketplace (Vella and Foxall, 2011, 2013). The corporate behavior setting is composed of the strategic scope of the firm, predominantly its product-market matrix which defines the kind of organization it is, its purpose, the nature of its customer base and therefore the wants it is attempting to fulfill. It will also embrace the firm's overall policies, goals and objectives, and, following its resource audit, its capabilities, all of which determine the way in which it views novel opportunities and dangers as signaled by the marketplace and comparative competitive advantages. The reception its marketing mixes receive from customers determines the success of the firm and thus the extent to which its overall behavior pattern remains constant (providing similar marketing mixes) or changes (devising new or modified mixes). The two aspects are related in that success or failure in the marketplace may lead to a reassessment of the firm's scope and a consolidation of or change in its strategic direction (Foxall, 2014b).

What these examples have in common is that they relate individual human behavior, which is a personal level phenomenon, to the super-personal level of environmental contingencies which in each case are observable and measurable; the pattern or sequence of such contingencies can, therefore, be related systematically to the pattern or sequence of individual behavior; the behavior can then be presented as a function of its consequences. The result is a functional explanation of molar patterns of behavior that invokes the correlational law of effect (Baum, 1973). The behavior of the firm as a whole, i.e., the emergent generation of a marketing mix, is by definition not a personal level phenomenon. We may designate it *supra-personal* insofar as it is different from, greater than, over-and-above the combined behaviors of the members of the firm. The fortunes of the firm, as we have argued, depend on the reinforcing and punishing consequences of such behavior which in turn rely on the reception the marketing mix receives from the consumerate. Such organizational behavior depends at some level on the neurophysiological events responsible for the behavior of the firm's individual members, just as it depends on those managers' behavior being reinforced and punished by its immediate consequences that determine the success or failure of each

manager. But there is no justification for ascribing a neurophysiological level of analysis to the organization. There is no way of combining or averaging the neurophysiological events of each manager to produce a composite measure that would explain the behavior of the organization. There is no bilateral contingency that links firm level behavior with that of the consumerate via meaningful neurophysiological mechanisms. All of the relevant interactions between firm and consumerate, i.e., those that predict and explain the behaviors of each, can be described at the supra-personal level (in the case of the firm) and the personal level (in the consumerate).

However, we can isolate a useful mode of explanation in terms of the emotional rewards that individual managers and individual consumers receive, each as a result of the behavior of the other. There is another useful explanatory mode at the level of neuroeconomic RPEs that result for managers from the behaviors of consumers and for consumers from those of managers. The managerial behavior that influences consumer choice may actually be that of the firm.

A FRAMEWORK FOR RESEARCH

The chief implications of the foregoing for organizational neuroscience lies in clarification of the kinds of investigation that can reasonably be conducted within this emerging framework of conceptualization and analysis. The argument is that neurophysiological explanation, in contrast to that of operant psychology, cannot be extended beyond the individual. This means that, although operant psychology may find an expression in the study of supra-individual systems such as organizations like the firm, this mode of investigation is denied to organizational neuroscience. The chief implication for the development of consumer behavior analysis and the concept of the marketing firm is that the super-personal level of analysis, in which the behavior of the firm is understood in terms of the effects that its emergent outputs (notably marketing mixes) have had on its primary environment, namely its consumerate, may be underpinned by organizational neuroscience as long as this is confined to the behavioral implications for individual managers and consumers and not abstracted to the organizational level of analysis. All of the modes of analysis advocated here can be supported by the identification of bilateral contingencies that closely link the behaviors of the transacting parties via observable and operational variables; those which have not been supported by the foregoing analysis are not realized in bilateral contingencies.

At the *supra-personal level* of exposition, firms' behaviors can be identified in terms of the marketing mix elements they introduce to the market (and these, in turn, can be traced back to their marketing intelligence procedures, their goal-formation through strategic audits of their comparative capabilities and the opportunities of the marketplace, their strategic and marketing planning, the devising and implementation of their marketing mixes). The fortunes of these marketing mixes can be ascertained through analysis of their impacts on sales and profitability. These are not easy measures to obtain in practice but attempts to secure them form part of the feedback mechanisms on which firms rely. It is feasible at this level of analysis to identify a firm-level behavior setting and learning history, and therefore a

firm-level situation; the behavior attributable to this corporate situation has implications for the behavior of the firm's consumerate whether this comprises a mass of individual consumers whose collective actions amount to what Biglan and Glenn (2013) nominate macro-behavior (Figure 9) or one or more corporate customers the behavioral outputs of which can be characterized as metacontingency (Figure 10).

The equivalent of supra-contingency at the level of the individual consumer or manager is the *super-personal level* of explanation. Super-contingency refers to the control of an individual's behavior by contingencies of reinforcement, the operant conditioning paradigm exemplified by the three-term contingency. Although this level of exposition stands alone as a means of predicting individual behavior, especially in the relatively closed settings of the operant chamber, its explanatory power may be extended by considering the sub-personal, neuronal, ramifications of operant reinforcement. As the earlier discussion shows, the receipt of reinforcers is mediated by RPEs and leads to emotional reactions that reflect the pattern of reinforcement. At the super-personal level of exposition, both consumer and managerial behavior can be associated with patterns of rewards and punishments: a large body of research on the BPM has established this for consumer behavior and a far larger range of research studies have endorsed the principle for managers.

At the *personal level* of exposition, intentional idioms may be ascribed in the explanation of behavior as long as the ascription is limited so as to be consonant with empirical research findings at the super-personal and sub-personal levels (see Foxall, 2004, 2007a,b, 2013). This personal level of exposition differs from the other levels in providing an interpretation of behavior that employs intention idioms rather than the extensional language of science. That is, it proceeds in terms of beliefs and desires, emotion-feelings and perceptions that are necessary to render the

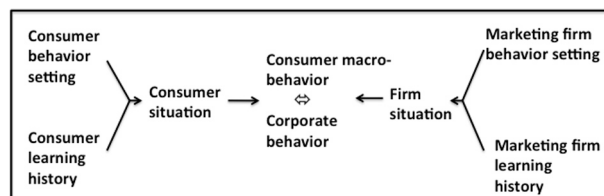


FIGURE 9 | Bilateral contingency between the marketing firm as a metacontingency and the macro-behavior of the consumerate of final buyers.

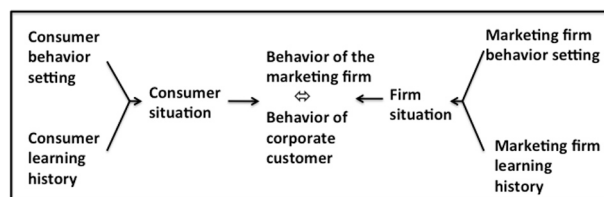
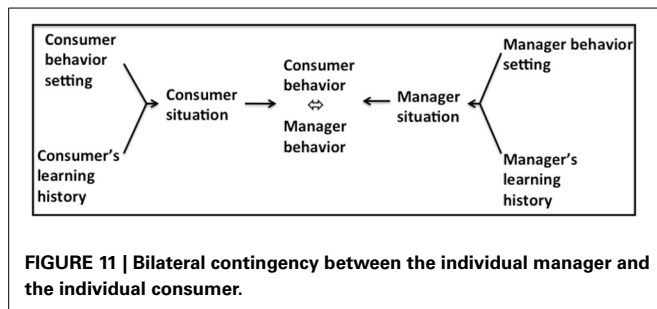


FIGURE 10 | Bilateral contingency between the marketing firm as a metacontingency and a corporate customer as a metacontingency.



behavior intelligible. Intentional exposition is used when extensional language no longer suffices to provide an understanding of behavior, principally when the stimuli responsible for behavior cannot be identified. The super-personal and sub-personal levels of exposition are integral to this personal level since they are instrumental in the creation and support of the intentional idioms that enter into personal level interpretation. Hence, in the context of neuropsychology, the *sub-personal level* of exposition involves the neurophysiological events that enter into interpretations of behavior in intentional and decision-making terms (Dennett, 1969; Foxall, 2007b,c).

The affect-reward and neuroeconomic levels of analysis introduced in this paper involve the super-personal, personal, and sub-personal levels of exposition. They refer to the behavior of single individuals rather than to organizational behavior (Figure 11)

CONCLUSIONS

This paper has sought to understand the managerial mechanisms that facilitate the operation of the marketing firm by enhancing its exchange relationships with its customer base. Drawing on the TME, it was suggested that the characterization of the parties to this bilateral transaction can be depicted as contextual systems, their behavior being explained in terms of the consequent products of the marketing firm and the customer base. The concept of bilateral contingency, which has been employed to describe the relatedness of the participants in marketing transactions to one another (Foxall, 1999a), is of value in emphasizing the interconnectedness of behavior systems that make up the marketplace. The various levels of analysis that have been considered suggest guidelines for the degree of abstraction with regard to relationships based on neurophysiological events can be justified in organizational neuroscience. The overall conclusion is that while firms and other organizations may be treated, by virtue of their generating outputs that are over and above the consequences of the behaviors of individual managers or their cumulative behavioral outputs, as contextual systems, only individual behavior may legitimately be explained by reference to a neurophysiological sub-personal level. Both individual organisms and human organizations may be treated as contextual systems but only the former constitute neurophysiological systems.

Future research on the marketing firm and bilateral contingency could usefully examine the role of the neuronal basis of cooperative behavior and trust as they are related to both intra-firm and extra-firm relationships. It would be particularly useful to understand better how trust and cooperation vary between (a)

firm ⇔ firm relationships and (b) those linking the firm and final consumers.

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Near-infrared spectroscopy (NIRS) as a new tool for neuroeconomic research

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Over the last decade, the application of neuroscience to economic research has gained in importance and the number of neuroeconomic studies has grown extensively. The most common method for these investigations is fMRI. However, fMRI has limitations (particularly concerning situational factors) that should be countered with other methods. This review elaborates on the use of functional Near-Infrared Spectroscopy (fNIRS) as a new and promising tool for investigating economic decision making both in field experiments and outside the laboratory. We describe results of studies investigating the reliability of prototype NIRS studies, as well as detailing experiments using conventional and stationary fNIRS devices to analyze this potential. This review article shows that further research using mobile fNIRS for studies on economic decision making outside the laboratory could be a fruitful avenue helping to develop the potential of a new method for field experiments outside the laboratory.

Keywords: mobile fNIRS, prefrontal cortex, real-world setting, neuroeconomics, decision making

INTRODUCTION

Over the last decade, the investigation of economic research questions by use of well-established neurological and neurophysiological methods such as fMRI, EEG, electrodermal activity (EDA) or eye-tracking has led to the new interdisciplinary research field called “neuroeconomics” (e.g., McClure et al., 2004; Bechara et al., 2005; Camerer et al., 2005; Kenning and Plassmann, 2005; Singer and Fehr, 2005; Brosch and Sander, 2013). In this field, the underlying neurophysiological processes of economic decision making have been increasingly elaborated with diverse research foci.

Different research studies focus on the neural correlates of social dimensions in economic markets (e.g., Fehr et al., 2005; Ruff et al., 2013), explore behavioral game theories through a new neurophysiological perspective (e.g., Sanfey et al., 2003; Bhatt and Camerer, 2005) and investigate brain activities related to investors’ financial decision-making behavior (e.g., McClure et al., 2004; Kuhnen and Knutson, 2005). Other research focuses on consumers’ decision-making processes and their corresponding brain activities (e.g., Yoon et al., 2006; Knutson et al., 2007; Hedgcock and Rao, 2009). Moreover, management researchers in the area of information system research have begun to use these neurophysiological methods and prior findings to investigate information system constructs, as well as users’ decision making in the online world (e.g., Dimoka, 2011; Kopton et al., 2013; Riedl et al., 2014). Recently, management research focusing on organizational behavior has also begun to develop a new interdisciplinary perspective by transferring prior neurological findings to extend organizational theories (e.g., Boyatzis et al., 2014).

This body of research has generally resulted in significant developments by adding a new theoretical perspective to economic research. However, the majority of these well-known neuroeconomic studies, all of which investigate decision making from different economic perspectives (Glimcher et al., 2013), were commonly investigated through fMRI-based research (Braeutigam, 2012).

Nevertheless, fMRI measurements have limitations with regard to how their real-world applicability corresponds to restricted external validity, so that many researchers question whether economic decision making can truly be measured and generalized in such a restricted situation (Shimokawa et al., 2009; Ariely and Berns, 2010; Ayaz et al., 2013). Only limited conditions can be tested in the fMRI-scanner, and only specific types of stimuli can be shown while the participant is lying in the scanner. For this reason, neuroeconomic studies, to date, have primarily focused on “fictive” tasks and not “real-world” situations (Ariely and Berns, 2010). Because of the technical limitations, the influencing stimuli in these studies were often reduced in complexity, suggesting that other measurements are necessary for future field experiments in neuroeconomics.

Against this background, mobile functional near-infrared spectroscopy (fNIRS) measurement seems to have strong potential for applicability in field studies. fNIRS can be defined as a non-invasive optical brain imaging technique that investigates cerebral blood flow (CBF) as well as the hemodynamic response in a local brain area during neural activity (Jackson and Kennedy, 2013). In different prior studies it has been demonstrated that, comparable to functional magnetic resonance imaging (fMRI), the fNIRS method is a reliable and valid measurement for cortical activations (see Ernst et al., 2013).

In response to the limited research, this paper aims to integrate various disciplinary fNIRS studies in economic decision making research which, up to now, have been examined mainly in isolation from each other. Moreover, we provide insight into the potential of fNIRS for measuring brain activations during different real-world situations of economic decision making.

RECENT CHALLENGES FOR NEUROECONOMICS

At present, researchers in (neuro-)economics are challenged by many new economic trends. Particularly, these trends increase the difficulty of using traditional neurophysiological methods such as fMRI to investigate research questions, for which measuring situational factors in the “real world” and outside the laboratory are highly important.

Three current examples of trends regarding consumers’ economic decision making effectively illuminate new challenges of (neuro-)economic research:

- (1) Integrating consumers into the innovation process is becoming increasingly essential (e.g., von Hippel and Katz, 2002; Jeppesen and Molin, 2003; Gassmann et al., 2010). In general, innovative products, ideas or concepts that are considered “radical” or that offer “incremental” developments show high failure rates in economic markets (Hauser et al., 2006), primarily because they often present high risks and costs resulting from uncertainty of consumer or user acceptance (Davis, 1989; Stevens and Burley, 2003; Joshi and Sharma, 2004). Therefore, economic researchers in the area of innovative product development are highly motivated to further investigate determinants of consumer acceptance, perception and preference (e.g., Herrmann et al., 2007; Ariely and Berns, 2010) during integration processes. In classical economic studies, this is often implemented with experiments that use real products and prototypes. The investigation of prototypes and their potential for consumer acceptance is often accomplished through market studies that use real products and prototypes. In general, such investigations raise questions regarding high external validity. These prevailing complexities related to the new trend of integrating real-world consumers into the product innovation process in order to increase certainty of consumers’ product acceptance show the necessity for new mobile measurements that can be used outside the laboratory.
- (2) Another new economic trend is the consumer tendency toward sharing and joint consumption (Bardhi and Eckhardt, 2012). Noting that these issues were a major topic at the 2013 Association for Consumer Research Conference, general indicators suggest that the phenomenon will continue to gain importance. Today, “Generation Y” has fully accepted the innovative trend of collaborative consumption and “non-possession” (Belk, 2010). In contrast to the conventions of earlier generations of consumers who placed value on owning as a sign of prestige, young consumers share such things as clothes, apartments, bicycles and cars, both with known or previously unknown persons (Bardhi and Eckhardt, 2012). Many new business models have emerged in response to this development, and are primarily framed around the idea of allocating market overcapacities (Botsman and Rogers, 2010). This socially based consumer movement will be increasingly relevant for future-oriented economic studies, and thereby will require extension of neuroeconomic theories on consumers’ decision making. In order to implement studies concerning the new trend of collaborative consumption, the consumers’ interaction in the real world will be an interesting and valuable new perspective. This consequentially arising complexity demands new mobile neuroimaging techniques that can be used for investigating consumers’ interactions outside the laboratory.
- (3) Investigating the operation of companies in new markets is an important area for the expansion of economic studies, and will also require new research methods. For example, an fMRI study about consumer preferences and decision making in new markets presents strong challenges, including the need for cooperation or collaboration with institutes that have easy access to fMRI scanners and clinics. Because of these challenges (particularly in new markets with inadequate infrastructure), new mobile neuroimaging techniques gain in importance and have strong potential, especially in the field of “cultural neuroscience” (Seligman and Kirmayer, 2008).

These three examples of new trends in economic research show the relevance for new methods in (neuro-)economic research outside the laboratory. Overall, neuroeconomic research is challenged by a number of changes that demand new methodological development toward flexible and mobile technologies such as fNIRS.

METHODOLOGICAL BACKGROUND OF fNIRS MEASUREMENT

An elaboration of the potential of fNIRS methods should begin by detailing the fNIRS methods that are applied for recording data and for analysis. This background both allows useful assessment of the potential of this new method, and brings to light its challenges. Jöbsis (1977) was first to explain how the optical measurement for cerebral hemodynamic response known as NIRS is performed by the irradiation of near-infrared light into participants’ head and its scattering position (Villringer et al., 1993; Funane et al., 2013).

Near-infrared light, with a wavelength spectrum of circa 650–950 nm, passes through biological tissue without difficulty, and can non-invasively illuminate several centimeters of the tissue (Lloyd-Fox et al., 2010; Jackson and Kennedy, 2013; Scholkmann et al., 2013). Because of this characteristic transparency, the spectrum of near-infrared light is often called an “optical window” (Jöbsis-vanderVliet, 1999). In general, it can be approximated that oxy-(O₂Hb) and deoxy-hemoglobin (HHb) are the main absorbers, so that the changes in oxy- and deoxy-hemoglobin can be assessed, allowing for the indirect quantification of neural activity (Jackson and Kennedy, 2013). Various existing studies calculate the optimal wavelength as well as the optimal number of different wavelengths for perfect illumination based on a mathematical optimization problem (Yamashita et al., 2001; Sato et al., 2004; Correia et al., 2010; Schelkanova and Toronov, 2012; Scholkmann et al., 2013). Based on these physical and

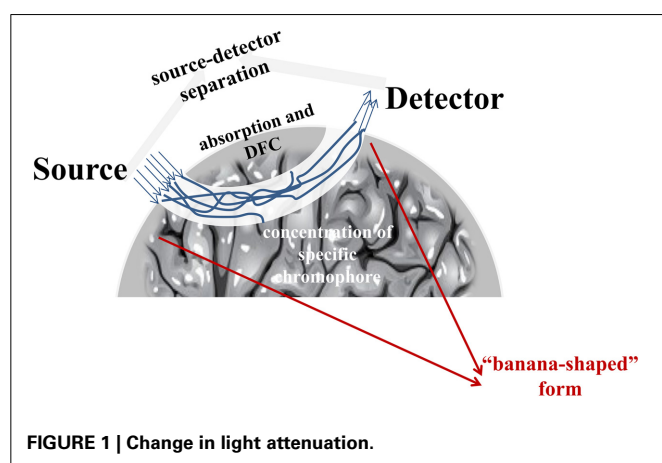
mathematical calculations, several techniques have been developed to measure the hemodynamic response. The majority of these studies implement the continuous-wave method (Lloyd-Fox et al., 2010). For oxy-(O₂Hb) and deoxy-hemoglobin (HHb) chromophores, dissimilar near-infrared light absorption properties can be anticipated, so that by using the absorption variation difference resulting from different chemical structure changes in blood oxygenation of the illuminated skin, the skull and some centimeters of brain tissue can be measured (Jöbsis, 1977; Lloyd-Fox et al., 2010).

The near-infrared light sources, which are laser-emitting diodes, are placed directly onto a participant's scalp and are sent—in a “banana-shaped” form (Okada and Delpy, 2003)—to the detectors, called optodes. The depth and exactness of measurement depends on the distance between the source and the detector. In different mathematical models, the correlation of the inter-optode distance and the depth of light penetration are assumed to be proportional (Nossal et al., 1988; Ehlis et al., 2005). However, the larger the distance, the more the light is scattered, so that the detector should not be placed more than 3 cm away from the source (Lloyd-Fox et al., 2010; Jackson and Kennedy, 2013).

For the conversion of the raw near-infrared light absorption and attenuation data into oxy- and deoxy-hemoglobin concentration, the most commonly used algorithm is the modified Beer–Lambert law (Kocsis et al., 2006; Scholkmann et al., 2013). In contrast to the original Beer–Lambert law, which generally allows the quantification of concentration only for non-scattering media (Scholkmann et al., 2013), the modified Beer–Lambert law considers a constant optical scattering of the light and relates the change in chromophore concentration to the change in light attenuation (see also Figure 1):

$$\Delta A = \alpha * \Delta c * L * DFC \text{ (Lloyd-Fox et al., 2010)}$$

with A, light attenuation; α , absorption coefficient; c, concentration of specific chromophore; L, source-detector separation; DFC, differential path length factor, which may vary according to specific wavelength, gender, age and difference in tissue type (Duncan et al., 1995, 1996).



To measure changes in oxy- and deoxy-hemoglobin, the brain needs to be illuminated with two different wavelengths, which in turn need to be integrated into two simultaneous equations in order to measure the blood oxygenation differences in the tissue (Lloyd-Fox et al., 2010).

In addition to the implementation of the modified Beer–Lambert law, fNIRS data analysis requires further preprocessing methods such as motion artifact correction, low- and high-pass filtering (for eliminating breathing, heartbeat and drift; see also Piper et al., 2014) and single-channel signal-to-noise analyses. Similar to fMRI studies, fNIRS data needs to be Bonferroni-corrected for multiple comparisons between channels. This implies that the *p*-values of multiple comparisons are adapted by the number of correlations performed (see also Ernst et al., 2013).

LITERATURE REVIEW OF NIRS STUDIES

A number of NIRS studies can be found in the literature, some using stationary NIRS machines and others using mobile, wireless and innovative NIRS prototypes. A general NIRS study classification separating “stationary” and “mobile” NIRS has been developed, designating specific subcategories of studies with emphasis on “economic decision making” and on “general decision making” (see Figure 2).

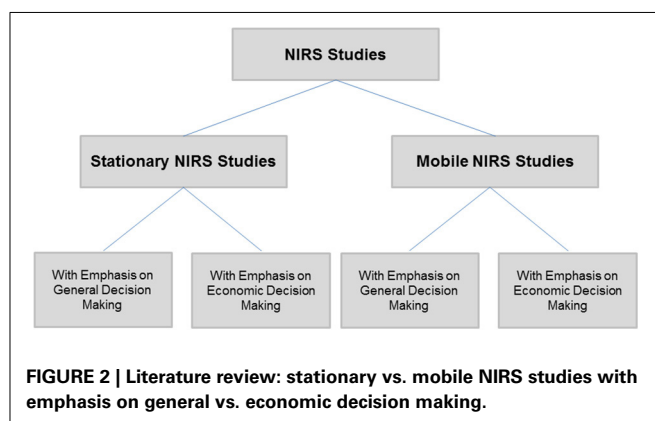
Based on these (Figure 2) classifications, the following section presents various NIRS studies.

STATIONARY NIRS STUDIES

Stationary NIRS studies with emphasis on general decision making

One group of stationary NIRS studies includes those without a concrete economic research frame, but that explore phenomena that have interest and strong relevance for economic research questions (see Table 1). The following decision making studies, with varied foci, are transferable to economic research questions.

- (1) Studies transferable to marketing research/transferable to design studies in information system research: Several NIRS studies explore the effects of different visual and auditory stimuli (Köchel et al., 2011; Plichta et al., 2011) on brain activations during participants' decision making. These NIRS studies could effectively complement the neuroeconomic fMRI studies that investigate these various aspects of



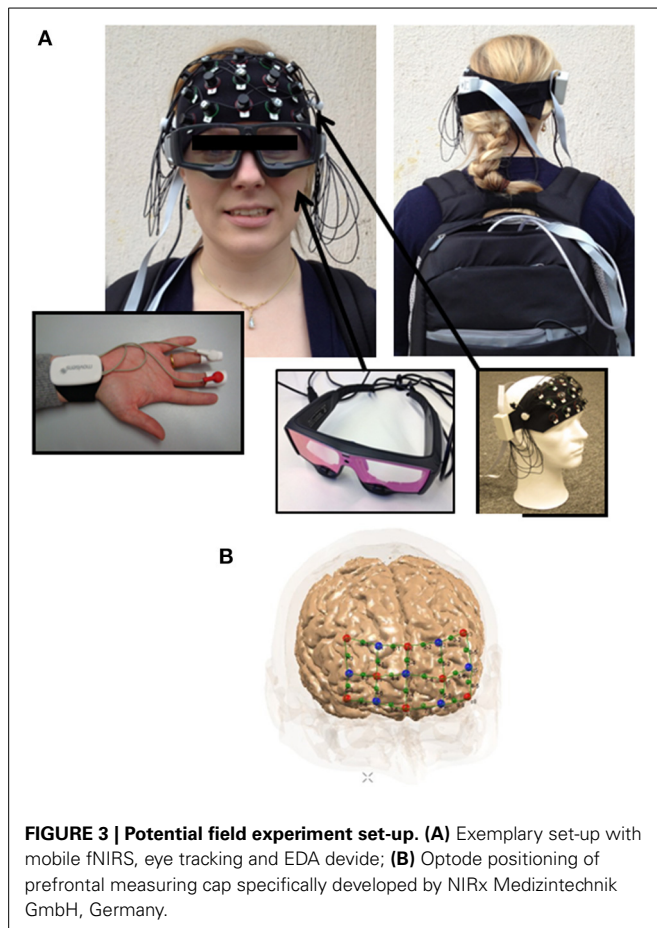


FIGURE 3 | Potential field experiment set-up. (A) Exemplary set-up with mobile fNIRS, eye tracking and EDA device; **(B)** Optode positioning of prefrontal measuring cap specifically developed by NIRx Medizintechnik GmbH, Germany.

influencing stimuli, such as the “First-Choice Brand Effect” (Deppe et al., 2005) or the effect of culturally familiar brands on preference (Schäfer et al., 2006). Moreover, these NIRS studies can be transferred to prior fMRI studies that investigate optimal user interface in social networks (Kopton et al., 2013).

- (2) Studies transferable to leadership research: fNIRS studies dealing with social functioning theory and emotion discrimination effects (Pu et al., 2012, 2013; Schneider et al., 2013) can give new impetus in the area of leadership research and organizational behavior. Few published research studies integrate neurophysiological methods into leadership and organizational research, and the few that do exist are not well known. This is astonishing, because the description, the explanation and configuration of human behavior in organizational systems is both central to and a main aspect of leadership and organizational research (Kenning and Kopton, 2013). Consequently, because interpersonal relationship systems play a major role in the organizational behavior of employees and managers, and in leadership behavior, fNIRS studies (with the potential of implementing field experiments with single trials during real human interpersonal interactions) promise to be highly relevant for this relatively new research area.

- (3) Studies transferable to interpersonal behavior studies in information systems research: Schneider et al. (2013) designed an experiment using avatar images to investigate participants’ brain activations during the judgment of different emotional faces. Riedl et al. (2014) used fMRI machinery to investigate online users’ interaction with avatars, as well as with real human beings, in the online world. Though these studies suggest that fNIRS studies can also easily be transferred to information system research, the implementation of NIRS as a tool for real-world settings is not as relevant for “computer interaction” studies. Accordingly, scientists should always deliberate the advantages and disadvantages of using fNIRS devices and fMRI machinery.
- (4) Studies transferable to decision making studies from strategic management and consumer research perspectives: NIRS studies about decision making under time pressure (Tsujii and Watanabe, 2010) and about decision-making processes investigating approach-avoidance theories (Ernst et al., 2013) are highly relevant for strategic managerial decision making, as well as for consumer decision making (e.g., buying decisions under time pressure). Management studies from various areas such as innovation management research (e.g., Dayan and Elbanna, 2011) and strategic management research (e.g., Sandler-Smith and Shely, 2004) focus on managers’ intuitive decisions and “gut feelings” under time pressure. Additionally, in the areas of marketing and consumer research, many studies address questions related to consumer decision making under time pressure (e.g., Reimann et al., 2012; Krishnan et al., 2013). The Ernst et al. (2013) NIRS study on approach-avoidance theory is another area of application.
- (5) Studies transferable to consumer research studies in the area of compulsive buying behavior/consumer protection research: A number of recent fNIRS studies about ADHD syndrome and other pathological behaviors (Moser et al., 2009; Gehricke et al., 2013) can be readily transferred to consumer research studies in compulsive buying (e.g., Otero-Lopez and Pol, 2013), as well as to consumer protection studies that currently have increasing importance (Lee and Mysyk, 2004; Kenning and Linzmayer, 2011; Kenning and Reisch, 2013).

Stationary NIRS studies with emphasis on economic decision making

In the last 5 years a number of new decision making studies investigating concrete and relevant economic research questions were applied to economic decision-making research questions:

- (1) Investors’ risky decision making: The experiments developed by Shimokawa et al. (2009, 2012) investigate investors’ decision making processes. The first study (Shimokawa et al., 2009) examines the medial prefrontal cortex (MPFC) and the orbital cortex (OFC) related to risk and reward prediction during decision making, using an fNIRStation from Shimadzu Corporation. In this study, 15 participants fictively received 1 million yen as total assets and were instructed to use a computer to decide a ratio of stock investment.

Table 1 | Stationary NIRS studies with emphasis on general decision making.

Transfer to marketing research/Transfer to design studies in information systems research	Transfer to leadership research/Transfer to interpersonal behavior studies in information systems research	Transfer to decision making studies from strategic management and consumer research perspectives	Transfer to consumer research studies in the areas of compulsive buying behavior/consumer protection research
Köchel et al., 2011	Pu et al., 2012, 2013	Tsujii and Watanabe, 2010	Moser et al., 2009
Content: Perception of pictures and imagery Transferable to: Transferable to product and promotion policy; e.g., influence of visual stimuli on advertising and (innovative) products (e.g., Schäfer et al., 2006) as well as to online design studies in Neuro-IS research (Kopton et al., 2013)	Content: Relationship between prefrontal function during a cognitive task and social functioning (motivation factor scores of SASS) Transferable to: Transferable to leadership and personal management research (e.g., investigating working behavior for practical implications; see Kenning and Kopton, 2013)	Content: Time pressure effect and the activity in the inferior frontal cortex (IFC) Transferable to: Managers' strategic decision making under time pressure, as well as consumer decision making under time pressure	Content: Results show that ADHD can be characterized by impairment of the dorsolateral prefrontal cortex Transferable to: Investigating studies of consumers' pathological decision making, such as research about compulsive buying (e.g., Manolis and Roberts, 2008)
Plichta et al., 2011	Schneider et al., 2013	Ernst et al., 2013	Gehricke et al., 2013
Content: Auditory cortex activation is modulated by emotion Transferable to: Transferable to promotion policy and POS-marketing (influence of, for example, music or voice on consumers' decision making; subliminal marketing)	Content: Emotion discrimination task with faceless avatars expressing different patterns (fearful, happy, sad, neutral, angry) and participants' judgment Transferable to: Transferable to managers' interpersonal exchange processes; human resource management with relation to the motivation of employees; interpersonal behavior in the online world (information systems research; e.g., Riedl et al., 2014)	Content: Cortical processes during automatic and regulated approach-avoidance reactions Transferable to: Findings for approach-avoidance theories are transferable to real-world economic decision making of consumers and managers; from a consumer perspective, testing of First Choice Brand Effect (Deppe et al., 2005)	Content: Investigation of how cigarette smoking affects prefrontal brain hemodynamics in smokers with and without ADHD Transferable to: Transferable to prior studies about consumers' pathological decision making (e.g., Otero-Lopez and Pol, 2013)

Participants were allowed to change their ratio occasionally, in response to stock prices, which were updated every 750 ms (experimental events). The results of this study show that the OFC is sensitive to responses to price changes (loss prediction), whereas MPFC changes accompany reward predictions. The second study (Shimokawa et al., 2012) confirms these findings regarding expected rewards, and future risks were further developed by investigating the extent to which information about brain activity can advance investment performance during investors' decision making.

- (2) Consumers' decision making and preferences: In their NIRS experiment, Luu and Chau (2009) address the phenomenon of subjective product preference. Nine adults participated in a computer experiment with a subjective preference task, based on 60 trials (in total) per participant. During these trials the participants were asked to look at two different drinks and to mentally evaluate their preference. The method applied the well-established shopping task of Knutson et al. (2007). For the measurement, a multichannel frequency domain NIRS device with 16 sources and three detectors was used. The results showed that subjective preference could be measured in the MPFC with 80 percent accuracy. Accordingly, this study shows high relevance for the research area of

consumer decision making processes, providing new and useful impetus for field experiments on consumer decision making.

MOBILE NIRS STUDIES

Mobile NIRS studies with emphasis on general decision making

One of the first mobile near-infrared spectroscopy systems was developed by Bozkurt et al. (2005), for the purpose of continuous monitoring of brain functions for newborns vulnerable to brain injuries (see **Table 2**). In this study the researchers present the low-cost, battery-operated continuous shot-limited SNR of 67 dB (with dual wavelength) that they had developed for newborns in neonatal intensive care units (NICUs). The phantom study tested the validity and reliability of the NIRS system, and demonstrated the potential of this technology as a clinical tool for measuring the metabolism of newborns in NICUs. Even though this first study had a clinical setting, the development was a first step toward application of a successful mobile tool.

In a later study, Muehlemann et al. (2008) developed a continuous wave near-infrared imaging (NIRI) with four sources and four detectors that was tested in a solid silicone phantom and in an *in-vivo* experiment with one male adult (see **Table 2**). The results of both phantom and *in-vivo* studies showed

Table 2 | Studies with mobile NIRS devices.

MOBILE NIRS STUDIES						
Authors	Area of interest	NIRS set-up	External validity	N	Method	Results
Bozkurt et al., 2005	New-born brain metabolism	Validity of the system	Relatively high external validity	1 (new-born) and prior phantom tests	NIRS prototype of a low-cost, battery-operated, dual wavelength, continuous wave	Shot-limited SNR of 67 dB for 10 Hz temporal resolution was achieved. Reliable clinical tool employed at bedside
Muehlemann et al., 2008	Tissue oxygenation and cortical hemodynamic response to sensory stimuli	Wireless NIRS device tested in a solid silicone phantom and an <i>in-vivo</i> experiment (4 sources, 4 detectors)	Very low external validity	1 phantom test and 1 male (<i>in-vivo</i> experiment)	<i>In-vivo</i> experiment: baseline; pneumatic pressure cuff attached to the upper arm	Tests with lightweight and inexpensive miniaturized wireless NIRS device show that the measurement accuracy is comparable to well-established instruments
Atsumori et al., 2009	Pre-frontal cortex while subject performed a word-fluency task	Functional wearable NIRS brain imaging with a prototype during reading	High external validity (but computer task)	1 (adult)	During the task periods, the subject was asked to think of as many words as possible that begin with the Japanese character	Typical changes in oxy-Hb and deoxy-Hb during the task. Therefore, prototype can be used to investigate functions in the prefrontal cortex
Yoshino et al., 2013a	Frontal lobe activations during car acceleration and deceleration	Functional wireless multi-channel system (FOIRE-3000, Shimadzu); 16 sources and 16 detection probes	Very high external validity (field experiment under specific driving conditions)	12 (adults)	Acceleration and deceleration	Results show that vehicle deceleration requires more brain activation, focused in the prefrontal cortex, than does acceleration
Yoshino et al., 2013b	Activation in the frontal lobe during driving operations	Functional wireless multi-channel system (FOIRE-3000, Shimadzu); 16 sources and 16 detection probes	Very high external validity (field experiment under specific driving conditions)	12 (adults)	Resting state, acceleration, deceleration, U-turn, stop	Powerful technique for investigating brain activations outdoors, proving to be sufficiently robust for use in an actual highway driving experiment in the field of intelligent transport systems
Piper et al., 2014	Motor cortex activity during bicycling (left hand gripping)	Functional wireless and mobile NIRS brain imaging during an outdoor activity	Very high external validity (field experiment with specific task conditions)	8 (adults)	Three different exercise conditions: (1) during outdoor bicycle riding; (2) while pedaling on a stationary exercise bicycle; (3) sitting still on a stationary exercise bicycle	Following left hand gripping, a significant decrease in the deoxy-hemoglobin concentration over the contralateral motor cortex could be found for all three conditions; outdoor and indoor conditions showed no significant difference in the shape or amplitude of HbR.

(Continued)

Table 2 | Continued

MOBILE NIRS STUDIES						
Authors	Area of interest	NIRS set-up	External validity	N	Method	Results
Holper et al., 2014	Simultaneous comparison with EDA; activity of lateral prefrontal cortex during risky decisions	Functional wireless and mobile NIRS brain imaging NIRS machinery with only one light-source	Relatively high external validity (but computer task)	20 (adults)	Risky decision-making task (Christopoulos et al., 2009; Tobler et al., 2009) and baseline recording	Enhanced activation in the lateral prefrontal cortex is related to high-risk decisions; reduced activation in this area is related to low-risk decisions. EDA revealed increasing responses for high-risk decisions

that measurement precision with the lightweight and lower-cost miniaturized NIRS is similar to well-established non-mobile NIRS instruments. Testing this prototype on an adult was an important step in the direction of wireless NIRS measurements.

To the best knowledge of the authors, Atsumori et al. (2009) were among the first to carry out a study combining a test for validity and reliability of a new system with an integrated participant task component (see Table 2). The Atsumori team created a small, light and wearable system that covers the participant's forehead in order to measure activation in the prefrontal cortex, and applied it to performing a word fluency tasks. From their study implemented with one Japanese adult, the results showed changes in oxy- and deoxy-hemoglobin that would be typical for this reading task, confirming that the prototype could be used to investigate the prefrontal cortex.

Moreover, a later study applied a wireless, mobile and miniaturized fNIRS prototype (16 channels) for neuroergonomic research (Ayaz et al., 2013). The goal of this prototype was to measure brain activation in naturalistic settings to obtain better knowledge for safety in air traffic control (see Table 2). Though this experiment was executed with only solid and liquid phantoms, the study shows the strong potential for using fNIRS in economic decision-making studies with high external validity.

In 2013, several different studies with wireless prototypes were implemented. One study ($N = 12$ adults) explored frontal lobe activation during car acceleration and deceleration, using a functional wireless multi-channel system (FOIRE-3000, Shimadzu; 16 sources and 16 detectors), and found that vehicle deceleration requires more brain activation—with focus on the prefrontal cortex—than does acceleration (Yoshino et al., 2013a). The study reveals very high external validity by testing participants in a real car in a real-world setting (see Table 2). A second study investigated these first findings regarding brain activations during driving further (Yoshino et al., 2013b). The second study also shows the robustness of using the mobile fNIRS method in a real highway setting. Piper et al. (2014) presented a prototype study of the first wearable multi-channel fNIRS system that could be used for freely moving subjects. In this study, the brain area of interest was the motor cortex activity observed during gripping of the left hand seated at rest, and while cycling outdoors. The experiment was implemented with eight adults and three different

exercise conditions (outdoor bicycle riding, riding a stationary exercise bicycle, and sitting still on a bicycle). The results showed a significant decrease in the deoxy-hemoglobin concentration (contralateral motor cortex) for all three cycling conditions, in comparison to the resting conditions. Furthermore, activation in the outdoor condition was not significantly different from riding a stationary exercise bicycle. Therefore, their prototype was assumed to be robust enough for implementation in real-world settings. At this stage, the technology allowed participants in the fNIRS studies to move freely, which is an important precondition for field experiments in naturalistic settings.

Mobile NIRS studies with emphasis on economic decision making

Very recently, Holper et al. (2014) presented the first study using wireless and mobile fNIRS machinery with a research question relevant to economics (see Table 2). The researchers tested the activity of the lateral prefrontal cortex during risky decision making, using a simultaneous comparison of the mobile fNIRS system and an EDA device ($N = 20$) in a computer experiment. Results showed that boosted activation in the lateral prefrontal cortex is related to high-risk decisions, and reduced activation in this area with low-risk decisions. Furthermore, the EDA revealed increased response for high-risk decisions. As the first economic decision-making study using mobile fNIRS, the study revealed a number of limitations, most notably that the NIRS machinery had only one light source, and the fictive task was implemented in front of a computer without integrating further situational factors.

However, these prototype studies generally show interesting new tendencies, providing foundation for application of the new wireless and mobile fNIRS techniques as potential measurement methodologies for neuroeconomic studies with high external validity.

Overall, the outline of published studies with stationary and mobile fNIRS machinery presented here indicates that interesting and notable findings exist. However, the area of neuroeconomics is still far away from a systematic integration of fNIRS. This may be due to the lack of a clear indication on the suitability of using fNIRS to study economic decision making. In addition, it may be that neuroeconomists are not trained in application of fNIRS. Regarding these two aspects, we will present a more detailed discussion about the positive and negative aspects of such uses for

fNIRS, and develop a decision table to aid in decisions about the suitability of fNIRS in neuroeconomics. Finally, we present a design for a first concept of potential field experiment set-up for neuroeconomic research questions.

DECISION ON THE SUITABILITY OF fNIRS METHODOLOGY FOR STUDYING NEUROECONOMICS

As shown, very few studies have investigated economic decision making with fNIRS measures, nor have used portable mobile fNIRS measures that allow participants to freely move around in a naturalistic setting. Many researchers are still working on basic methodological studies to optimize the methodology and the analyses of the near-infrared light data. However, the characteristics of the measurements suggest that fNIRS has many strengths, and offers significant potential for neuroeconomics, particularly for research with a high external validity. In order to determine the suitability of using fNIRS, we provide a decision-table for judging the potential for integrating fNIRS studies into neuroeconomic research (see **Table 3**). Based on this decision-table, neuroeconomic researchers can assess the potential of fNIRS studies for answering their specific research questions.

In the following, we elaborate on the various assessment criteria of this decision-table:

- (1) Spatial resolution: Compared to fMRI, the spatial resolution of fNIRS is less precise. For some research questions, the lower spatial resolution of fNIRS (compared to fMRI) makes it challenging to distinguish cortical areas that are positioned close to each other, so that in earlier multi-channel NIRS studies researchers proposed different algorithms to separate these close regions (Koenraadt et al., 2012; Thanh Hai et al., 2013). These new algorithms are valuable for better identification of cortical sources. Moreover, in contrast to EEG (which measures scalp activity), fNIRS methods are appropriate for specific research

questions regarding brain cortical activity (e.g., hypotheses regarding attention/cognition levels and sensory activations). As mentioned in the prior review section, some fNIRS decision studies have investigated cortical and prefrontal processes (e.g., Ernst et al., 2013; Pu et al., 2013; Yoshino et al., 2013a), and can be transferred to economic decision-making questions. Furthermore, some sensory studies (e.g., for advertisement studies) with a focus on perception and imagery processing (e.g., Köchel et al., 2011) are equally transferable.

- (2) Brain areas in deep brain regions: This aspect is in line with Criteria 1. Cortical and prefrontal areas can be reached effectively by fNIRS studies (e.g., Pu et al., 2012; Ernst et al., 2013; Yoshino et al., 2013a). However, for studies that investigate deeper brain structures (such as the nucleus accumbens) as the concrete region of interest (e.g., Reimann and Bechara, 2010), the fNIRS methodology is less appropriate. This aspect is often mentioned in the limitations of current fNIRS studies (e.g., Pu et al., 2012, 2013) and should be considered when developing a research design for an fNIRS study.
- (3) Temporal resolution: Generally, in terms of temporal resolution, fNIRS (for the ETG-100 machinery; e.g., 100 ms) is a good compromise between fMRI and EEG/MEG. fNIRS technology supports fast acquisition of data from numerous positions (Ehliis et al., 2005; Huppert et al., 2006; Sitaram et al., 2009). In their NIRS time pressure study, Tsujii and Watanabe (2010) noted activity in the prefrontal cortex (IFC), which demonstrates that fNIRS may provide a good measurement for studies having similar research questions. Tsujii and Watanabe's study (2010) can easily be transferred to neuroeconomic research questions—for example, regarding managers' strategic decision making under time pressure, as well as consumers' decision making under time restrictions. Therefore, this relatively high temporal

Table 3 | Potential of fNIRS for neuroeconomics.

Potential of fNIRS for answering research questions neuroeconomic studies is...
high, if...

low if...

- (1)... there is **medium high** need for spatial resolution.
- (2)... there is **low** need for investigating areas in deeper brain regions.
- (3)... there is a **medium high** need for temporal resolution.
- (4)... there is a **low abstraction** faculty of the research objects/**high** need for external validity.
- (5)... there is a **high sensitivity** of study regarding movement artifacts.
- (6)... there is a **high** need for quiet.
- (7)... there is a **high** need for compatibility with other methods.
- (8)... there **exist several** fNIRS studies regarding a comparable behavioral phenomenon.
- (9)... there is a **limited budget** available.
- (10)... there is a **high** need for pleasant consumer experience.
- (11)... there is **low** possibility to cooperate with institutes in different countries.
- (12)... there is a **high** possibility of working together with fNIRS experts.

- (1)... there is **very high** need for spatial resolution.
- (2)... there is **high** need for investigating areas in deeper brain regions.
- (3)... there is **very high** need for temporal resolution.
- (4)... there is a **high abstraction** faculty of the research objects/**low** need for external validity.
- (5)... there is **low sensitivity** of study regarding movement artifacts.
- (6)... there is **low** need for quiet.
- (7)... there is **no/low** need for compatibility with other methods.
- (8)... there is no **existence** of fNIRS studies regarding a comparable behavioral phenomenon.
- (9)... there is a **high budget** available.
- (10)... there is a **low** need for pleasant consumer experience.
- (11)... there is a **high** possibility to cooperate with institutes in different countries.
- (12)... there is a **low** possibility of working together with fNIRS experts.

resolution of fNIRS shows a strong potential for fNIRS methodological investigations regarding time restrictions and limitations in economic settings.

- (4) Abstraction faculty of the research object: Generally, prior neuroeconomic studies with fMRI investigations have explored economic constructs on a high level of abstraction (e.g., Knutson et al., 2007; Riedl et al., 2010; Kopton et al., 2013). However, for some research questions and concrete economic constructs that need to be examined on a neural basis, limitations exist with regard to the faculty in abstraction. The fNIRS-based driving studies of Yoshino et al. (2013a,b) are a good example of these limitations. fMRI studies could not effectively monitor real driving experiences such as acceleration or deceleration events with external validity. Also, concrete limitations of abstractions exist, with regard to economic constructs—for example, trust in real exchange processes or real-world interpersonal situations. The mobile and wireless capabilities of fNIRS (see also Kober et al., 2013; Yoshino et al., 2013a,b; Piper et al., 2014) indicate optimal possibilities for field experiments in economics.
- (5) Sensitivity of study regarding movement artifacts: In contrast to fNIRS methodology, fMRI is relatively sensitive to body-motion artifacts (Aihara et al., 2012). The low sensitivity of motion artifacts creates strong potential for fNIRS studies with application in the real world (Nambu et al., 2009; Lloyd-Fox et al., 2010; Kober et al., 2013; Piper et al., 2014). For example, in consumer neuroscience research it is highly relevant to consider consumers' decision-making processes by evaluating not only pictures but also real three-dimensional products (e.g., cars or food items). Studies have often provided evidence that consumers' decision making and affects differ when real products are shown, as compared to pictures (e.g., Bushong et al., 2010). Furthermore, the opportunity to touch or experience real products—in such situations as sitting inside a car or touching clothing—is relevant for some research questions (e.g., Peck and Childers, 2006). These examples suggest that using mobile fNIRS machinery, which is relatively robust to movements, can be a fruitful method for measuring economic decision-making constructs. Nevertheless, researchers who want to investigate economic decision making in real-world settings need to be aware that the mobile prototype machineries are still not immune to movements that are very sudden.
- (6) Quiet: In contrast to fMRI, fNIRS is an extremely quiet neuroimaging technique (Plichta et al., 2011). This feature gives fNIRS strong relevance for future studies in which auditory sounds play an important role. As an example, a study by Plichta et al. (2011) that shows enhanced activations of sensory brain areas in response to emotional auditory stimuli would be highly transferable to consumer neuroscience studies, as well as to organizational and (neuro-)leadership studies, confirming the significant potential offered by fNIRS studies regarding research questions with auditory stimuli. For instance, it could be both interesting and useful to observe how consumers in real-world shopping situations react to characteristic voices (friendly/unfriendly) of salespeople, or to study the influence of a leader's voice on team or group members.
- (7) Compatibility with other methods: fNIRS compatibility with other measurements such as EDA is very high (see, for example, Holper et al., 2014). Especially for field experiments with complex stimuli, this possibility could be valuable—for instance, by combining fNIRS with eye-tracking data. Further, because of the quietness of the fNIRS machinery, the method also has very high compatibility with research techniques such as well-established interpersonal market research interviews, which are often used in studies with marketing and strategic management focus. This ability makes the method highly relevant and useful for economic researchers.
- (8) Existence of several fNIRS studies regarding a comparable behavioral phenomenon (nomological validity): The potential of the fNIRS method for neuroeconomic research studies increases with regard to the number of existing fNIRS studies relative to comparable behavioral phenomenon. Therefore, for basic neuroeconomic research studies using fNIRS methodologies, we suggest a research agenda based on existing inquiries. As mentioned in the review section of the present article, research studies that focus on impulsivity and ADHD syndromes are available, but no studies with a focus on impulsive or compulsive consumer decision making apply fNIRS methodologies. Consequently, exploring consumer impulsivity and compulsivity (e.g., Manolis and Roberts, 2008; Hubert et al., 2013) with the new and still relatively unknown fNIRS measurement has strong potential for generating valuable results for real-world neuroeconomic research. Furthermore, neuroscience studies focused on picture and imagery processing have been implemented, with results suggesting that fNIRS analysis of advertising images could produce valuable new theories for real-world economic applications.
- (9) Limited budget: In general, fMRI is an expensive neuroimaging method, whereas fNIRS is relatively inexpensive, and the machinery is easily accessible for economic researchers (Shimokawa et al., 2009; Weiskopf, 2012; Kober et al., 2013; Moriguchi and Hiraki, 2013). Therefore, fNIRS studies may have a relatively strong potential for pretest studies, for which researchers would like to test first for expected effects, and have value for economic researchers who have no direct access to fMRI machineries or clinical settings, as well as those who have a relatively low budget. These attributes will enable researchers carrying out fNIRS experiments to include more participants for larger group analyses.
- (10) Pleasant consumer experience: Marketing or strategic management researchers recognize the value of working with customers of a company, particularly for implementing a study that is pleasant and not uncomfortable for the customers. Doing so prevents conditions that may discourage customers from future interactions with the company, or that may inhibit further buying decisions. This is especially the case for typical market research projects. The use of fNIRS is a relatively pleasant experience for participants. As

an example, in contrast to EEG measurements, no electrical gel is needed, so that the montage of NIRS optodes is also much faster than the montage of EEG electrodes (Kober et al., 2013). The montage of the machineries for participants with dark hair can take a bit more time, however, because dark hairs between the optodes and the head can cause light attenuation. Though this complication can be diminished by brushing participants' hair out of the way to ensure good skin contact for sources and detectors, the preparation can be time-consuming for researchers (Lloyd-Fox et al., 2010; Holper et al., 2012). For analyses where only the frontal areas are regions of interest, specific fNIRS caps can be used, measuring only the forehead where no hairs disturb the positioning of the optodes (e.g., Atsumori et al., 2009). Overall, NIRS is a very suitable method when there is a need for pleasant consumer experiences.

- (11) Intercultural study: possibility of cooperating with institutes in different countries: This feature in the decision-list is related to the prior aspect. Building on studies showing that culture has influence on social and interpersonal behavior (Wallendorf and Arnould, 1988; Strombach et al., 2013), it can be anticipated that intercultural aspects have a strong influence on social life and decision making. For real-world conditions where researchers are investigating consumer behaviors in countries other than their own, and where there may be limited ability to cooperate with institutes (China or Africa, for instance), the ability to travel that mobile fNIRS offers to researchers could make it a highly practical tool.
- (12) Possibility of working with fNIRS experts: For economic researchers who want to answer research questions using fNIRS technology, there is strong advantage in working cooperatively with neuroimaging/optical experts or specific fNIRS experts. In general, the standardization of fNIRS data analysis remains an issue that needs further attention, and many researchers in this area continue to work on their own prototype software to analyze their findings. Therefore, economic researchers who are not yet experts in fNIRS would find particular value in working with experts during the data analysis stage. It should be noted that because there are currently very few fNIRS studies with neuroeconomic focus, comparability between results of different studies continues to be relatively difficult.

In summary, the present discussion, in combination with the elaborated continuum (Table 3), offers neuroeconomic scientists a decision agenda for evaluating the potential of fNIRS methodology, and its usefulness for their specific research questions, aims, and areas of interests.

INSIGHT INTO A POTENTIAL FIELD EXPERIMENT SET-UP

As discussed, fNIRS might be a promising and new tool for neuroeconomic research under certain circumstances, especially regarding mobile technologies. In the following, therefore, we will report first insight about a potential experimental set-up using mobile fNIRS in combination with further neurophysiological methods for studies outside the laboratory. The aim of this section

is to provide neuroeconomists with greater ability for developing fNIRS studies.

For the application of a mobile fNIRS device in a field experiment, a wearable multi-channel fNIRS system with a specifically developed prefrontal cap is typically used. For our economic decision-making studies (with regard to the measurement restrictions of fNIRS in deeper brain regions), we are mainly interested in the prefrontal areas of the brain.

Even if scientists keep the design of a field experiment very simple and integrate no complex treatment conditions, questions arise regarding how to control external influencing variables, and how to reconstruct aspects such as consumer behavior for the analysis. These questions are extremely relevant, because consumers in field experiments can move freely and without exact timing conditions, which presents challenges for neurophysiological measurements. For the optimal measurement of consumers' decision making outside the laboratory, a number of reasons can be identified for developing a multifaceted experimental set-up not only with fNIRS measurement, but also with eye-tracking and EDA devices (Figure 3).

The eye-tracking device enables researchers to both follow consumers' eye movements objectively, and to develop a baseline for analysis of the field experiments. Thus, in a field experiment, for example, about consumers' decision making about innovative prototype products such as cars, the eye-tracking data can give important information regarding the stimulus that is being observed by the consumer at a specific time (in seconds) during the decision-making phase. With parallel eye-tracking measurements as baseline and timeline, therefore, participants' individual differences during the experiment outside the laboratory can be controlled. This element of integrating eye-tracking has potential usefulness in neurophysiological field experiments using a portable fNIRS device. Furthermore, comparing fNIRS activation and electrodermal arousal reactions (as additional controls) could be useful for measuring not only eye-tracking but also ("EDA"; e.g., Greenwald et al., 1989) simultaneously with fNIRS (Holper et al., 2014). Prior studies have revealed that specific activations in prefrontal areas have an effect on EDA (Tranel, 2000; Critchley, 2002; Figner and Murphy, 2010; Holper et al., 2014).

Finally, for the successful implementation of experiments outside the laboratory, specific additional operating procedures need to be considered. Consumers should close their eyes ("resting conditions") before observing objects/stimuli (e.g., car exteriors/interiors), and should walk at a constant speed (to control for potential movement artifacts), in experiments with several rounds and a number of treatment conditions. Moreover, the supervisor of the experiment needs to simultaneously observe each participant, take notes regarding potential outliers (of external variables), and trigger the mobile fNIRS device concerning specific upcoming situations and pre-defined conditions. These operating procedures are relevant for subsequent successful data preprocessing.

CONCLUSIONS

Generally, most prior neuroeconomic studies were implemented with the fMRI scanner, but the fMRI technology also has

limitations that have often been criticized—especially concerning the generalizability and the restrictions regarding the integration of situational factors in a lab, and regarding external validity (Braeutigam, 2012). Some of these limiting factors and critical aspects could be countered with new technological tools such as mobile fNIRS devices that support investigation of economic decision making outside the laboratory. Currently, however, few neuroeconomic studies applying mobile NIRS methods are available. The reason for this research gap might be that the use of mobile and wireless NIRS is in its early stages, and many researchers still work on prototypes for optimal data acquisition (e.g., Muehleemann et al., 2008; Atsumori et al., 2009; Piper et al., 2014). The aim of this paper was to demonstrate, and to discuss, the potential that fNIRS methods offer for neuroeconomic research questions in which situational factors outside the laboratory play a major role (e.g., in consumer decision making at the point of sale).

To fulfill our objectives, we reviewed existing studies with relevance to (economic) decision making and presented a decision-table for neuroeconomic researchers that may enable better determination of the suitability of fNIRS for studying neuroeconomics. To the best of our knowledge, this is the first article investigating the fNIRS method as a new and prospective tool for economic research questions outside the laboratory. By integrating studies from various disciplines, we developed a decision-table to support future application of fNIRS methods. Finally, we presented a first concept of a potential field experiment set-up for a neuroeconomic research question.

Overall, this present article shows that further research using (mobile) fNIRS for studies on economic decision making outside the laboratory could be a fruitful avenue. As well, the paper helps to validate the potential of a new method regarding different aspects and to develop a more effective application outside the laboratory.

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Ideology in organizational cognitive neuroscience studies and other misleading claims

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As part of this forum on “*Society, Organizations and the Brain*,” Butler (2014) contributed an article on how to operationalize interdisciplinary research by way of introducing “a model of co-production in organizational cognitive neuroscience (OCN)” (p. 1).

While I appreciate his work as an extension of prior research, there are some misleading claims in his article in terms of associating my previous work with what he terms “science ideology” (a term he does not define), and a misleading representation of key arguments presented in that body of work (Lindebaum, 2013b). Consequently, my aim in this article is twofold. First, I demonstrate that Butler uses the term “ideology” incorrectly. Second, I contrast his depiction of my work with what it actually states. Note that, consistent with previous work (Lindebaum, 2013a), I am explicit that a multitude of opinions on this seemingly touchy topic is likely to yield richer insights than any one dominant view alone. However, I highlight a need for accurate usage of terms and accurate engagement with each others’ work, however much we might beg to differ on the topic.

IDEOLOGY IN SCIENCE

The topic of ideology has been a contested line of inquiry in management studies for some time (see e.g., Alvesson and Willmott, 1992; Raftopoulou and Hogg, 2010). Key to Butler’s (2014) brief exegesis on ideology is the role of dominant actors when knowledge becomes “ideological and biased in favor of particular actors through a conflictual process” (p. 4). However, more elaboration is in order on a topic as complex as ideology. To begin

with, it is important to understand what scholars mean when they refer to ideology. For instance, Van Dijk (1995) defines ideology along these lines.

“Ideologies are basic frameworks of social cognition, shared by members of social groups, constituted by relevant selections of socio-cultural values, and organised by an ideological schema that represents the self-definition of a group. Besides their social function of sustaining the interests of groups, ideologies have the cognitive function of organizing the social representations (attitudes, knowledge) of the group, and thus indirectly monitor the group-related social practices and hence also the text and talk of its members” (p. 248).

In other words, ideologies are characterized as a system of values, ideas, and beliefs that seek to legitimize extant hierarchies and power relations and preserve group identities. Therefore, ideology operates in the process of meaning in everyday life by way of common-sense and taken-for-granted assumptions that work to legitimize existing power relations (e.g., Fairclough, 1992). The focus upon meaning implies that ideology is viewed as an imaginary relationship of individuals to their real world, rather than a reflection of the real world (Althusser, 1971). If we take ideology and combine it with the scientific knowledge we share, it is clear that knowledge is *never free* of ideological influences. Thus, neither the work of advocates nor the work of skeptics of OCN is ideologically free. That is, neither camp can cast off its “ideological boundedness” (Fairclough, 1995). The problem arises if, among a set of ideologies,

some exercise a more powerful influence than others, which then starts constrain some lines of enquiry while privileging others.

Having defined “ideology,” it is now possible to examine Butler’s (2014) association of my previous work with “science ideology.” He states that “within the UK,” I am seemingly “a key voice for critique, however, [I am] perceived by colleagues as straying into science ideology” (p. 4). However, does this accurately reflect the power balance between advocates and skeptics of OCN? In terms of numbers of publications in flagship US management journals, my counting reveals a score of at least 15 to 0 in favor of advocates¹, so I cannot see that my work is part of an existing hierarchy that dominates the field. In this respect, I am reminded of Gabriel’s (2010) observation that “what gets published and what gets rejected ... are barely concealed exercises in power and resistance ... what gets published is one of the most political processes” in today’s academia (p. 761). Thankfully, other thought-provocative and original journals like the *Journal of Management Inquiry* or

¹This score is calculated taking into account three publications in the *Journal of Management*, four in *Leadership Quarterly*, one in *Organization Science*, one in *Academy of Management Perspectives*, one in the *Journal of Applied Psychology*, two in *Strategic Management Journal*, and three in *Organizational Behavior and Human Decision Processes*. These publications represent those I am aware of, hence excluding any forthcoming or in press articles that have not been cited widely yet. I admit that there is a possibility that an article has escaped my attention. Even so, this is unlikely to fundamentally change the score presented. Due to space limitations, I cannot include the whole list here. However, it is available upon request.

Human Relations (Lindebaum and Zundel, 2013) have been more receptive to my work².

I also would like to briefly reflect on Butler's (2014) words to the effect that I am "*perceived by colleagues as straying into science ideology*" (p. 4). The first part (in italics for emphasis) of that sentence requires attention. Specifically, I wonder whether Butler (2014) intended to make a factual statement, or whether his comment is based upon hearsay of the kind we can read in tabloids. If it is the former, the reader would appreciate evidence in support of his claim. If it is the latter, I am not sure whether this statement adds substance to his article.

MISLEADING CLAIMS

The second point I would like to raise in response to Butler (2014) is his depiction of key points I offered previously. To explicate, consider the following first quote from his article:

"On the one hand, Lindebaum and Zundel (2013) rightly maintain that without explicit consideration of, and solutions to, the challenges of reductionism, the possibilities to advance leadership studies theoretically and empirically are limited" (p. 4).

While it is gratifying to see one's work being cited, it is also important that this is executed correctly in congruence with academic conventions of citation practice. In this case, the above statement is taken *ad verbatim* (starting with "maintain" and ending with "limited") from Lindebaum and Zundel (2013) and, therefore, must be accompanied by the page number (i.e., p. 857). However, this is not the case.

²If we follow Duster (2006) in his claim that funding in the US is increasingly directed toward "markers inside the body" as predictors of socio-economic and health outcomes, then this tendency suggests another leverage of the OCN ideology and its associated power. The term "power" is most suitable here, as Scott (1992) defines it as having access to resources (in this case, research funding). Indeed, President Obama has just recently announced a US\$100 million dollar brain-mapping research initiative. See <http://blogs.nature.com/news/2013/04/obama-launches-ambitious-brain-map-project-with-100-million.html>, accessed 21 October 2013.

There are two more problems with Butler's depiction of my work on the topic in the following statement:

"On the other hand, it has been argued that Lindebaum (2012) mischaracterizes neuro-feedback processes for the purpose of leader development, which then leads to misinformed statements about its potential ethics (Cropanzano and Becker, 2013)" (pp. 4–5).

The first problem is the reference to Lindebaum (2012). This study is not devoted in any way to OCN (instead it focuses on emotional standardizations at work). The second point pertains to the statement that I "*mischaracterize neuro-feedback processes*" as applied to leader development, "*which then leads to misinformed statements about its potential ethics.*" Readers who have perused my 2013(b) article will quickly see that I have characterized the neurofeedback process by first defining it according to the view of the *International Society for Neurofeedback and Research* (Hammond et al., 2011). I have also provided more characteristics of the neurofeedback process with reference to the Waldman et al. (2011) study (often using direct quotes from that study). Consequently, I cannot discern where a mischaracterization has occurred. The same applies to "*misinformed statements about potential ethics,*" a point allegedly made by Cropanzano and Becker (2013) in response to my article. What Cropanzano and Becker (2013) suggest, however, is that they "*strongly endorse [my] call for scholars and others to pay closer attention to ... ethical concerns*" (p. 306) when neuroscience is used in leadership research. Of course, Cropanzano and Becker (2013) also offer divergent and complementary views on my critique, especially when they argue that my "*ethical inquiry does not go far enough*" and that "*a more complete analysis suggests that there are additional matters that should also be considered*" (p. 306). However, it is somewhat curious that Butler takes this to imply "*misinformed statements about its potential ethics.*" For further clarification on Cropanzano and Becker's (2013) article, please consult Lindebaum (2013a).

CONCLUDING THOUGHTS

Butler (2014) deserves credit for bringing into the open the role of ideologies in the construction of knowledge, especially on a topic that enjoys hardly any substantive critique, least of all in flagship US management journals. However, the clarification of ideological charges against my work reveals that the exact opposite of Butler's (2014) argument is the case, namely, that advocates of OCN represent a dominant ideological movement, one which, through a system of ideas and beliefs, aims to legitimize extant hierarchies and power relations and preserve group identities as indicated by the score presented earlier. It is, therefore, important for future debates to be based upon informed views, which correctly and unequivocally reveal how the meaning of a term is employed. Since neuroscience as a theoretical and empirical toolkit is likely to further consolidate its influences in management studies (and how they fit with the theme of this research forum), it is all the more imperative to avoid terms being used to silence dissenting views or discredit prior work (for instance, by discarding them as lacking relevance and rigor). For a healthy unfolding of the debate, I suggest it is also necessary to engage more accurately with each others' work, for doing otherwise is likely to unnecessarily create deeper chasms rather than aiding to bridge them. I hope this article serves this purpose.

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NOTE

This article by Lindebaum refers to a previous version of the opinion article "Operationalizing interdisciplinary research—a model of co-production in organizational cognitive neuroscience" by Butler, which first appeared online in provisional form on 11 October 2013 before undergoing final publication. In light of a potential conflict of interest identified after the initial peer review, the opinion article by Butler underwent an additional round of review and was then published in its current form. The final publication differs from the original version that first appeared online.

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The evolution of leader–follower reciprocity: the theory of service-for-prestige

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We describe the service-for-prestige theory of leadership, which proposes that voluntary leader–follower relations evolved in humans via a process of reciprocal exchange that generated adaptive benefits for both leaders and followers. We propose that although leader–follower relations first emerged in the human lineage to solve problems related to information sharing and social coordination, they ultimately evolved into exchange relationships whereby followers could compensate leaders for services which would otherwise have been prohibitively costly for leaders to provide. In this exchange, leaders incur costs to provide followers with public goods, and in return, followers incur costs to provide leaders with prestige (and associated fitness benefits). Because whole groups of followers tend to gain from leader-provided public goods, and because prestige is costly for followers to produce, the provisioning of prestige to leaders requires solutions to the “free rider” problem of disrespectful followers (who benefit from leader services without sharing the costs of producing prestige). Thus service-for-prestige makes the unique prediction that disrespectful followers of beneficial leaders will be targeted by other followers for punitive sentiment and/or social exclusion. Leader–follower relations should be more reciprocal and mutually beneficial when leaders and followers have more equal social bargaining power. However, as leaders gain more relative power, and their high status becomes less dependent on their willingness to pay the costs of benefitting followers, service-for-prestige predicts that leader–follower relations will become based more on leaders’ ability to dominate and exploit rather than benefit followers. We review evidential support for a set of predictions made by service-for-prestige, and discuss how service-for-prestige relates to social neuroscience research on leadership.

Keywords: leadership, followership, reciprocity, collective action, evolutionary psychology, social status, dominance, prestige

INTRODUCTION

Leadership and followership have evolved to facilitate information sharing and coordinated group action in a wide variety of species (King et al., 2009). Humans are apparently adapted for complex cooperative behaviors that require high levels of expertise, coordination, and solutions to collective action problems (Tooby et al., 2006), and it would not be surprising if they, like so many other species, have also evolved psychological adaptations for leadership and followership (Van Vugt and Ahuja, 2010; Van Vugt and Ronay, 2014). In this article, we propose that such adaptations have indeed evolved, and that they govern the dynamics of leader–follower relations in human organizations. Our focus is specifically on leader–follower relations in humans, as opposed to any other species. We describe a theory of leader–follower relations which we think will ultimately enhance social neuroscientists’ understanding of the neural processes that enable these relations. Scientists are still in the early stages of understanding how the mind is adapted to lead and follow, and of developing neuroscientific methods for identifying psychological adaptations (Van Vugt, 2014). Nevertheless, the key conceptual elements of a coherent and plausible

evolutionary theory of leader–follower relations are already in place (Price and Van Vugt, in press), and neuroscientists have already begun using evolutionary theories of psychological adaptation to guide their research on social interactions (Rilling and Sanfey, 2011). Thus, we propose that evolutionary social psychologists and social neuroscientists should begin engaging with each other more on the topic of leader–follower relations, and thinking about ways in which evolutionary approaches to these relations could both inform and be informed by neuroscientific research.

From the perspective of evolutionary psychology (Tooby and Cosmides, 1992, 2005), voluntary social relationships are likely to evolve if they provide all partners in the relationship with individual fitness benefits – that is, with benefits that enhance the survival and reproduction of the individual (and/or the individual’s very close genetic kin). We take this perspective on leader–follower relations, so a key question driving our analysis is: how might leader–follower relationships have been mutually fitness-enhancing for both leaders and followers in the environments of the evolutionary past? We pay close attention to past evolutionary environments, because any evolved psychological

mechanisms that exist today in the minds of modern humans, including those governing leader–follower relationships, could exist only if they functioned adaptively in these environments (Tooby and Cosmides, 1990).

We propose that voluntary leader–follower relationships – that is, interactions in which followers voluntarily follow, and leaders voluntarily lead, because they each perceive some positive incentive to do so – were adaptive in the past for both leaders and followers because they involved mutually beneficial exchange. In this exchange, leaders enhanced the fitness of followers by providing them with collectively shared benefits and resources (often in the form of “public goods”) that enhanced followers’ wealth, status, and ability to function in coordinated and cooperative groups, and followers enhanced the fitness of leaders by providing them with prestige. As we will discuss in more detail below, by “prestige” we mean social status that is voluntarily conferred on those who are useful to others, as distinguished from “dominance,” which is status that is attained coercively by those who are threatening to others (Henrich and Gil-White, 2001). Evidence suggests that prestige and dominance are two distinguishably different paths that individuals can take in order to increase their social status (Von Rueden et al., 2011; Cheng et al., 2012).

The more equal the social bargaining power of leaders and followers (i.e., the more equal their abilities to confer benefits and/or impose costs on one another; Sell et al., 2009), the more likely the leader–follower relationship would have remained voluntary, mutually fitness-enhancing, and maximally beneficial overall. However, the greater the bargaining power of leaders relative to followers, the more likely the relationship would have been to transition from being reciprocal and prestige-based to being coercive, exploitative, and dominance-based. This transition should occur because from the leader’s perspective, the leader–follower relationship is advantageous primarily as a means of acquiring and maintaining high social status. When followers have relatively high relative bargaining power (e.g., high freedom to exit the group, high power to reject or retaliate against leaders), the easiest way for leaders to achieve high status will be to make themselves useful to followers by offering them benefits in exchange for prestige. In these situations, if leaders attempt to claim high status without offering followers anything in return, or by attempting to dominate and coerce followers, then their would-be followers can simply reject them (e.g., exit the group or depose the leader). However, when followers have relatively low bargaining power, leaders will have increased ability to gain and maintain status based on their ability to dominate, rather than benefit, followers. For example, if followers have low power to exit a group or to strip a leader of his or her high status, then the leader will have little need to offer them benefits, in order to compel them to (a) stay in the group or (b) grant the leader high status in exchange for these benefits. Leaders may sometimes perceive dominance, as compared to reciprocity, to be an appealingly cheap and efficient route to high status, as it saves them the costs of having to produce benefits for followers.

We refer to the above theory of how and why leader–follower relationships vary from reciprocity to dominance as *service-for-prestige* (Price and Van Vugt, in press).

HOW ARE LEADER–FOLLOWER RELATIONS DIFFERENT IN HUMANS THAN IN OTHER SPECIES?

As noted above, leader–follower relations have evolved in a wide variety of species to allow individuals to share information and coordinate their behavior (King et al., 2009). For instance in many taxa, individuals share knowledge in order to lead followers to the locations of food, water, and other resources (examples include ravens, elephants, and most famously honeybees, who map out directions to resources via waggle dances); in many fish species, leader–follower dynamics result in groups (shoals and schools) that are helpful for avoiding predators and finding food; and among some primates such as chimpanzees, alpha males lead aggressive group actions against enemy groups and predators (Boehm, 1999; Krause and Ruxton, 2002; King et al., 2009). In the human lineage, just as in other species, leadership probably evolved initially to solve problems related to information sharing and social coordination. However, we propose that eventually, evolution enabled humans to use reciprocity to enhance the benefits of leadership.

To understand why reciprocity could enhance leadership, consider that leader–follower dynamics often evolve in situations where individuals are better off acting in groups as opposed to acting alone, for example, because group membership increases one’s likelihood of finding resources or escaping predators (Hamilton, 1971; Van Vugt and Kurzban, 2007). Such group movements present coordination problems, however, associated with determining who will lead and who will follow. For example, if Individuals A and B both have an interest in visiting a waterhole together (because there is safety in numbers), and have several waterholes to choose from, how will they choose which one to visit? There are several ways in which leader–follower dynamics could emerge to solve this problem (Van Vugt and Kurzban, 2007). For example, imagine that A prefers a particular waterhole but B has no preference, and as a result A moves first to choose the preferred waterhole. Once A has made this move, B is best off following A, as opposed to making a dangerous solo journey to a waterhole that offers B no additional benefits. Leadership may have evolved in many species to solve coordination problems such as these, when there has been a fitness advantage to the individual in assuming a leadership role (Van Vugt, 2006).

However, what about situations in which the individual is disadvantaged by assuming a leadership role? Many leadership roles may involve substantial costs to leaders, and individuals may need special incentives to accept these roles. If followers stand to benefit from a leader’s assumption of a costly role (e.g., if this leadership would provide protection for followers), then it might profit followers to provide the leader with these incentives. This potential for reciprocity could provide new opportunities for leadership to evolve, such that leader–follower relations could become not just matters of coordination but also matters of exchange. We propose that leader–follower relations evolved as service-for-prestige transactions in contexts such as these, to enable leadership behaviors that would otherwise have been prohibitively costly. However, engagement in reciprocity, particularly in the complexly cooperative social environments of human beings, requires specially designed social-cognitive abilities that are uniquely sophisticated in humans (Tooby and Cosmides, 1996; Hammerstein, 2002;

Tooby et al., 2006; Bowles and Gintis, 2011). Therefore, we propose that service-for-prestige exchange is a crucial aspect of leader–follower dynamics in humans, but not necessarily in any other species.

THEORETICAL FOUNDATIONS OF SERVICE-FOR-PRESTIGE: SYNTHESIZING THEORIES OF RECIPROCITY AND COLLECTIVE ACTION, AND ACCOUNTING FOR EVOLUTIONARY MISMATCH

EVOLUTIONARY THEORIES OF RECIPROCITY

Human leader–follower relationships are cooperative interactions that occur between people who are not necessarily close genetic kin. One of our key theoretical tools, therefore, will be the main concept used by evolutionists to explain non-kin cooperation: reciprocity (Trivers, 1971; Alexander, 1979; Tooby et al., 2006). Reciprocity theories assume that because cooperative individuals incur fitness costs in order to deliver fitness benefits to others, they must receive some return benefit from others as compensation for these costs. In the absence of such compensation, cooperation will be maladaptive for cooperators and will not evolve.

The most basic form of reciprocal cooperation is direct reciprocity, described originally by Trivers (1971) as “reciprocal altruism.” Trivers (1971) described mutually beneficial exchange between a cooperator (or “altruist”) and a reciprocating partner. For example, if X pays a cost of size 1 to provide Y with a benefit of size 2, and Y precisely returns the favor, then X and Y will each have paid a cost of 1 and received a benefit 2, and the exchange will be mutually profitable. However, it is crucial to note that Y could have profited even more by “cheating,” that is, by taking X’s 2 without reciprocating 1. In order for reciprocity to evolve in direct exchange contexts, cooperators must somehow avoid being exploited by cheaters, for example, by avoiding them altogether, or by neutralizing their advantage via punishment. If cheaters consistently tend to come out ahead in these interactions, they will eventually exploit cooperators to extinction and cooperation will not evolve (Hamilton, 1964; Trivers, 1971; Henrich, 2004; Price and Johnson, 2011). Individuals should thus be predisposed to cooperate with reciprocators, and be averse to cooperating with cheaters. This prediction is supported by a large body of evidence from several behavioral science fields (Price, 2006a). Reciprocity has long been considered a fundamental attribute of human social systems cross-culturally (Gouldner, 1960), and it is generally considered to be a universal, species-typical, and highly fitness-relevant human behavior (Brown, 1991; Rilling and Sanfey, 2011).

The reciprocity theory presented by Trivers (1971) primarily describes reciprocity that is direct and dyadic (i.e., involving direct exchange between two individuals). However, extensions of this theory have been used to explain other forms of reciprocity. The best known example is “indirect reciprocity,” that is, interactions in which X’s altruism toward Y is reciprocated not by Y but by a third party (Alexander, 1979; Nowak and Sigmund, 2005). There have also been attempts to apply reciprocity theory to direct exchanges between one individual and a group of other individuals (Boyd and Richerson, 1988; Price, 2003, 2006a; Tooby et al., 2006; Takezawa and Price, 2010). Because leader–follower relations often (although not exclusively) involve interaction between one leader

and multiple followers, this kind of reciprocity would seem most relevant to an understanding of leader–follower exchange. However, it is not widely accepted among evolutionary researchers that direct reciprocity can explain the evolution of cooperation in group contexts such as these (Boyd and Richerson, 1988; Henrich, 2004; Bowles and Gintis, 2011). In the view of these researchers, direct reciprocity can explain the evolution of simple dyadic cooperation, but totally different processes such as cultural group selection are required to explain cooperation in groups. Our application of reciprocity to these contexts, then, does not represent the consensus view of evolutionary researchers, and important theoretical questions still need to be resolved about precisely how leader–follower exchange could evolve.

Nevertheless, despite this lack of a theoretical consensus, we agree with previous suggestions (Price, 2003, 2006a; Tooby et al., 2006) that direct reciprocity (in combination with indirect reciprocity) may be a key factor in the evolution of group cooperation in humans, and we do not think that it is premature or implausible to suggest that leaders and followers often engage in mutually beneficial exchange. We propose that reciprocity theory provides the most appropriate and predictive evolutionary framework for understanding voluntary human leader–follower interactions, because (1) leaders often incur costs in their efforts to provide benefits for followers, (2) followers often incur costs in order to provide prestige which benefits leaders, (3) in order for each of these costly provisioning behaviors to be adaptive in the ancestral past, both leaders and followers would have needed to recoup these costs somehow, and (4) this recoupment could plausibly have occurred via a process in which leader-produced benefits were exchanged for follower-produced prestige. Illustrations of why it is often costly for leaders to provide public goods and for followers to provide prestige, and of why prestige entails fitness benefits, are presented below.

LEADER–FOLLOWER RECIPROCITY AS A COLLECTIVE ACTION PROBLEM

Our second key theoretical tool is Olson’s (1965) theory of collective action, which states that even if group members benefit on average if their group cooperates effectively, individual members can often reap the greatest private profits if they “free ride” while the rest of the group pays the costs of cooperation. This free rider problem – the private incentive that each individual member has to free ride on everyone else’s contributions – often seriously undermines group efforts to cooperate, and is considered by behavioral scientists to be the fundamental obstacle to successful collective action (Yamagishi, 1986; Boyd and Richerson, 1988, 1992; Ostrom, 1990).

Service-for-prestige regards leader–follower reciprocity as a collective action problem because many benefits provided by a leader (e.g., increased group status, improved group defense, and access to resources) will be public goods, shared widely and more or less equally by followers. A leader’s motivation to provide such benefits will thus also constitute a (second-order) public good. The public goods provided by the leader will often be costly to produce, and if increased prestige is what motivates the leader to pay these production costs (as service-for-prestige predicts), then followers must succeed in providing the leader with prestige, in order to

maintain production of these public goods. If the prestige allocated to leaders is costly for individual followers to provide, then its allocation will present a collective action problem for followers (Price, 2003; Price and Van Vugt, in press).

To understand why prestige allocation should constitute a collective action problem for followers, it helps to first consider social power more abstractly. Emerson (1962) provides a simple and useful definition of social power when he notes the reciprocal relationship between power and dependence: Individual X has power over Individual Y to the extent that Y must depend exclusively on X for the achievement of some goal, that is, to the extent that Y's ability to achieve the goal is controlled by X. Similarly, because Y's goals will generally involve the acquisition of benefits and avoidance of harm, the power of X (i.e., the dependence of Y on X, and X's control over Y's goal achievement) can also be thought of as X's ability to confer benefits and/or impose harm on Y (Sell et al., 2009). If X has high power, this should improve X's access to many kinds of resources: if X is highly able to benefit and/or harm others, then those whom X can benefit/harm will be motivated to act in ways that promote X's welfare, so that they can remain in good standing with X and thus acquire these benefits and/or avoid this harm. As a result, people will tend to go out of their way to promote X's welfare (Henrich and Gil-White, 2001; Sell et al., 2009), for example, by deferring to X's interests, sharing resources with X, taking pains to avoid causing harm to X, and cooperating with X. High social power ("status") is therefore expected to benefit X's fitness by improving X's access to many kinds of resources (Von Rueden et al., 2011, in press; for more on the nature of these resources, see below section on small-scale societies).

The notion that social power is rooted in ones' ability to benefit and/or harm others corresponds well to Henrich and Gil-White's (2001) conceptualization of prestige and dominance as two different kinds of social status (noted above), with prestige being status that is voluntarily conferred on those who are perceived as offering benefits, and dominance being status that is attained coercively by those who are perceived as threatening harm. (However, note that these two paths to status will rarely be completely distinct, since traits that lead to prestige can frequently lead to dominance, and vice versa; Henrich and Gil-White, 2001; Von Rueden et al., 2011). If prestige is conceptualized as something that is freely conferred, then efforts made by the prestige allocator to promote the prestigious individual's welfare ought to be thought of – like any kind of behavior in which one individual intentionally and voluntarily incurs costs to deliver benefits to another individual – as a kind of biological "altruism" (Tooby and Cosmides, 1996). We believe that conceptualizing prestige in this way, and distinguishing it from dominance, are useful means of understanding the different ways in which leaders can acquire status. However, unlike the service-for-prestige theory we present here, Henrich and Gil-White (2001) regard prestige as something that is offered in exchange not for public goods but for a private good: the privilege of affiliating socially with the prestigious individual. In their view, individuals with high levels of expertise are allocated prestige by those who wish to learn from and copy their behavior; by allocating prestige to an expert (i.e., by acting in ways that benefit the expert's welfare), followers can ingratiate themselves to, and

thus enhance their own ability to copy, the expert. Although we do agree that prestige allocation may often occur as a way to compensate experts for providing private goods, we suggest that it also often occurs as a way to compensate leaders for providing public goods.

If prestige is indeed allocated in exchange for public goods, and if prestige and its behavioral consequences are indeed costly to produce, then it becomes easy to see why the allocation of prestige to leaders will entail a collective action problem. In order for followers to motivate leaders to provide public goods, they must collectively pay the costs of respect. That is, they must as a group incur costs to allocate prestige to the leader – and the increased access to the group's material, reproductive, and social resources that this prestige will entail – to an extent that compensates the leader for the cost of providing public goods. Because this represents a collective action problem, a follower could gain a free rider's advantage by accepting the benefits of leadership while refusing to pay these costs. For example, consider a leader who routinely incurs costs (e.g., risks his own life in battle, assumes stressful responsibilities, works long and hard on military strategy) in order to guide his group to success in war. His services enable his followers to acquire public goods such as better territory, shared resources, and increased group status. Imagine two followers in this group, both of whom benefit equally from the leader's services. Follower 1 is respectful, and tends to engage in costly acts that benefit the leader (e.g., does favors for and shares resources with the leader; refrains from having an affair with the leader's wife; takes pains to look out for the welfare of the leader's children; strives to comply with the leader's directives; pays taxes or tribute to the leader; takes risks to ensure the safety and health of the leader). Follower 2 free rides on the leader's services by doing none of these things, and thus enjoys higher net benefits (benefits received from the leader's services, minus costs paid to be respectful) than Follower 1. Because each follower in this scenario has a personal incentive to free ride, there is the risk that the collective effort will fail to produce sufficient prestige to compensate the leader for the costs of providing public goods.

Just like cheaters in reciprocal exchanges, free riders in collective actions will exploit cooperators to extinction unless their advantages are neutralized (Yamagishi, 1986; Boyd and Richerson, 1992). As a result, cooperators strive to neutralize free riders' advantages via punishment or social exclusion (Fehr and Gächter, 2002; Price and Johnson, 2011). The collective action scenario described here is unusual in that it is a collective action for the purpose of engaging in reciprocity. Collective actions are typically conceptualized as functioning to produce or acquire some shared material resource (for example, a group of citizens jointly generating tax revenue, or a group of hunters jointly killing a large game animal), but in this case, the joint effort is focused on producing sufficient prestige to compensate the leader for services rendered. As a result, Follower 2 above is in the unusual position of simultaneously representing both a cheater in a reciprocal interaction (for failing to engage in a service-for-prestige transaction with the leader) and a free rider in a collective action (for failing to cooperate with fellow followers in collectively producing prestige for the leader). Follower 2 will therefore be a prime target for hostility within the group: both

the leader and the other followers have incentives to punish or ostracize Follower 2.

Because service-for-prestige is unique (as far as we know) in regarding the allocation of prestige to leaders as a collective action problem, it is also unique in predicting that this problem will need to be solved via the punishment and/or social exclusion of disrespectful followers. We say more about this prediction and related predictions below.

MISMATCH THEORY: ANCIENT ADAPTATIONS IN MODERN ENVIRONMENTS

A final key component of service-for-prestige is mismatch theory. Because psychological adaptations evolved in ancestral environments that may be quite different in certain respects than present environments, we cannot always expect for adaptations to function adaptively in modern societies (Tooby and Cosmides, 1990). A common example is human gustatory preferences for fats, sugars, and salts. Because these nutrients were essential but difficult to acquire in ancestral environments, people have apparently evolved to be strongly motivated to consume them. These motivations may function maladaptively in environments where these nutrients are easily obtained, by leading to health problems associated with over-consumption (Nesse and Williams, 1994). Some aspects of leader–follower relations may represent mismatches with modern environments (Van Vugt et al., 2008b); we provide several examples below.

LEADER–FOLLOWER RELATIONS IN THE HUMAN EVOLUTIONARY PAST

Before we focus on service-for-prestige in modern contexts, we will examine how leadership and followership operated in small-scale (i.e., hunter-gatherer and tribal) societies that most closely approximate those in which our ancestors spent the vast fraction of their evolutionary history.

The available evidence suggests that leadership and followership are universal aspects of human nature: these behaviors appear at all levels of social organization that have existed since prehistoric times, including hunter-gatherer and tribal societies (Brown, 1991; Van Vugt et al., 2008a). Leadership is used in these societies to facilitate cooperation in activities such as warfare, forging political alliances, maintaining within-group order, big game hunting, and moving camp (Service, 1966; Johnson and Earle, 1987), all of which are vital to the success, status, and fitness of individuals living in groups. Ethnographic accounts of leaders in these domains generally describe the leaders as men, rather than women (Service, 1966; Johnson and Earle, 1987). However, although women only rarely hold the most directly influential political positions in small-scale societies, they commonly lead in more indirect ways by exerting substantial influence on political affairs (Low, 1992; Yanca and Low, 2004; Bowser and Patton, 2010).

A common observation about leadership in small-scale societies is that it tends to be informal and based on achievement (Fried, 1967; Kelly, 1995). Compared to leaders in industrialized societies, these leaders have little power to force others to do what they say. This is especially true in nomadic hunter-gatherer societies, which, compared to sedentary small-scale societies, involve smaller group sizes and lower population densities. There

are usually no formal leadership offices or duties in nomadic hunter-gatherer societies, and leaders tend to lead by persuasion and demonstrations of their expertise and ability to benefit others (Service, 1966; Johnson and Earle, 1987). Nomadic hunter-gatherers rarely recognize anyone as a formal headman and tend to express low tolerance for domineering leaders (Service, 1966; Turnbull, 1968; Lee, 1993).

Small-scale societies also tend to recognize different leaders in different domains (cf. the concept of distributed leadership; Gronn, 2002). Leadership requires expertise, and different people may have expertise in different activities (Service, 1966). For instance, the leader of a hunting expedition may not be the same person who organizes an alliance with a friendly group or a raid against an unfriendly one. The traditional authority system of the Navajo, for example, included war leaders, peace leaders (who organized friendly political interactions), hunt leaders, medical leaders, and ceremonial song leaders (Shepardson, 1963).

By assisting the group in domains such as political relations with external groups, maintenance of internal order, big game hunting, and camp movements, leaders provided followers with public goods. For instance, success in war can bring a wide variety of collective benefits, including increased access to territory, mates, and other resources (Keeley, 1996), and success in hunting large game produces meat that is widely shared among the entire residential group (Kelly, 1995). Leaders often incur large costs to generate these public goods. Big game hunting, for example, can involve large investments of time and effort and significant risks. A survey of “persistence hunts” among Kalahari hunter-gatherers suggests that members of hunting parties chase large game for 3–6 h across distances of 20–35 km (12–22 mi), in difficult conditions such as extreme heat and dense bush (Liebenberg, 2006). War leadership represents another example of costly public goods provisioning; war leaders gain reputations for bravery by taking risks (for example, fighting in the front lines) that enable their groups to effectively compete for resources (Meggitt, 1977; Chagnon, 1988).

Why are leaders willing to incur large costs in order to provide followers with public goods? Plausibly because provisioning of public goods is a key way in which members of small-scale groups can acquire social status (Price, 2003, 2006a,b). Because leaders in small-scale societies have little power to coerce and dominate followers, their high status appears to be more similar to voluntarily conferred prestige than to dominance (Henrich and Gil-White, 2001; Van Vugt and Ahuja, 2010). These leaders benefit from their high status: prestigious individuals are highly valued by others as friends and allies and therefore social and material resources tend to flow their way. Leaders’ increased access to these resources may sometimes be observable only over the long-term, as opposed to the immediate short-term (Von Rueden et al., in press); for example, among Ache forager-horticulturalists, those who consistently produce and share large amounts of food appear to be rewarded over the long-term by receiving more food from others when they are sick or injured (Gurven et al., 2000). In a community of Tsimane hunter-horticulturalists, the most prestigious and influential men did not receive more shared food over the short-term, but were more likely to receive social support (e.g., help with labor), food, and cash during times of crop failure (Von Rueden, 2011).

Similarly, magnanimous leadership among the Martu Aborigines in Australia is believed to be rewarded over the long-term with social and political support (Bird and Bliege Bird, 2010).

A further important way in which status enhances male fitness in these societies is by contributing to reproductive success. Status is attractive both to women (Ellis, 1992; Li, 2007) and to parents who wish to betroth their daughter to a high status man as a way of creating a useful ally (Hart and Pilling, 1960; Kelly, 1995). Ethnographic evidence suggests that in these societies, higher status men – or leaders – have more wives and sexual partners, as well as higher-fertility wives and more surviving offspring (Levi-Strauss, 1967; Chagnon, 1979, 1988; Betzig, 1986; Von Rueden et al., 2008, 2011). For example, relatively high levels of status and reproductive success are attained both by leaders in the hunting domain who provide their group with large game as a public good (Hawkes, 1993; Hawkes and Bliege Bird, 2002), and by leaders in the war domain who contribute to their group's ability to compete for resources (Matthiessen, 1962; Meggitt, 1977; Chagnon, 1988).

The importance of leadership in small-scale societies tends to correlate positively with the degree to which settlement patterns are sedentary as opposed to nomadic, because sedentism permits larger residential group sizes and higher population density (Fried, 1967; Johnson and Earle, 1987; Marlowe, 2011). When groups are larger, coordination and collective action problems involved in group action are harder to solve, and leadership is relatively more important (Carneiro, 2000; Tooby et al., 2006; Hooper et al., 2010). Within-group disputes between members (e.g., dyadic conflicts) may also become more frequent in larger groups, necessitating leadership to resolve them. Further, when population density is lower and it's easier to move camp, individuals can more freely leave and switch groups. Nomadic hunter-gatherers exhibit “fission–fusion” social organization, with unstable group membership rosters. Groups may break apart or join together, depending on the abundance of local resources and the quality of social relationships within the group (Turnbull, 1968; Kelly, 1995). This arrangement makes it relatively easy for group members to escape a leader who becomes too dominant. But with increases in sedentism and population density, fission–fusion social organization becomes less tenable, and followers become less capable of exiting groups with dominant leaders (Boehm, 1999; Price and Van Vugt, in press). Sedentism may also be associated with more powerful leadership if it is enabled by the presence of a “patchy” resource (i.e., one concentrated in a fixed location) that can be monopolized and controlled by leaders, such as the salmon runs of the Northwest Coast described below (Kelly, 1995).

The transition to agriculture is associated with increases in group size, population density, and sedentism, as well as increases in the power and dominance of leaders. Typical nomadic hunter-gatherer bands consist of 25–50 members, but typical hunter-horticulturalist villages consist of 100–400 residents (Johnson and Earle, 1987; Kelly, 1995). Leaders are more powerful in hunter-horticultural compared to nomadic hunter-gatherer societies, with formally recognized “Big Men” exhibiting enduring political authority, and with social organization becoming more hierarchical (Meggitt, 1977; Johnson and Earle, 1987; Chagnon, 1997; Boehm, 1999). Greater sedentism and population density

also mean that hunter-horticultural settlements are more “socially circumscribed” (i.e., hemmed in by neighboring settlements) than the camps of nomadic hunter-gatherers (Chagnon, 1997), which reduces the feasibility of fission–fusion organization and the ability of followers to escape overly dominant leaders.

However, it is not agriculture *per se*, but rather the increased group size and population density that agriculture permits, that seems to lead to increases in the power and dominance of leaders. The Indians of the American Pacific Northwest Coast provide a useful illustration of how leaders can become more powerful and dominant with increases in group size and population density, even in the absence of agriculture (Price and Van Vugt, in press). By residing near salmon-rich rivers, these hunter-gatherers could maintain sedentary villages of 500–800 people and population densities of one to two people per square mile, both unusually high figures for either hunter-gatherers or hunter-horticulturalists (Johnson and Earle, 1987). These villages required strong leaders because it is challenging to organize large groups for collective action and resource redistribution (Fried, 1967; Johnson and Earle, 1987). Accordingly, Northwest Coast leaders were much more powerful than typical hunter-gatherer leaders, and are regarded by anthropologists as being the key to the functioning of the Northwest Coast political economy (Johnson and Earle, 1987). These leaders were clearly identified by followers as chiefs and as essential group representatives in political interactions, and they broadcast their wealth and status in lavish potlatch ceremonies in which they distributed and sometimes destroyed large collections of their material goods.

Not only were followers more dependent on leaders in the environments of the Northwest Coast, they were also more helpless to escape dominant leaders, due to the unfeasibility of fission–fusion organization (that is, the sedentary lifestyle and high population density made it more difficult for group members to hive off from groups with bad leaders, in order to live and forage in a different territory). Moreover, the patchy distribution of salmon runs enabled chiefs to control access to the region's most important food resource, which further increased follower dependence (Kelly, 1995). The decreased exit options and increased dependence of followers seem to have increased the extent of dominance-based leader–follower relationships: although slavery is rare in hunter-gatherer societies, it was common throughout the Northwest Coast, with slaves composing 7–15% of a typical community (Kelly, 1995). As noted above, this association between reduced follower bargaining power and increased dominance in leader–follower relations is a prediction of service-for-prestige, which assumes that leaders tend to maintain their high status in the least costly way that they can; if they can maintain it without having to pay the costs of providing benefits for followers, they will tend to do so. That is, when followers are more powerless to escape, reject, or retaliate against leaders, leaders will more likely attempt to maintain their status via their ability to dominate and exploit followers, as opposed to their ability to engage in reciprocity with them.

The positive relationships between group size/population density and more powerful leadership can also be observed not just by comparing different societies but by comparing different settlement patterns within the same society. Carneiro (2000) describes

how these patterns changed seasonally among North American Plains Indians. For most of the year they lived in small bands of about 50 people, but during the summer buffalo hunt 20 or more of these bands would coalesce to form a much larger group. The dramatic size increase was accompanied by an equally dramatic elaboration of leadership structure. Whereas leadership in the single band involved little power and few duties (i.e., it was fairly typical of a small nomadic foraging society), leadership in the large aggregation involved a tribal council of band leaders headed by a designated tribal chief, as well as several men's societies, including one that acted as a police force to maintain order in the settlement.

Like the different small-scale societies discussed above, the hunter-gatherer societies of the human evolutionary past have probably varied considerably in terms of key demographic factors such as group size and population density (Kelly, 1995). We suggest that this variation affected the balance of power between leaders and followers and therefore influenced the prevalence of reciprocal versus coercive leadership of these societies. We also suggest that human mental adaptations for leadership and followership were designed by the selection pressures that existed across this range of different environments, and so are calibrated to generate a range of behavioral outputs, depending on the balance of power between leaders and followers that is perceived in the environment.

SERVICE-FOR-PRESTIGE IN INDUSTRIALIZED SOCIETIES

The human mind was designed by and for the environments of small-scale ancestral societies (Tooby and Cosmides, 1990, 1992, 2005). The above examination of leader–follower relations in such societies therefore provides an essential foundation for our next task, which is to evaluate the extent to which predictions of service-for-prestige are supported by observations of leader–follower relations in industrialized societies.

PREDICTION 1: FOLLOWERS PREFER TO CHOOSE THEIR OWN LEADERS, BY ALLOCATING PRESTIGE TO THOSE WHO PROVIDE THEM WITH BENEFITS

Experimental evidence suggests that people in industrialized societies, just like in small-scale societies, prefer to follow leaders who they have chosen themselves, rather than leaders who have been imposed on them by an external agent (Van Vugt et al., 2004). Further, their mechanism for choosing leaders is similar to that used in small-scale societies (Price, 2003, 2006a,b): they reward group-beneficial contributions with prestige (Price and Van Vugt, in press). Studies conducted among both university students and business employees indicate that when group members are allowed to allocate status to the co-members of their choosing, they allocate it to those who have demonstrated their willingness and ability to benefit the group (Flynn, 2003; Hardy and Van Vugt, 2006; Anderson and Kilduff, 2009; Willer, 2009). This process of status acquisition via engagement in group-beneficial tasks has been termed “competitive altruism” (Roberts, 1998; Barclay, 2004; Hardy and Van Vugt, 2006; McAndrew and Perilloux, 2012): because group members obtain an individual advantage by achieving high status, and because status can be acquired via pro-group altruism, members compete with each other to be the most group-beneficial.

Representative governments (e.g., forms of democracy) are also characterized by processes whereby followers can choose their own leaders, and award prestige to leaders who benefit them (e.g., by voting them into office). Political philosophers have long noted that these processes are key reasons why representative governments tend to be more effective in delivering benefits to citizens, compared to less reciprocal arrangements such as monarchy (Locke, 1689; Mill, 1861). In most businesses, however, such democratic processes are absent, and leaders are simply imposed on followers. Thus a central dynamic of leader–follower reciprocity – the process whereby followers choose their leaders, and allocate prestige to them based on their ability to provide group benefits – cannot occur in most businesses, which probably results in followers becoming alienated and losing motivation to cooperate voluntarily with leaders (Price and Van Vugt, in press). Some successful businesses, however, are exceptions to this rule. Leaders at W. L. Gore and associates, for example, are selected via a process in which employees choose who they want to follow, rather than one in which bosses are imposed on employees. The philosophy behind this practice – “if you attract followers, then you're a leader” – recalls the bottom-up process of leader selection that prevails among nomadic hunter-gatherers. W. L. Gore's very low employee turnover rate suggests that they are implementing this practice to good effect (Van Vugt and Ahuja, 2010).

PREDICTION 2: PREFERENCES FOR LEADERS WILL BE BIASED IN FAVOR OF PHYSICALLY FORMIDABLE AND INTELLIGENT MALES, AND MAY BE MISMATCHED WITH MODERN ENVIRONMENTS

Because of processes in sexual selection (Darwin, 1871; Trivers, 1972), men are on average more physically formidable (e.g., taller and stronger) than females. In the ancestral-type environments of small-scale societies, some of the most important domains in which leadership is required are male-dominated activities requiring high physical formidability, such as hunting and war. The leaders who are chosen in such domains are almost always males (Service, 1966; Johnson and Earle, 1987). As a result, our minds may have evolved to be biased toward assuming that all else equal, physically formidable males make the most appropriate leaders (Van Vugt and Ahuja, 2010). (Indeed more generally, people seem to cognitively encode the concept of political power as a human body, with higher power represented by a more formidable body; Holbrook and Fessler, 2013).

Followers do appear to exhibit such biases in industrialized societies: experimental and field studies of general leadership preferences suggest that people tend to prefer leaders who are male (Carlson et al., 2006; Elsesser and Lever, 2011), who are perceived as taller based on their stature or facial height (Judge and Cable, 2004; Gawley et al., 2009; Blaker et al., 2013; Re et al., 2013), and who are perceived as healthier based on their bodily motion (Kramer et al., 2010). Facial appearance may also provide cues to pubertal testosterone levels and thus to physical formidability. For example, male military academy graduates who were rated as appearing more dominant in their student portraits went on to achieve higher status in their careers (Mazur and Mueller, 1996). Another formidability-related cue is physical attractiveness; traits that are perceived as attractive are believed to be those which would

have indicated health and biological quality in the ancestral past (Grammer et al., 2003). Accordingly, followers express preferences for physically attractive leaders (Anderson et al., 2001; Van Vugt and Ahuja, 2010).

Preferences for physically formidable male leaders may, however, be mismatched with leadership requirements in modern organizations (Van Vugt et al., 2008b). Our ancestors' need for expertise in male-dominated, physically aggressive coalitional activities such as hunting and war is much-reduced in modern businesses, but biases in favor of physically formidable males persist. As a result of such biases, people in industrialized societies may, for reasons that have become largely obsolete, tend to overlook females and physically unimpressive males as candidates for leadership positions, even if these candidates are in fact well-suited for leadership in modern contexts (Van Vugt et al., 2008b; Price and Van Vugt, in press). On the other hand, even if there is less of a genuine need for physically formidable leaders in modern organizations than there was in the ancestral past, such leaders may nevertheless perform especially effectively in some kinds of leadership roles, due to how they are perceived by others. For example, a leader's high formidability could increase his bargaining power in social interactions by making him seem more intimidating to others (Sell et al., 2009; Lukaszewski, 2013); as a result that leader might be relatively effective in tasks like deterring uncooperative behaviors among followers and winning negotiations with external groups.

Other leader traits that tend to be widely preferred are intelligence and communication skills (Den Hartog et al., 1999; Judge et al., 2004). These preferences also seem consistent with the requirements of leadership roles in the ancestral past (Tooby et al., 2006; Van Vugt et al., 2008a). For instance, intelligence is necessary for making decisions that will affect group welfare in a positive way (e.g., developing a strategy for successful group cooperative action), and communication skills are essential for implementing these decisions (e.g., persuading followers about the wisdom of that strategy, and ensuring that the group acts out that strategy in a precise and coordinated way). Unlike traits related to physical formidability, however, intelligence and communication skills are probably just as genuinely relevant to leadership roles in modern environments as they were in the ancestral past. Competent leadership in an industrialized society generally has little to do with killing large game or physically dominating rivals, but continues to have much to do with devising and communicating a successful strategy for collective action (Price and Van Vugt, in press).

PREDICTION 3: PREFERENCES FOR LEADERS WILL BE DIFFERENT IN DIFFERENT DOMAINS, AND MAY BE MISMATCHED WITH MODERN ENVIRONMENTS

Leadership ability can be domain specific, and just as small-scale societies distinguish among several kinds of leaders (as noted above), members of industrialized societies prefer different leaders for different roles (Price and Van Vugt, in press). This may be a major reason why leadership is often shared in successful organizations (Wassenaar and Pearce, 2011). For example, experimental participants prefer leaders with a more masculine facial appearance (like John McCain) in the context of war and intergroup

competition, and prefer leaders with a more feminine face (like Barack Obama) in peaceful contexts (Little et al., 2006; Spisak et al., 2012a,b). Domain-specific leadership preferences may even be strong enough to override the general bias in favor of male leaders, noted above: experimental evidence suggests that although male leaders are preferred in times of intergroup competition, female leaders are preferred when there is a need for conflict resolution within the group (Van Vugt and Spisak, 2008).

On the other hand, our bias toward domain-specific leadership may sometimes lead us astray, and can be another example of mismatch (Van Vugt and Ronay, 2014; Price and Van Vugt, in press). Hunter-gatherer collective actions tend to be small and therefore relatively simple to organize and manage, so domain-specific expertise (as opposed to management skills) may often be the most important requirement for competent leadership. It might make sense, for example, to choose the leader of a three-member hunting expedition based on hunting expertise. In a complex modern organization, however, the gulf between domain-specific expertise and leadership can be more vast, and managerial roles can require skills that have very little to do with this expertise itself. In many professional sports, for example, great former players are often preferred as managers, despite an absence of evidence that better players make better managers (Van Vugt and Ahuja, 2010). We should question our bias toward assuming that superior ability in a specific activity will make one particularly well-suited to lead an organization related to that activity.

PREDICTION 4: FOLLOWERS WILL PREFER COMPETENT, PROSOCIAL, AND “FAIR” LEADERS, BUT SOME PREFERENCES MAY BE MISMATCHED WITH MODERN ENVIRONMENTS

According to service-for-prestige, followers are adapted to favor leaders who are willing and able to provide them with benefits (Price and Van Vugt, in press). Accordingly, research suggests that people from a wide variety of cultures do prefer leaders who score highly on both prosociality and competence (Van Vugt et al., 2008a). The 61-culture GLOBE survey of universally valued leader traits (Den Hartog et al., 1999) indicates that prosocial disposition (e.g., trustworthiness, fairness) and possession of group-beneficial skills (e.g., intelligence, competence) are consistently valued attributes of leaders cross-culturally. These findings complement a review by Hogan and Kaiser (2005), which identified traits indicating prosociality (e.g., modesty, humility, and integrity) and group-beneficial skills (e.g., decisiveness, competence, and vision) as the most important characteristics of successful leaders. With regard to these prosocial traits, note that Hogan and Kaiser (2005) define integrity as “keeping one's word, fulfilling one's promises, not playing favorites, and not taking advantage of one's situation” (p. 173). Integrity is thus essentially synonymous with trustworthiness, which is an essential trait in a reliable reciprocal partner (Price, 2006a; Rilling and Sanfey, 2011). The emphasis on modesty and humility suggests that followers prefer leaders who are not overly self-centered, which would allow them to focus more on the interests of followers (Price and Van Vugt, in press). Indeed, other results from the GLOBE survey indicate universal distaste for traits associated with leadership that is self-serving and

unconcerned with the interests of followers (e.g., dominance, selfishness).

This aversion to overly self-centered leadership is the flip side of the preference for prosocial leaders: leaders are reviled if they control groups in a manner that benefits themselves while harming followers (Tooby et al., 2006). A recent event that epitomizes this principle is the extent to which New Jersey Governor Chris Christie has been excoriated for his perceived role in the “Bridgegate” scandal. Christie’s political allies allegedly orchestrated the partial closure of the Fort Lee bridge from New Jersey to New York – the busiest motor-vehicle bridge in the world – in order to punish Fort Lee’s mayor for not endorsing Christie’s candidacy (Kleinfeld et al., 2014). The lane closures caused traffic chaos and imposed large costs on Christie’s own electorate, all for the intended purpose of generating a narrowly selfish and relatively trivial benefit for Christie. It is also worth considering, in this context, that the extreme levels of income inequality that can obtain in modern businesses may be perceived by followers as exploitative failures of reciprocity. CEOs in the United States between 2000 and 2013, for example, made 200–400 times as much as the average worker (Mishel and Sabadish, 2013), a level of inequality that far exceeds those observed in hunter-gatherer societies (Smith et al., 2010). Leaders who accept salaries that are massively higher than those of followers may be seen as hoarding group resources for their own selfish ends (Price and Van Vugt, in press; Van Vugt et al., 2008a).

Finally, note that although people universally prefer “fair” leaders (Den Hartog et al., 1999), this universality probably masks some important underlying variance. Because different types of followers prefer different kinds of fairness, it will often be difficult for a leader to achieve reciprocity with all followers simultaneously. Whereas some followers may perceive social equality as maximally fair, others may see some forms of inequality as maximally fair, for example, inequality that results from socially sanctioned competition (such as better-qualified job candidates competing successfully for higher-paying jobs). Increased approval of inequality and competition is expressed by individuals who are better-positioned to win competitions for status and resources, such as the highly educated, the wealthy, and members of ethnic majorities (Ritzman and Tomaskovic-Devey, 1992; Pratto et al., 2006; Kunovich and Slomczynski, 2007).

Other traits associated with approval of inequality and competition may be more comprehensible in terms of ancestral environments than modern ones. For example, men who are relatively muscular are more likely to approve of social and economic inequality (Price et al., 2011), particularly if they are relatively wealthy (Petersen et al., 2013; however, this research also found that relatively muscular men are *less* approving of inequality if they are relatively poor). Muscular men are also more likely to endorse aggressive methods of conflict resolution, including war (Sell et al., 2009; Price et al., 2012). These preferences may have been adaptive ancestrally, when muscularity was relatively key to success in social competitions, but seem less rational in modern contexts in which such success has more to do with education and technology. Thus, the kind of “fair” leaders that followers prefer may sometimes be mismatched with aspects of modern environments.

PREDICTION 5: FOLLOWERS WILL PREFER LEADERS WHO DELIVER INGROUP ADVANTAGE

Ancestrally, one of the most vital benefits leaders could provide was expertise in matters of intergroup competition, and in modern environments, followers prefer leaders who are perceived as ingroup members and strong representatives of ingroup interests (Hogg, 2001). At times when the ingroup is threatened by an external enemy, members will most exhibit this pro-ingroup bias and be most supportive of their leader (the “rally effect”; Van Vugt et al., 2008a). The rally effect benefits followers, who gain security via their increased willingness to cooperate with the leader’s efforts to organize them against the enemy, and it also benefits leaders, who gain status due to their increased ability to benefit the group (Van Vugt and De Cremer, 1999). Because the rally effect enhances the leader’s status, there is the potential for abuse; leaders could exaggerate or provoke an external threat in order to consolidate their own power (Price and Van Vugt, in press).

On the other hand, leaders can also use the rally effect in a less self-serving and more group-beneficial way. If followers are persuaded by a leader of a great need to beat a competitor, they may cooperate particularly effectively: experimental evidence suggests that groups are more cooperative and productive when they perceive a competitive threat from an external group (Van Vugt et al., 2007; McDonald et al., 2012). Note, however, that this tendency appears to be stronger in males than females, which suggests that it evolved in conditions of male coalitional violence (Van Vugt et al., 2007). This suggestion is also made by evidence that people who are experiencing or have experienced life during wartime tend to play economic games in a more cooperative and egalitarian manner (Gneezy and Fessler, 2012; Bauer et al., 2014).

PREDICTION 6: DOMINANT LEADERSHIP EMERGES WHEN FOLLOWERS LACK EXIT OPTIONS

Service-for-prestige predicts that leaders benefit by adopting a more dominant and coercive leadership style when they can get away with it, because this saves them the costs of delivering benefits to followers. Leaders should be able to get away with this more in modern contexts in which their bargaining power relative to followers is increased for whatever reason, for example, due to it becoming institutionally normalized (Henrich and Gil-White, 2001) in a way that increases follower dependence (Emerson, 1962). One of the most important ways in which leaders’ relative power will be increased in modern societies, however, is if followers have reduced power to exit groups. It was noted above that leadership in small-scale societies seems to become more dominant and less reciprocal when followers have better exit options, and it has long been suggested that a similar pattern exists in industrialized societies, with leadership becoming more autocratic when members have fewer exit options (cf. Hirschman, 1970).

In consideration of the above, service-for-prestige expects that leaders of modern organizations will more likely adopt a dominance-based leadership style when employees are less able or willing to leave their jobs, or to otherwise reject or retaliate against non-beneficial leaders (Price and Van Vugt, in press). In such situations, it will be less necessary for leaders to pay the costs of providing benefits to followers in order to compel them

to remain in the organization. This may explain why employees with better exit options tend to receive a greater share of organizational rewards (Rusbult et al., 1988). If leaders adopt a coercive leadership style when their followers do possess good exit options, they will likely lose followers: in experimental research by Van Vugt et al. (2004), members defected more from groups if they were led by autocratic-style instead of democratic-style leaders.

When followers lack exit options, and thus have reduced bargaining power to demand reciprocity with leaders, a more comfortable niche is created for leaders who are concerned only with maximizing their own power and who have no genuine regard for follower interests (Price and Van Vugt, *in press*). Such toxic leadership may be exhibited by those with high scores on at least one of the “dark triad” traits of Machiavellianism, narcissism, and psychopathy (Paulhus and Williams, 2002; Van Vugt and Ahuja, 2010). Such traits appear to be more prevalent among corporate leaders than among the general population (Babiak et al., 2010), and employees who serve under leaders high in such traits report reduced well-being and job satisfaction (Mathieu et al., 2014).

PREDICTIONS 7 AND 8: DISRESPECTFUL FOLLOWERS OF BENEFICIAL LEADERS WILL ATTRACT SOCIAL PENALTIES (PUNISHMENT AND/OR SOCIAL EXCLUSION) FROM OTHER FOLLOWERS, WHEREAS DISRESPECTFUL FOLLOWERS OF NON-BENEFICIAL LEADERS WILL ATTRACT SOCIAL REWARDS (ENHANCED REPUTATION AND PRESTIGE) FROM OTHER FOLLOWERS

We conclude this section by looking at some of the novel predictions that service-for-prestige is able to make because it regards leader–follower reciprocity as a collective action problem. As noted above, service-for-prestige predicts that leaders provide public goods to followers in exchange for prestige, which followers must collectively supply. As in any collective action, this presents a free rider problem: a follower who took leader-provided benefits without paying the costs of respect (by going out of one’s way to promote the welfare and interests of the leader, including by deferring to and cooperating with the leader) would be advantaged over respectful followers. In order to solve this problem, this advantage would have to be neutralized or reversed. As in other collective actions, this neutralization/reversal would be expected to occur via the imposition of social penalties on the free rider, in the form of punishment (e.g., physically harming or appropriating resources from the disrespectful follower) and/or social exclusion (i.e., preventing the disrespectful follower from participating in advantageous social and cooperative interactions; Fehr and Gächter, 2002; Price and Johnson, 2011). Thus, a general prediction of service-for-prestige is that disrespectful followers of beneficial (i.e., public-good-provisioning) leaders will tend to attract social penalties from other members of their group. Note that because such a penalty would represent a cost imposed on not only a free rider in a collective action but also a cheater in a reciprocal exchange (with the leader), it could take the form of negative indirect reciprocity (Alexander, 1979; Nowak and Sigmund, 2005), whereby one follower imposes costs on another for failing to engage in reciprocity with the leader.

In considering the various ways by which social penalties could be imposed on disrespectful followers, it is important to keep in

mind that to the extent that a penalty is costly to impose, it could lead to a second-order free rider problem (Yamagishi, 1986; Boyd and Richerson, 1992). Second-order free riders in this situation would be followers who paid the costs of respect, but who did not penalize disrespectful followers; they would obtain the benefit produced by these penalties (i.e., the leader’s continued motivation to produce public goods), but by avoiding the costs of administering these penalties, they would acquire higher net benefits than followers who paid to allocate both prestige and penalties. There are a variety of ways in which evolution could overcome the recursive nature of free rider problems and there is no consensus about how it does so (Price, 2003). However, researchers do agree that evolution overcomes these problems somehow (Boyd et al., 2003; Barclay, 2006; Bowles and Gintis, 2011).

Researchers also agree that the penalties used to solve these problems can take the form of direct punishment, and that cooperators in collective actions tend to experience punitive sentiment toward free riders (Price et al., 2002; Mathew and Boyd, 2014). Punitive sentiment leads those who experience it to support and advocate the punishment of free riders, and may lead them to administer this punishment themselves (Fehr and Gächter, 2002; Price, 2005). It is therefore plausible that respectful followers experience punitive sentiment toward disrespectful followers, and act on this sentiment either by punishing these followers themselves, or else by advocating and supporting the punishment of these followers by other group members. This punishment could be administered by one specific member (O’Gorman et al., 2009), including the leader him/herself. Even in situations in which leaders impose such penalties themselves, we would expect for followers to experience punitive sentiment, as it would lead them to lend political support to the leader’s punitive actions. Punishment could also be administered in a coordinated manner by more than one member; coordinated punishment could reduce the per capita costs of punishment and thus mitigate the second-order free rider problem (Boyd et al., 2010; Guala, 2012).

The social penalties of free riding do not have to involve direct or explicit punishment, and in both small-scale and industrialized societies they may take the form of informal social sanctions that lead to reputational damage (Fried, 1967; Falk et al., 2005). Among hunter-horticultural Shuar, for example, villagers who are perceived as being less respectful of a popular leader are themselves respected less (Price, 2003). The main costs of such reputational damage may involve exclusion from advantageous social interactions (Barclay and Willer, 2007; Sylwester and Roberts, 2010; Baumard et al., 2013). In modern organizations, employees who act disrespectfully toward popular leaders may be sanctioned by other employees via social exclusion processes that are facilitated by gossip (Barkow, 1992; Williams, 2007).

Note that the prediction of social penalties (punishment and/or social exclusion) for disrespectful followers only applies to situations in which leaders are providing followers with public goods, because this is the only context in which followers will need to engage in reciprocity with leaders by collectively providing them with prestige. If followers do not perceive that a leader is providing them with benefits, they should not be motivated to generate prestige for that leader, nor to impose costs on other followers who

fail to generate prestige. On the contrary, if the leader is unpopular, followers should tend to regard disrespectful followers in a positive light. Leaders will be unpopular if they are seen as failing to provide public goods for one reason or another, for example, because they are incompetent or exploiting followers for their own narrowly selfish ends (Tooby et al., 2006), and followers face the problem of how to collectively strip such leaders of status. A disrespectful follower of an unpopular leader risks retaliation from the leader, and so will be seen by co-members as a selfless and prestige-worthy contributor to the public good: if you brave the wrath of Darth Vader, you will become a hero to the rebellion. Thus according to service-for-prestige, rescinding status from a non-beneficial or exploitative leader, just like supplying it to a beneficial one, is a collective action problem (Price and Van Vugt, *in press*). Accordingly, service-for-prestige predicts that disrespectful followers of such leaders will attract social rewards from other followers. These rewards will come in the form of enhanced prestige, which like all forms of prestige (as discussed above) should afford increased access to material, reproductive, and/or social resources.

DISTINGUISHING SERVICE-FOR-PRESTIGE FROM OTHER LEADERSHIP THEORIES

NOVEL PREDICTIONS OF SERVICE-FOR-PRESTIGE

A Lakatosian view (Lakatos, 1978) suggests that a progressive scientific theory will make not only correct predictions shared by other theories, but also novel correct predictions. Some predictions of service-for-prestige presented above may be shared with many leadership theories (e.g., that followers will prefer leaders who are intelligent, competent, and able to deliver ingroup advantage). We included these predictions not to suggest that they are unique to service-for-prestige, but in order to demonstrate that service-for-prestige is consistent with a broad range of well-supported observations about leader–follower relations. These are observations that any useful theory of leader–follower relations should explain, even if other theories can explain them as well. In order to judge the added value of service-for-prestige, however, we must focus on whether it makes any novel predictions.

Because of its evolutionary foundations, service-for-prestige makes some predictions that are not shared by most non-evolutionary theories. These include predictions related to mismatch theory, such as that followers will judge leaders based on characteristics that are more relevant to small-scale societies than to modern organizations (e.g., physical formidability). However, most of these mismatch-related predictions are also made by the evolutionary leadership theory presented by Van Vugt and Ahuja (2010). What truly distinguishes service-for-prestige is not its evolutionary foundations *per se*, but rather its assumption that leader–follower relations evolved via a reciprocal interaction that entailed collective action problems for followers. Thus, the most important novel predictions made by service-for-prestige are those which emanate directly from this assumption, specifically, predictions seven and eight above: disrespectful followers of beneficial leaders will attract social penalties from other followers, whereas disrespectful followers of non-beneficial leaders will attract social rewards from other followers. As far as we are aware, no other theory of leader–follower relations makes not only predictions 1 through 6 above, but also predictions 7 and 8.

COMPARING SERVICE-FOR-PRESTIGE TO OTHER EVOLUTIONARY THEORIES FOR WHY IT PAYS TO LEAD

Predictions 7 and 8 distinguish service-for-prestige not just from the evolutionary leadership theory mentioned above (Van Vugt and Ahuja, 2010), but also from two other notable evolutionary theories of leadership. Both of these theories address the issue of why, given the costs that leaders must incur in order to generate public goods for followers, it would be adaptive for leaders to lead.

The first of these theories is costly signaling theory, which proposes that acts of providing public goods to one's group can serve as a valuable opportunity to advertise one's desirable qualities to potential allies, cooperative partners, and mates (Gintis et al., 2001; Hawkes and Bliege Bird, 2002). For example, the opportunity to lead a hunt might afford one an opportunity to show off attractive traits such as hunting skill, health, and formidability. This advertising could lead to fitness-enhancing social and mating opportunities that would compensate the leader for leadership costs. Although costly signaling offers a plausible explanation for some aspects of leadership, it is distinguishable from service-for-prestige because it does not predict that followers face the collective action problem of generating prestige. Instead, it presumes that the increased social affiliation that a follower offers a leader represents a private good for both leader and follower. This focus on private goods is why costly signaling theory does not make predictions 7 or 8 above (Price, 2003).

The second evolutionary theory of leader compensation could be called the “asymmetric interest” model. From this perspective, leaders of collective actions are compensated by virtue of the fact that they have a greater interest in the success of the collective action than do most followers. Their interest may be greater, for example, because compared to followers they stand to acquire a larger share of the resource produced, or because this resource is inherently more valuable to them (Tooby and Cosmides, 1988; Ruttan and Borgerhoff Mulder, 1999; Hooper et al., 2010). Before examining how this theory is distinguishable from service-for-prestige, it is important to note that some versions of it could in fact be identical to service-for-prestige in everything but name. This would be the case if the leader's increased interest in the collective action were the result of collectively allocated prestige from followers, for example, if this prestige led followers to jointly and voluntarily grant the leader a relatively large share of the spoils. If the leader's increased interest in the collective action were not the result of such prestige, however, then this theory would make different predictions than service-for-prestige. Because it would predict that the leader was leading the collective action out of a private interest in collective success, it would not predict that the leader would require any additional compensation from followers (e.g., prestige), nor that followers would face a collective action problem in generating this prestige. Therefore this theory would not even make the prediction that leaders will acquire more prestige than followers, let alone predictions 7 and 8 above.

COMPARING SERVICE-FOR-PRESTIGE TO EXISTING NON-EVOLUTIONARY LEADERSHIP THEORIES

Service-for-prestige has some important aspects in common with previous exchange theories of leadership that are not explicitly

grounded in evolutionary theory (Price and Van Vugt, *in press*). One of these is leader–member exchange theory (LMX; Graen and Uhl-Bien, 1995), which suggests that leadership quality depends heavily on the quality of social relationships between a leader and individual followers. Transactional theories of leadership are also exchange theories; the exchange process that is usually emphasized in these theories is one in which leaders use punishments and rewards to motivate followers to achieve group goals (Bass, 1991). Interestingly, however, Hollander (1992) suggests that this transaction may take the form of leaders providing benefits to followers in exchange for esteem. Also relevant is servant leadership theory (Greenleaf, 2002; Gillet et al., 2011), which emphasizes that the influence of good leaders stems from their compassion, altruism, moral authority, and ability to benefit followers.

Despite some clear points of similarity with these theories, service-for-prestige possesses several unique attributes (Price and Van Vugt, *in press*). Unlike servant leadership, service-for-prestige sees the “altruism” of good leaders as something that not only benefits followers, but also ultimately profits leaders (because leaders exchange this altruism for prestige). Unlike LMX, service-for-prestige focuses on relationship quality not in general but specifically in terms on how evolution designed both leaders and followers to achieve an efficient exchange of fitness-relevant benefits. Further, service-for-prestige examines relationships between leaders and groups of followers, whereas LMX focuses on dyadic leader–follower relationships. Only service-for-prestige, therefore, predicts that followers face a collective action problem in generating leader prestige. And unlike either servant leadership or LMX, service-for-prestige attempts to explain not only how leadership can most benefit followers, but also how it can most harm them.

Finally, service-for-prestige can potentially explain not only the transactional, material rewards and punishments provided by leaders to followers, but also the “symbolic” benefits of leadership such as enhanced cohesion and identity; such relatively abstract benefits may plausibly have contributed to the fitness of individual group members in the past, if they improved the group’s solidarity and hence ability to compete for resources with other groups. In other words, symbolic benefits may represent proximate mechanisms that over evolutionary time have enabled leaders and followers to achieve more ultimate (fitness-related) goals. In this respect, service-for-prestige has as much in common with transformational leadership models of leadership (Bass, 1991, 1998) as with transactional or social identity models of leadership (Price and Van Vugt, *in press*).

SERVICE-FOR-PRESTIGE AND SOCIAL NEUROSCIENCE

Service-for-prestige proposes that voluntary leader–follower relations involve many of the same behaviors that are involved in cooperative interactions more generally, such as reciprocal exchange, collective action, and punishment of non-cooperators. A growing body of social neuroscience research focuses on these behaviors, especially exchange and punishment (Rilling and Sanfey, 2011). Most of this research has examined cooperation in dyadic contexts and relatively little has focused on group behaviors, which to some extent limits the direct applicability of this research to the group contexts of leadership. However, the science is developing

rapidly, and interest is now turning to the neuroscience of group cooperation as well (Zak and Barraza, 2013).

As social neuroscience is uniquely poised to reveal the specific neural systems that are involved in cooperative behaviors, it may ultimately provide the best methods for testing some of the most fundamental claims of service-for-prestige. One such claim is that voluntary leader–follower exchange evolved as an elaborated form of dyadic cooperation, which allowed for reciprocity to occur between an individual and multiple group members. If correct, then the same core neural systems involved in dyadic cooperation are likely also involved in voluntary leader–follower exchange. If social neuroscience could shed light on the validity of this assumption, it would contribute to the resolution of a debate among evolutionary researchers, some of whom claim that cooperation between an individual and multiple group members is likely to involve direct reciprocity (Price, 2003, 2006a; Tooby et al., 2006) and some of whom claim such cooperation could evolve only via completely different processes such as cultural group selection (Boyd and Richerson, 1988; Henrich, 2004; Bowles and Gintis, 2011).

If service-for-prestige is correct to expect that neural systems that evolved to enable dyadic reciprocity are also fundamental to leader–follower exchange, then there already exists a fairly large body of social neuroscience research that is relevant to service-for-prestige. There has been quite a bit of neuroscience-related research on behavior in the ultimatum game, for example, and this game can be interpreted as a simple form of leader–follower exchange. The ultimatum game is a two-player economics experiment involving a proposer and a responder. The proposer is given a sum of funds and decides how much to offer to the responder. If the responder accepts the offer, then the deal goes through. For example, if the proposer offers 40% of \$10 to the responder and the responder accepts, then the proposer keeps \$6 and the responder takes home \$4. If the responder rejects the offer, however, then both players get nothing. The “rational” decision for responders is to accept any offer greater than 0, even if it is very low, because if they reject they will always get 0. By the same token, the rational decision for proposers would be to offer the lowest possible amount above 0. However, research shows that responders tend to reject offers that are too far below 50%, and that proposers’ offers tend to be close to 50% (Bowles and Gintis, 2011). The proposer can be seen as the leader, and the proposer characteristics that cause cooperation to fail in the game – that is, selfishness and unfairness – are those that followers associate, as noted above, with dominant and “bad” leadership (Den Hartog et al., 1999). A rejected offer in the ultimatum game, therefore, is essentially similar to a case of failed leadership.

Most studies on the neural and hormonal correlates of behavior in the ultimatum game are concerned with responder behavior, but a few focus on proposers. For instance, one study shows that patients with damage to the ventromedial prefrontal cortex (VMPFC), a condition associated with impaired concern for other people, made more selfish proposals. Compared with a control group these patients offered significantly less and seemed less motivated by the emotion of guilt (Krajchich et al., 2009). These results suggest that such individuals would be less likely to emerge as successful leaders in the context of service-for-prestige

exchanges. Other research found that men who received a small dose of testosterone, a hormone associated with aggression and status competition, made more unfair offers compared to men who received a placebo (Zak et al., 2009; cf. Burnham, 2007, who found no significant relationship between circulating testosterone levels and ultimatum game offers in men). Considering that unfair offers are more likely to be rejected, this result suggests that some neurological effects of testosterone in men may reduce effectiveness as a service-for-prestige leader (however, other effects of testosterone, such as those increasing physical formidability, may increase perceived suitability for leadership). A recent study among a sample of managers shows that baseline testosterone levels correlate positively with a more dominant leadership style, and negatively with a laissez-faire leadership style (Van der Meij et al., unpublished data).

Other studies have been conducted to examine the neural correlates of responder behaviors in the ultimatum game, which can be conceived of as a measure of followership. Data on patients with brain damage, especially in the VMPFC, show that they are more likely than healthy participants to reject offers that are deemed unfair (Koenigs and Tranel, 2007). This brain area is thought to be important for emotion regulation. Other studies have suggested that people with higher levels of serotonin – which has been linked to aggression, hostility and impulsivity – are less likely to accept unfair offers from proposers (Crockett et al., 2008; Emanuele et al., 2008). Higher levels of circulating testosterone have also been linked to increased rejection of unfair offers (Burnham, 2007). Taken together, these studies on VMPFC damage, serotonin and testosterone support the view that rejection of unfairness is related to impulsivity and negative emotion, and that individuals who are less able to regulate negative emotion will be less likely to emerge as followers in unequal leader–follower relationships. On the other hand, better ability to regulate negative emotion might make one more likely to accept unequal (e.g., highly dominant) leadership. An fMRI study by Kirk et al. (2011) compared ultimatum game behavior in people who regularly perform Buddhist meditation (entailing training in the regulation of negative emotion) and a control group. Meditators accepted unfair offers more often than controls, and displayed reduced activity in the anterior insula, an area associated with the emotion of disgust.

Studies have also begun to indicate the general brain regions involved with the punishment of non-cooperators in dyadic trust game contexts (de Quervain et al., 2004; Singer et al., 2006). With increased methodological precision, and as studies broaden their focus to include punishment of free riders in collective actions, we will become increasingly able to answer punishment-related questions raised by service-for-prestige, such as: when a follower who respects a leader perceives another follower to be disrespecting that leader, does he or she experience punitive sentiment that is similar (in terms of the neural systems involved) to the anti-free-rider punitive sentiment experienced by high-contributing members of other kinds of collective actions (Fehr and Gächter, 2002; Price et al., 2002)? Such results will shed additional light on debates between evolutionary researchers, mentioned above, about the extent to which leader–follower relations were designed by the same evolutionary processes that enable reciprocity and collective action in other cooperative contexts, as opposed to being

designed by qualitatively different processes such as cultural group selection.

CONCLUSION

Service-for-prestige does not claim that either kind of leader–follower relationship described above – prestige-based reciprocity or dominance-based coercion – is more “natural” than the other; people are adapted for both kinds of interaction. However, reciprocity clearly involves the greater degree of mutual benefit. Unlike coercion, reciprocity allows followers to act on their leader preferences, and collectively award prestige to people who, via their ability to benefit followers, they deem worthy of leadership roles. Reciprocity is also more closely associated with what most would consider “good” leadership (Den Hartog et al., 1999), that is, leadership that most helps followers to achieve their shared goals, as opposed to primarily serving the narrow interests of the leader (Price and Van Vugt, in press).

There is also much that service-for-prestige does not explain about the evolution of leadership. Most importantly, as noted above, it does not explain why leadership has evolved in so many non-human species, nor why it first appeared in the human lineage. Leadership has evolved in many species to solve problems related to information-sharing and coordination problems (King et al., 2009), and these were probably its initial functions among human ancestors as well (Van Vugt and Kurzban, 2007; Van Vugt et al., 2008a). However, we suggest that humans, much more than any other species, have been able to use reciprocity to enhance the benefits of leadership, by providing leaders with prestige in exchange for services that would otherwise have been too costly for leaders to provide. Our theory applies to humans much more than any other species, because humans are uniquely well-adapted for sophisticated cooperative behaviors such as collective action and various forms of reciprocity (Tooby and Cosmides, 1996; Hammerstein, 2002; Tooby et al., 2006; Bowles and Gintis, 2011).

By considering the kinds of problems that evolution had to solve in order to enable leaders and followers to interact adaptively in human ancestral environments, service-for-prestige is able to make novel predictions about leader and follower behaviors in modern environments. Service-for-prestige also promotes a synthesis of the theoretical frameworks of positive reciprocity and collective action. Although each of these frameworks has had an enormous independent influence in behavioral science, they are thought of by many evolutionary researchers as distinct and non-overlapping (Boyd and Richerson, 1988; Henrich, 2004; Bowles and Gintis, 2011). We suggest, as others have previously (Price, 2003, 2006a; Tooby et al., 2006), that reciprocity and collective action are not as distinct as these researchers suggest, and that syntheses of these theories will enable more predictive evolutionary theories of complex human cooperation. Social neuroscience is in a unique position to help resolve debates about the extent to which these theories can in fact be integrated. If service-for-prestige is correct, then many of the same neural systems involved in cooperative behaviors such as reciprocity, collective action, and free rider punishment should be similarly involved when these processes occur in the specific context of leader–follower relations. Neuroscientific methods are already proving useful in identifying

and illuminating the nature of these systems, and as they become increasingly precise, they will become increasingly essential for answering fundamental questions about how humans are adapted for leadership, followership, and indeed all forms of social behavior. More frequent occasions for interaction between evolutionary social psychologists and social neuroscientists, such as that provided by this special issue, will enable us to take full advantage of these new research opportunities.

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Recommendations for sex/gender neuroimaging research: key principles and implications for research design, analysis, and interpretation

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Neuroimaging (NI) technologies are having increasing impact in the study of complex cognitive and social processes. In this emerging field of social cognitive neuroscience, a central goal should be to increase the understanding of the interaction between the neurobiology of the individual and the environment in which humans develop and function. The study of sex/gender is often a focus for NI research, and may be motivated by a desire to better understand general developmental principles, mental health problems that show female-male disparities, and gendered differences in society. In order to ensure the maximum possible contribution of NI research to these goals, we draw attention to four key principles—overlap, mosaicism, contingency and entanglement—that have emerged from sex/gender research and that should inform NI research design, analysis and interpretation. We discuss the implications of these principles in the form of constructive guidelines and suggestions for researchers, editors, reviewers and science communicators.

Keywords: brain imaging, sex differences, sex similarities, gender, stereotypes, essentialism, plasticity

INTRODUCTION

Over the past few decades, psychologists have documented a tendency for lay-people to hold “essentialist” beliefs about social categories, including gender (for summary, see Haslam and Whelan, 2008). Essentialist thinking about social categories involves two important dimensions (Rothbart and Taylor, 1992; Haslam et al., 2000). Essentialized social categories are seen as “natural kinds”, being natural, fixed, invariant across time and place, and discrete (that is, with a sharply defined category boundary). In addition, essentialized social categories are “reified”, being seen as “inductively potent, homogenous, identity-determining, and grounded in deep, inherent properties” (Haslam and Whelan, 2008, p. 1299).

Gender is a strongly essentialized category, particularly in the degree to which it is seen as a natural kind (Haslam et al., 2000), with interpersonal differences spontaneously interpreted through a gendered lens (Prentice and Miller, 2006). 3G-sex (that is, the genetic, gonadal, and genital endowment, of an individual (Joel, 2011)) is indeed highly—although not completely—internally consistent, discrete and invariant across time and place and thus much more of a “natural kind”. Yet decades of gender scholarship have undermined the traditional essentialist view of the behavioral manifestations of masculinity and femininity, and their neural correlates, which are of interest to neuroscientists (Schmitz and Höpner, 2014).

The key principles from gender scholarship of overlap, mosaicism, contingency, and entanglement, reviewed in the

following sections, offer a serious challenge to essentialist notions of sex/gender¹ as fixed, invariant, and highly informative. This is an important message for neuroscientists because, unless they have specific expertise or knowledge in gender scholarship, they too are laypeople with respect to gender research, and may also be susceptible to gender essentialist thinking. Indeed, sex/gender NI² research currently often appears to proceed as if a simple essentialist view of the sexes were correct: that is, as if sexes clustered distinctively and consistently at opposite ends of a single gender continuum, due to distinctive female vs. male brain circuitry, largely fixed by a sexually-differentiated genetic blueprint. Data on the sex of participants are ubiquitously collected and available; the two sexes may be routinely compared with only positive findings reported (Maccoby and Jacklin, 1974; Hines, 2004); and

¹As we describe below, neural phenotypes represent the complex entanglement of biological and environmental factors, such that it is generally not possible to entirely isolate the two. Thus, we use the composite term “sex/gender” as a way to refer to this irreducible complexity (see also Kaiser, 2012).

²Our focus in this paper is on the use of Magnetic Resonance Imaging MRI techniques, both structural and functional (fMRI). The majority of studies in this area, particularly those most commonly cited in the public domain, use MRI/fMRI techniques. We are aware that techniques with better temporal resolution such as electroencephalography (EEG) and magnetoencephalography (MEG) have been used in this field (and may, indeed, be more appropriate for the cognitive processes being investigated) but detailed inclusion of these is beyond the scope of this review. Almost all of the identified implications and recommendations will also be relevant to EEG and MEG research.

the emphasis on difference is institutionalized in databases that allow only searches for sex/gender differences, not similarities (Kaiser et al., 2009).

The all but ubiquitous group categorization on the basis of biological sex seems to suggest the implicit assumption that a person's biological sex is a good proxy for gendered behavior and that therefore categorizing a sample on the basis of sex will yield distinct "feminine" vs. "masculine" profiles. The small sample sizes common in fMRI investigations reporting female/male differences (Fine, 2013a) suggests the implicit assumption that female vs. male brain functioning is so distinct that true effects can be identified with small numbers of participants. Conversely, with large sample sizes (seen mostly in structural comparisons), the publication of statistically significant effects suggests the implicit assumption that they are also of theoretical and functional significance. The readiness with which researchers draw on gender stereotypes in making reverse inferences (Bluhm, 2013b; Fine, 2013a) suggests an implicit assumption of distinctive female vs. male brains giving rise to "feminine" and "masculine" behavior, respectively. Finally, the common use of single "snapshot" female/male comparisons (Schmitz, 2002; Fine, 2013a) is in keeping with the implicit assumption of gendered behavior and female and male brains as fixed and non-contingent, meaning that such an approach promises to yield "the" neural difference between the sexes for a particular gendered behavior.

Thus, our goal in this article is to draw attention to the four key principles of overlap, mosaicism, contingency and entanglement that have emerged from sex/gender research, and discuss how they should inform NI research design, analysis and interpretation.

PRINCIPLES FROM SEX/GENDER SCHOLARSHIP OVERLAP

Studies examining sex/gender typically categorize participants as female or male and apply statistical procedures of comparison. Sex/gender differences in social behavior and cognitive skills are, if found, far less profound than those portrayed by common stereotypes. As Hyde (2005) found in her now classic review of 46 meta-analytic studies of sex differences, scores obtained from groups of females and males substantially overlap on the majority of social, cognitive, and personality variables. Of 124 effect sizes (Cohen, 1988)³ reviewed, 30% were between (+/−) 0 and 0.1 (e.g., negotiator competitiveness, reading comprehension, vocabulary, interpersonal leadership style, happiness), while 48% were between (+/−) 0.11 and 0.35 (e.g., facial expression processing in children, justice vs. care orientation in moral reasoning, arousal to sexual stimuli, spatial visualization, democratic vs. autocratic leadership styles). There is non-trivial overlap even on "feminine" and "masculine" characteristics such as physical aggression (d ranges from 0.33 to 0.84), tender-mindedness ($d = -0.91$), and mental rotation (d ranges from 0.56 to 0.73). More recent reviews have also emphasized the extent of this overlap (Miller and Halpern, 2013; Hyde, 2014).

³By convention, a positive effect size refers to greater average male score, while a negative effect size refers to a greater average female score.

There are more significant differences between women and men in other categories of behavior, such as choice of occupations and hobbies (Lippa, 1991). However, regardless of how one wishes to characterize the data (that is, as demonstrating that females and males are "different" or "similar"), or the functional significance of differences of a particular size (considerable or trivial), the important point for NI researchers is that the distributions of social cognitive variables typically of interest in research are likely to be highly overlapping between the sexes, and this has implications for research design. It has also been argued that many small differences may "add up" to very significant differences overall (Del Giudice et al., 2012; Cahill, 2014, although for critique of the latter, see Stewart-Williams and Thomas, 2013; Hyde, 2014). However, not only does this argument overlook the "mosaic" structure of sex/gender (discussed in the next section) but, additionally, NI researchers will generally be interested in isolating just one or two behavioral variables.

Overlap in behavioral phenotype does not necessarily imply overlap in cortical structural and functional phenotype, since potentially the same behavioral ends may be reached via different neural means—an important point when it comes to interpretation of group differences in neural characteristics (Fine, 2010b; Hoffman, 2012). Indeed, it has been noted in non-human animals that one average difference between the sexes in a brain characteristic may compensate for another, giving rise to behavioral similarity (De Vries, 2004). However, it nonetheless appears to be the case that establishing non-ephemeral sex/gender differences in cortical structures and functions has proved difficult. One commonly cited difference, supported by several meta-analyses and reviews, is that absolute brain volume is greater in men than in women (Lenroot and Giedd, 2010; Sacher et al., 2013) even when body size is controlled for (Cosgrove et al., 2007), although, as with psychological characteristics, the distributions overlap considerably. The significance of this is that, once volume differences are controlled for, many previously reported *regional* differences in specific structures disappear (e.g., Leonard et al., 2008). For instance, the claim that callosal size is greater in males is not supported when there is careful matching between the sexes in brain-size (Bishop and Wahlsten, 1997; Jäncke et al., 1997; Luders et al., 2014). However, this may not invariably be the case, with clusters of regional female/male differences in gray matter found to persist even in female and male participants matched for brain size (Luders et al., 2009), consistent with some previous findings (e.g., Good et al., 2001; Luders et al., 2006) but not all (Lüders et al., 2002). In addition, Giedd et al. (2012) note that the non-linear scaling relationship between brain size and brain proportions affects white to gray matter ratios, which could account for female/male differences in this measure.

It is also important to note that it has proved difficult to replicate well-accepted reports of sex/gender differences in *functional* organization of brain regions underpinning specific cognitive skills. A salutary example of this is the long-standing hypothesis that the male brain is more lateralized for language processing. A high-impact report that partially supported this hypothesis (Shaywitz et al., 1995, see Kaiser et al., 2009) was subsequently

shown to be spurious in two meta-analytic studies (Sommer et al., 2004, 2008).

The substantive point here is not to argue that there are *no* structural or functional brain differences between the sexes, but to draw attention to the fact that neural characteristics are not so distinctly different in the sexes that reliable differences are easily identified. These data make it clear that dimorphism, the existence of two distinct forms, is not an accurate way to characterize sex/gender differences in neural phenotype.

MOSAICISM

Developments in understanding of the structure of gender (that is, the traits, roles, behaviors, attitudes, and so on, associated with femininity and masculinity) have challenged the earlier assumption that the sexes cluster distinctively and consistently at opposite ends of a single gender continuum (Terman and Miles, 1936) or can be located on two discrete “feminine” and “masculine” dimensions (Bem, 1974). Because different feminine and masculine characteristics are only weakly inter-correlated, if at all, gender is now understood to be multi-factorial, rather than one- or two-dimensional (Spence, 1993). Similarly, Carothers and Reis (Carothers and Reis, 2013; Reis and Carothers, 2014), applying taxometric methods to analyze the latent structure of gender, have recently concluded that females’ and males’ psychological attributes mostly differ in ways that are continuous rather than categorical.

Similarly in neuroscience, the phenomenon of brain mosaicism has been recognized for decades (Witelson, 1991; Cahill, 2006; McCarthy and Arnold, 2011, see also Joel, 2011). That is, an individual does not have a uniformly “female” or “male” brain, but the “male” form (as statistically defined) in some areas and the “female” form in others, and in ways that differ across individuals. (Nor is this necessarily static, with animal research indicating that even brief experiences such as stress exposure can change brain characteristics from the “female” to the “male” form, and vice versa; see Joel, 2011).⁴ Thus, having a region in (say) the corpus callosum where a structural or functional characteristic has been shown to be statistically more characteristic of females is not a good predictor for whether the same individual brain will also have a region in (say) the amygdala that is associated with females. An implication of this mosaicism is that specific brain areas that are labeled as having a “female” or “male” phenotype can only be detected through group-level statistical comparisons. In other words, just as individuals are not comprehensively feminine or masculine in traits, roles attitudes, etc., so too is it not possible for an individual to have a “single-sex” brain.

Mosaicism of gendered behavior and brains is a critically important point, because it conflicts with the more (although not absolutely) categorical nature of biological sex, in which female/male differences in sex chromosomes, gonads and genitals are roughly dimorphic and highly interrelated, such that

individuals mostly have a unitary “male” or “female” phenotype. As Joel (2012) has put the issue, “Using 3G-sex (genetic-gonadal-genitals) as a model to understand sex differences in other domains (e.g., brain, behavior) leads to the erroneous assumption that sex differences in these other domains are also highly dimorphic and highly consistent” (p. 1). Even where mosaicism is acknowledged, the evidence may be undermined by common terminology such as “female or male phenotype” (for describing global brain structure or psychology) or “sex dimorphism” (Jordan-Young, 2014).

CONTINGENCY

Gendered behavior arises out of a dauntingly complex, reciprocally influencing interaction of multi-level factors, including structural-level factors (e.g., prevailing cultural gender norms, policies and inequalities), social-level factors (e.g., social status, role, social context, interpersonal dynamics) as well as individual-level factors such as biological characteristics (see “entanglement” principle in the following section), gender identity, gendered traits, attitudes, self-concepts, experiences, and skills. A few illustrative examples, which depart from the more “intuitive” conception of sex/gender differences as emerging from a causal pathway that runs from genes to hormone to brain to behavior to social structure, may be useful.

At the group level, women’s expression of “masculine” personality traits (such as assertiveness) appears to be responsive to cultural shifts in social status and role (Twenge, 1997, 2001), while in the shorter term, gendered behavior is flexibly responsive to social context and experience. For example, a meta-analysis conducted by Ickes et al. (2000) found that a moderate female advantage in empathic accuracy was only observed if participants were also asked to make self-ratings of their accuracy (hypothesized to preferentially enhance women’s motivation to perform well). Another well-known example of social contextual effects on gendered behavior is the “stereotype threat” phenomenon whereby, for instance, female mathematical performance is diminished when tests are presented in a way that makes salient the stereotype that females are poor at mathematics (Nguyen and Ryan, 2008; Walton and Spencer, 2009), although we acknowledge the more sceptical conclusion regarding the size, robustness, and generality of the stereotype threat effect from the meta-analysis by Stoet and Geary, 2012. As a third example, the average male advantage in mental rotation is diminished by altering how the task is framed (e.g., Moè, 2009). Moreover, the beneficial effects of training, including video-gaming, points to the contribution of gendered experience to this skill (Feng et al., 2007). (For numerous additional examples of stereotype threat effects on sex/gender differences, see Fine, 2010a).

From this brief discussion it should therefore not be surprising that, in contrast with the near complete consistency of genetic, gonadal and genital differences between the sexes, female/male differences in *behavior* are variable across time, place, social or ethnic group, and social situation. Indeed, intersectionality—the principle that important social identities like gender, ethnicity, and social class “mutually constitute, reinforce, and naturalize one another” (Crenshaw, 1991, p. 302)—is an important tenet of gender scholarship (Crenshaw, 1991; Shields, 2008). For example, as

⁴The terms “female” and “male” here do not indicate an “innate” or “natural” neural maleness or femaleness, but are rather place-holders for a statistical approach that involves calculating the effect size of sex for a particular brain-related data set.

reviewed in Hyde (2014), female/male differences in mathematics in the USA have not only decreased over time but also vary or even reverse according to ethnic group. A review of differences in math achievement in 69 nations by Else-Quest et al. (2010) revealed that gender differences were not only very small, but highly variable, with effect sizes ranging from -0.42 (a moderate difference favoring females) to 0.40 (a moderate difference favoring males); socio-cultural factors such as women's parliamentary representation, equity in school enrolment, and women's share of research jobs were significant predictors of gender gaps in math achievement. As with cognitive skills, female/male differences in personality (e.g., neuroticism/anxiety) or well-being (e.g., self-esteem) that are seen in one country or ethnic group are not necessarily observed in others (Costa et al., 2001, reviewed in Hyde, 2014).

ENTANGLEMENT

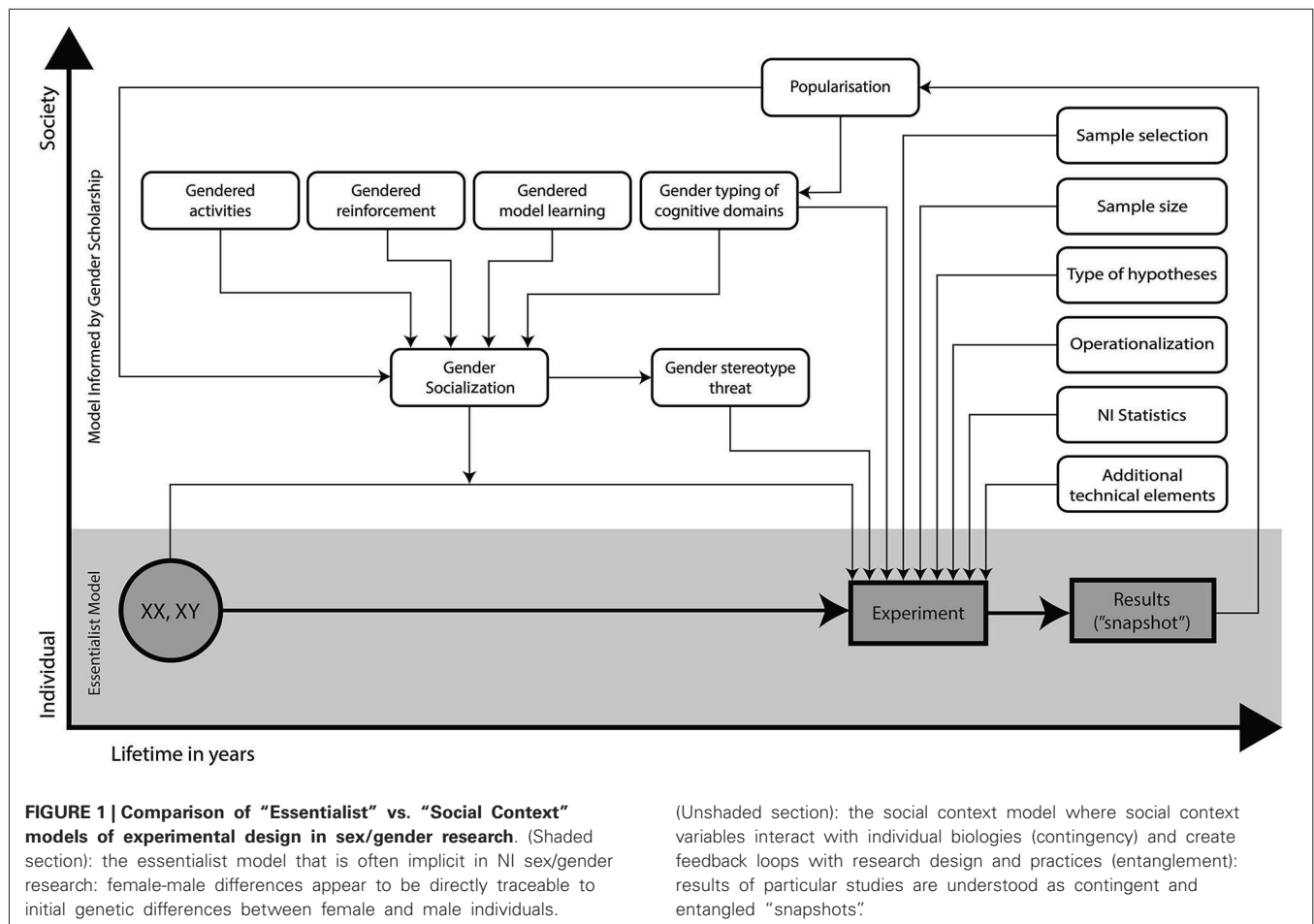
As indicated above, there is considerable evidence that average female/male differences can be modified, neutralized, or even reversed by specific context, for example the manipulation of the salience of such differences, or by chronic structural factors in the environment, such as national wealth or gender equity (reviewed in Miller and Halpern, 2013; Hyde, 2014). Clearly, this will be reflected in the neural substrates of such behavior, which therefore cannot be universal or fixed (see Fine, 2013b). This type of finding is in keeping with the rejection of early models of the relationship between brain and behavior in the study of sex/gender. These were based on a fairly simple, almost unidirectional concept of "hard-wiring", in which brain characteristics were conceived as being predetermined by the organizational effects of genetically-programmed prenatal hormonal influences (Phoenix et al., 1959). Here, each individual is endowed with a "female" or "male" brain that gives rise to feminine and masculine behavior, respectively; a neural substrate that social factors merely influence. This assumption of distinctive female vs. male brain circuitry, largely fixed by a sexually-differentiated genetic blueprint, is now clearly challenged by changed models of neurodevelopment and widespread consensus of on-going interactive and reciprocal influences of biology and environment in brain structure and function (Li, 2003; Lickliter and Honeycutt, 2003; van Anders and Watson, 2006; Hausmann et al., 2009; McCarthy and Arnold, 2011; Miller and Halpern, 2013). As NI research itself has been instrumental in demonstrating, such interactions leave neural traces. A recent review by May (2011) summarizes the evidence that new events, environmental changes and skill learning can alter brain function and the underlying neuroanatomic circuitry throughout our lives. Such changes could be brought about by, for example, normal learning experiences such as learning a language (Stein et al., 2012) or specific training activities such as taxi-driving or juggling (Maguire et al., 2000; Draganski et al., 2004; Chang, 2014). Other research demonstrates brain characteristics that vary as a function of socio-economic status (Hackman and Farah, 2009; Noble et al., 2012) or even subjective or perceived socio-economic status (Gianaros et al., 2007). Despite the key role played by NI research in the emergent concept of the permanently plastic brain, only a few NI studies have demonstrated how neuronal plasticity has been related to sex/gender. Wraga et al. (2006), using a direct

comparison of task-related positive and negative stereotype priming, showed that the neural correlates of performance of the same task reflected this priming, demonstrating short-term plasticity of neural function. Longer-term functional and structural plasticity was indicated in another within-sex study investigating the neural effects in adolescent girls of 3 months of training with the visuo-spatial problem solving computer game Tetris (Haier et al., 2009).

This dynamic and interactive conception of brain development means that biological sex and the social phenomenon of gender are "entangled" (Fausto-Sterling, 2000). That is, as a categorization linked to social difference and inequality, an individual's biological sex systematically affects their psychological, physical, and material experiences (Cheslack-Postava and Jordan-Young, 2012; Springer et al., 2012). For example, because gender is an important organizing principle for social life, giving rise to intensive gender socialization, including self-socialization processes (e.g., Bussey and Bandura, 1999; Martin and Ruble, 2004; Leaper and Friedman, 2007; Tobin et al., 2010), both formal training (e.g., school and vocational instruction) and daily experiences (e.g., sports involvement, hobbies, games, poverty, and harassment) are, at the group level, different for females and males. It will be critical for NI work investigating hormone-brain relations to take into account important insights into entanglement from social neuroendocrinology. Contemporary models identify hormones such as testosterone as key mediators of behavioral plasticity, with animal research indicating both genomic and non-genomic mechanisms involving both long-term structural reorganization and short-term modulation of sensitivity of neural circuitry (Adkins-Regan, 2005; Oliveira, 2009). This enables animals to be flexibly responsive to social situations that, in humans, incorporate gendered norms with respect to social phenomena such as competition, sexuality, and nurturance (van Anders, 2013). For example, it has been shown that fatherhood can reduce testosterone levels in males and that this effect varies with the extent of paternal care and physical contact with offspring (Gettler et al., 2011). Furthermore, a comparison of two neighboring cultural groups in Tanzania found lower testosterone levels among fathers from the population in which paternal care was the cultural norm compared with fathers from the group in which paternal care was typically absent (Muller et al., 2009). Entanglement thus refers to the fact that the social phenomenon of gender is literally incorporated, shaping the brain and endocrine system (Fausto-Sterling, 2000), becoming "part of our cerebral biology" (Kaiser et al., 2009, p. 57).

KEY PRINCIPLES: SUMMARY

The issues identified above indicate that, for NI researchers wishing to examine sex/gender variables in studies of the human brain, there are key factors which need to be taken into consideration in the design, analysis, and interpretation of research in this category. As illustrated in **Figure 1**, there will need to be adjustments made to the assumptions underlying current typical research practices. As will be clear from the discussion of the key principles of sex/gender scholarship, gender essentialist assumptions are inappropriate, and the experimental context complex and contingent. Any one sample will consist of individuals with an intricate mosaic of gendered attributes, the distributions for many



of which will be largely overlapping and may not differ at the group level in that particular sample. Similarly, the individuals in the sample will not have “female” or “male” brains as such, but a mosaic of “feminine” and “masculine” characteristics. Whatever female/male behavioral and therefore brain differences are observed in that particular sample are contingent on both chronic and short-term factors such as social group (such as social class, ethnicity), place, historical period, and social context and therefore cannot be assumed a priori to be generalizable to other populations or even situations (such as the same task performed in a different social context). Each individual’s behavioral and neural phenotype at the moment of experimentation is the dynamic product of a complex developmental process involving reciprocally influential interactions between genes, brain, social experience, and cultural context. Simpler, implicitly essentialist models (see lower, shaded portion of **Figure 1**) will need to be replaced by more complex multivariate models which acknowledge the interactive contribution of many additional sociocultural factors (see upper portion of **Figure 1**).

So what strategies do these key principles of sex/gender scholarship imply for NI sex/gender research design, methodology, and interpretation? We now outline some of the key implications and recommendations for research design, data analysis, and interpretation, which we hope will result in changes

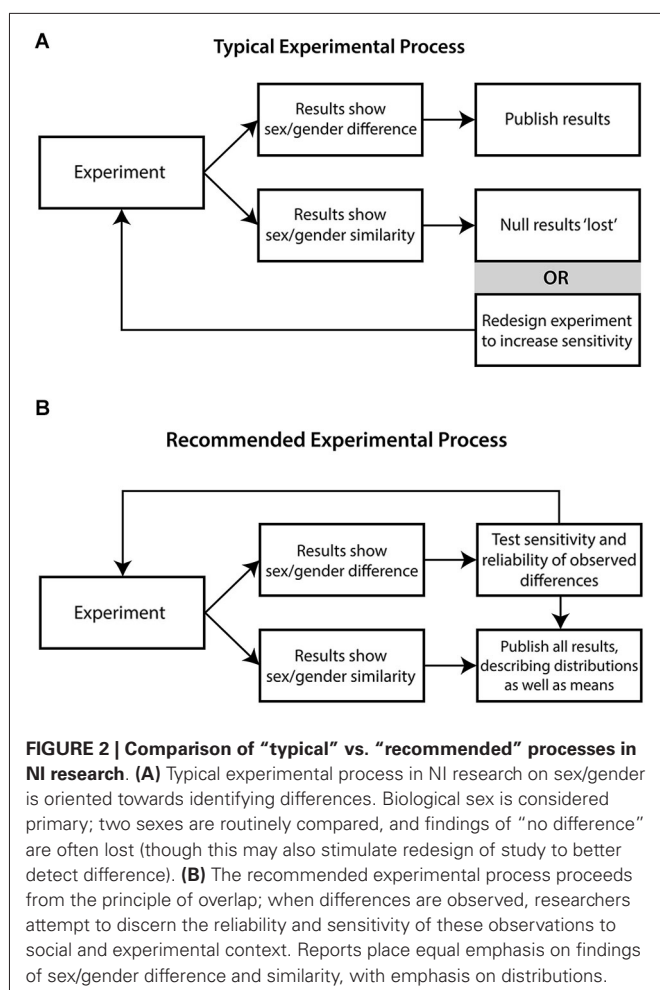
from standard practices (as illustrated in **Figure 2A**) to greater acknowledgment of gender similarities as well as differences, follow-up replication studies, and assessment of effect stabilities where differences are found (see **Figure 2B**). We conclude with a few comments concerning how these issues relate to ongoing discussions regarding discipline-wide practices.

RECOMMENDATIONS

RESEARCH DESIGN

Sample size

Ultimately, sex/gender social and cognitive neuroscience is concerned with the relationship between behavior and the brain, and it is therefore critical that researchers be aware that the key principle of overlap means that participants divided on the basis of biological sex cannot be assumed to have neatly distinct behavioral or cortical structural or functional profiles. Where there is considerable overlap in distribution of scores between a grouping factor (e.g., sex) and the dependent variable of interest, the magnitude of any difference, or effect size (Cohen, 1988) will be very small. Research designed to measure such a difference will obviously need an adequately large sample size to reliably and consistently identify such differences. Small sample size and associated reduced statistical power has been identified as a central problem in NI research (Carp, 2012; Button et al., 2013), as well



as in sex/gender fMRI studies (Kaiser, 2010; Fine, 2013a). This clearly raises a concern regarding the high probability of false-negative findings. However, the low statistical power of many studies also validates considerable concern that many reported statistically significant findings are “false positive”. False-positive errors are arguably the most costly errors in science (Simmons et al., 2011), and can be remarkably persistent despite documented null findings (Fidler, 2011; Fine, 2013a). Although, in theory, the probability of false positive errors should remain the same regardless of sample size, as Fine and Fidler (2014) have noted, a combination of publication bias, data noise, large intersubject variability, and considerable scope for researcher discretion about the construction of dependent variables may mean that, in practice, this is not the case. The difficulty, to date, of establishing reliable, non-controversial sex differences in the brain becomes less surprising in light of the key sex/gender principles discussed here and indicates that studies with small sample sizes will lack adequate statistical power and produce unreliable findings.

Independent and dependent variables

The evidence that gendered characteristics are often overlapping and multi-dimensional indicates the usefulness of a dimensional trait-based, rather than categorical sex-based, approach to

research (Jordan-Young and Rumiati, 2012). Although in psychology the experimental registration of sex/gender in a multi-parametric way is in its infancy, attempts are being made to trace the many different facets of what is an “enormous conglomeration of socialized, behavioral, cognitive, and culturally embedded biomarkers” (Kaiser, 2014). To give some examples, relevant and multiple information about sex/gender can be assessed through the utilization of questionnaires assessing gendered personality dimensions (Personal Attributes Questionnaire, PAQ; Spence and Helmreich, 1978), gender attitudes (Ambivalent Sexism Inventory, ASI; Glick and Fiske, 1996), self-attributed gender norms (Conformity To Masculine Norms Inventory, Mahalik et al., 2003, Conformity To Feminine Norms Inventory, CMFI; Mahalik et al., 2005), specific aspects of gender socialization (The Child Gender Socialization Scale, Blakemore and Hill, 2008), gender identity (Joel et al., 2013) and others (for reviews, see Smiler and Epstein, 2010; Moradi and Parent, 2013). A multi-parametric registration of sex/gender combines multiple binary classifications in various ways, similar to the mosaic-approach of Joel (2011). Most importantly, it promises to emphasize the multi-dimensionality of the factor sex/gender which is usually only measured by checking the F or M box (see Figure 1). In this way, specific sex/gender related information about gendered experiences, gendered socialization, gendered behavior, gendered cognition could be collected. With the emergent availability of large neuroimaging (NI) datasets, much more subtle interrogation of these data would be possible if the demographic data collected on the participants reflected the entangled complexity of their psychological, physical, and material experiences, rather than just their age and sex, as is currently typically the case.

As discussed above, there are physical characteristics of participants that are specifically relevant to sex/gender NI research such as head size (Barnes et al., 2010), given its relationship to brain volume. Similarly, height and weight should be noted in order to carry out the appropriate adjustments to brain volume measures; failure to do this must undermine the validity of any reports of sex differences in brain structure, as acknowledged by Ruigrok et al. (2014). There is the possibility that variations in hormone levels might produce (or mask) relevant sex/gender differences in brain structure and function. There is not currently strong evidence for such effects, but future research should be sure to take into account a range of sources of variation (e.g., diurnal, seasonal, and activity-related), and investigate variations in all research participants, as opposed to a singular focus, for example, on menstrual cyclicity and variations in women only. If there is a focus on hormonal variables, it should be noted that menstrual cycle phase is not, in fact, a good proxy for hormone fluctuations and direct measures will be required (Schwartz et al., 2012). Researchers should also be aware that popular beliefs/well-publicized claims regarding the psychological effects of menstrual phase on mood and male attractiveness ratings, have not been supported by recent meta-analyses (Romans et al., 2012; Wood et al., 2014, for contrary conclusion, see Gildersleeve et al., 2014, for critique, see Wood and Carden, in press).

If the basis of the research question is a link between measured differences in brain structure or activation patterns and behavioral or cognitive profiles, then a study’s dependent

variables should obviously include appropriate measures of the relevant behavior or cognitive skill, and not just assume that such differences are well-known (and therefore do not need measuring) (Tomasi and Volkow, 2012). Whatever behavioral measures researchers choose in order to investigate the phenomenon of interest, it will be necessary to acknowledge that no sex/gender differences are “fixed” but contingent, the implication being that research findings will at best be a snapshot of the relationship of interest. Thus, an important research possibility is to additionally draw on the principles of contingency and entanglement to challenge the *stabilities* of observed differences and similarities, by experimenting with context or population, for example. This can be seen, for example, in studies investigating the extent to which training can alter pre-existing sex/gender differences in visuo-spatial processing (Feng et al., 2007). This type of research design would enable researchers to perform a “sensitivity analysis” of the conditions under which sex/gender is related to some kind of neural function or structure, facilitating knowledge of the stability and contingency of observed group differences. Hyde (2014) has similarly recommended a focus on the exploration of contexts in which gender differences appear and disappear as a way forward in such research.

Research models and hypotheses

Although whole brain analysis is possible with all NI techniques, many researchers choose to specify Regions of Interest (ROIs), particular areas of the brain identified as of interest due to previous research findings or predictions from particular neurocognitive models. This approach can, for example, reduce the multiple comparison problem resulting from comparing voxels across the whole brain. Where an ROI approach is chosen for either structure or function measures, the regions need to be clearly specified in advance (Poldrack et al., 2008) which may be difficult in the absence of a well-specified neurocognitive model (see Bluhm, 2013a). Researchers may instead be drawn to a priori hypotheses based on gender stereotypes (see Bluhm, 2013b), but clearly it needs to be carefully established whether such stereotypes are more than trivially true.

Changing models of brain–behavior relationships require adaptation of research exploring such relationships with attention to more and/or different categories of independent variables, including ways of capturing the role of the environment. McCarthy and Arnold (2011, p. 681) note the need for a “more nuanced portrayal of the types of variables that cause sex differences”, acknowledging that environmental influences “have an enormous effect on gender in humans and are arguably more potent in sculpting the gender-based social phenotype of humans” (p. 682). Jordan-Young (2010) and Jordan-Young and Rumati (2012) similarly identify problems associated with the hard-wiring, “brain organization” theory in brain and brain development research and note that if researchers wish to bring understanding of how differences arise, then there is a need to focus more on the *dynamic* aspects of brain development, on the plasticity of the brain, and on identifying those events that enhance or change the course of development. For example, Cheslack-Postava and Jordan-Young (2012) reviewed research on the epidemiology of autism, focusing on studies that described or

advanced explanations for the observed male preponderance in autism diagnosis. They found no studies that explored potential biosocial interactions of sex-linked biology and gender relations. Instead, the female/male difference was attributed to biological factors by default, though multiple lines of evidence suggest that gender could play a role in either the development of the disorder, or the likelihood of diagnosis once it is developed.

Given the major role played by NI itself in transforming our understanding of brain plasticity, it is surprising that there are so few examples of study design, cohort selection, and/or data interpretation where the entanglement of sex and gender is considered. The predominant approach is a “snapshot” comparison of females and males, which will only give limited insights regarding why, when or in whom such differences exist (Schmitz, 2002; Fine, 2013a,b). Importantly, although neuroscientists are well-aware that “in the brain” does not mean “hardwired”, the predominant use of “snap-shot” comparisons in sex/gender NI is guaranteed not to produce data that might challenge the idea of universal, fixed female/male brain differences (Fine, 2013a). The limitations of a “snapshot” approach should be acknowledged in the research design, where the choice of participants and/or their demographics should reflect more than just their biological sex (and possibly age) but also perhaps factors such as educational history and socio-economic and occupational status, with these factors controlled for in any subsequent analyses. Particular attention should be paid to the fact that there will be missing information concerning gendered socialization of participants. It is very probable that attitudes and behaviors of an individual have been sex-typically reinforced by the environment throughout her/his life and that development has been influenced by the particular importance of social learning in humans in combination with culturally shared gender stereotypes, norms, and roles (see Wood and Eagly, 2013). As identified above, assessment tools for measuring information about individual gender socialization are rare (Blakemore and Hill, 2008), no doubt in part because the whole process of gender socialization is highly complex and long-lasting, but also because it is mostly implicit and habitual, rather than deliberate. However, measures of gendered personal traits, attitudes, or cognitive development can indirectly reflect the effects of gender socialization.

Fine and Fidler (2014) have argued that the principles of overlap and mosaicism, together with the complexities arising from the consequences of contingency and entanglement, raise the important conceptual question of whether it makes sense at all to try to identify an effect size of the impact of biological sex on brain structure or function. But whatever precise research question is pursued, uncovering what are undoubtedly highly complex interactions against a background of noise and considerable individual differences will require more complex experimental designs. As the complexity of design increases, with multiple groups and multiple comparisons, so too must the sample size increase if adequate statistical power is to be achieved.

DATA ANALYSIS

Given the overlapping nature of sex/gender differences, it is important that effect sizes for each of the individual variables are reported. When studies reporting sex/gender differences only provide information about statistical differences, a

misleading impression can be given of a near distinctive—or even oppositional—dichotomous finding. This was recently well illustrated by a large-scale ($n = 949$) report of significant sex differences in the structural connectome of the human brain (Ingalhalikar et al., 2014), accompanied by statements that the results “establish that male brains are optimized for intrahemispheric and female brains for interhemispheric communication” (p. 823). This was suggested to underpin “pronounced [behavioral] sex differences” (p. 826). However, no corrections for brain volume were made, and the actual effect sizes for brain differences were unreported, while behavioral differences in the larger population from which the sample were drawn were very modest (Joel and Tarrasch, 2014), being between 0 and 0.33 for behavioral differences, with 11 of 26 effect sizes being null/ $d < 0.1$ (Gur et al., 2012).

A second statistical issue relating to the presentation of findings is the problematic statistical practice observed in neuroscience generally (Nieuwenhuis et al., 2011), as well as in NI sex/gender research (Kaiser et al., 2009; Bluhm, 2013a), of analyzing group data separately and then doing a “qualitative” comparison. Thus in sex/gender research, if a difference is found in one group and not the other, it is reported as a sex difference, even though no statistically significant difference has been established. In some cases, both within-group and direct comparisons are carried out, but only the former reported on. As Bluhm (2013a) points out, only by a direct statistical comparison, can a genuine difference be established, which should be illustrated by a single image showing the group differences, not 2 separate images for the 2 groups.

As will by now be clear, sex/gender NI research will require complex statistical frameworks to integrate the key variables associated with the participant cohort, to deal with the presence of potential nuisance variables, as well as incorporating imaging and behavioral data. This is obviously true of all NI research, and currently generally addressed by the use of General Linear Models (GLMs). However, the particularly “entangled” nature of the demographic, biological, and psychological variables in sex/gender research and the associated non-parametric nature of much of the data should be acknowledged if using a standard GLM analysis (Poline and Brett, 2012)—or, better, non-parametric methods such as permutation tests could be applied (Winkler et al., 2014). It is important that, whatever it comprises, the analysis pipeline is clearly specified (Bennett and Miller, 2010; Carp, 2012).

INTERPRETATION

The principle of overlap in gendered behavior is particularly important to bear in mind when it comes to inferring functional interpretations from neural differences (Fine, 2010b; Roy, 2012). It would seem obvious to add that this should be particularly true where there is no actual measure of the behavior/cognitive skill. The problematic nature of “reverse inference” is, of course, well-known in the neuroscientific community (e.g., Poldrack, 2006). In reverse inference, activation in particular brain regions is taken to equate to a specific mental process and, by extension, differences in activation can be taken to indicate differences in ability or efficiency. The danger is that gender stereotypes are

inappropriately drawn upon in making such reverse inferences. This can happen particularly readily when, as is very often the case, there is no a priori neurocognitive model guiding hypotheses (Bluhm, 2013a; Fine, 2013a). This can lead to “stereotype-inspired” reverse inferences even where these are contradicted by behavioral similarity (see Fine, 2013a). In making reverse inferences that are consistent with gender stereotypes, different groups of researchers may even make precisely opposite assumptions about the behavioral significance of more vs. less activation in the same brain region (Bluhm, 2013b).

Although reverse inference is a generic issue in NI research, the ease and intuitive plausibility of such inferences in sex/gender NI studies makes it of particular concern. Reverse inference can certainly be a useful research tool when used to generate hypotheses to put to test in further work (Poldrack, 2008), and Fine (2013b) has noted the legitimacy of such an approach as part of a strategy of systematic development and testing of neurocognitive models and predictions. However, what is more common is to draw on stereotypical (and often inaccurate) assumptions about female/male differences in behavior or skill set *post hoc* to inform these inferences (Fine, 2013a). Given the sex/gender principle of overlap, this is poor scientific practice.

A final point of interpretation relates to entanglement. A recent review of sex/gender differences in decision-making “noted that we will use sex differences rather than gender differences in this review as we are focussed on biologically founded rather than culturally or socio-economically founded differences” (Van de Bos et al., 2013, p. 96). However, it is the nature of the entanglement problem that the variables of sex and gender are irreducibly entwined—it is not, in practice, possible to “control” for the gendered environment and examine only sex. This should be acknowledged, then, in the interpretation of findings. In addition, any evidence that the dependent variables being measured may be subject to alteration by training or focussed intervention should also be recognized. In addition, researchers should avoid framing findings of female-male differences as being “biological” or “fundamental”. Likewise, it is generally advisable to avoid the language that some variable is “affected by sex”, because that suggests the effect of biology apart from the gendered environment. Instead, the language “affected by sex/gender” or “linked with sex” would be preferable. It should, indeed, be considered that a study that approaches sex/gender as subject variable is only an ex-post facto study and, thus, it cannot demonstrate that sex/gender *causes* differences in any behavior (Brannon, 2008).

DISCIPLINE-WIDE IMPLICATIONS

While the aim of the recommendations above is to inform the planning, interpreting, and quality assessment of sex/gender research, we also think it is worth relating these issues to ongoing discussions regarding collective, discipline-wide strategies that could be helpful for ameliorating some of the issues in NI sex/gender research. One interesting proposal to consider is that of the “pre-registration” of protocols. This “in principle acceptance” (IPA) has recently been suggested in psychology circles (Chambers, 2013). A study protocol is submitted for peer review *before* the study is carried out; details include the relevant background literature and hypotheses, together with the

specific procedures and analysis protocol (including sample size and a priori power analysis). Once accepted, the study is carried out exactly according to the agreed procedures and all findings published. This process could overcome many of those factors we have identified in this paper as significantly detrimental to NI sex/gender research. Publication bias could be reduced, as manuscript acceptance would be a function of the significance of the research question and associated methodology, not whether or not the results exceeded the magical $p < 0.05$ threshold. Thus, over time, it would be possible to better ascertain the ratio of negative to positive findings in any research sphere. While we acknowledge the value and role of exploratory research in the scientific research, declaring the analysis pipeline in advance would put constraints on practices such as *post hoc* data mining (Wagenmakers et al., 2011) and ensure that any failures to support hypotheses were identified as well as the converse. It could also preclude the *post hoc* introduction of interpretations, e.g., stereotypical assumptions about participant characteristics that were not measured as part of the study.

A long-standing proposal also relevant to some of the issues discussed here (see Fine and Fidler, 2014) is that of following the discipline of medicine in shifting away from null hypothesis significance testing towards an estimation approach of effect sizes and measures of their associated uncertainty, and greater use of meta-analysis. Proponents of the estimation approach (for extensive reviews, see Kline, 2004; Cumming, 2012), argue for a number of advantages over a null hypothesis significance testing approach, including reduced scope for false positive and false negative errors, and diminished conflation of statistical significance with practical or theoretical significance.

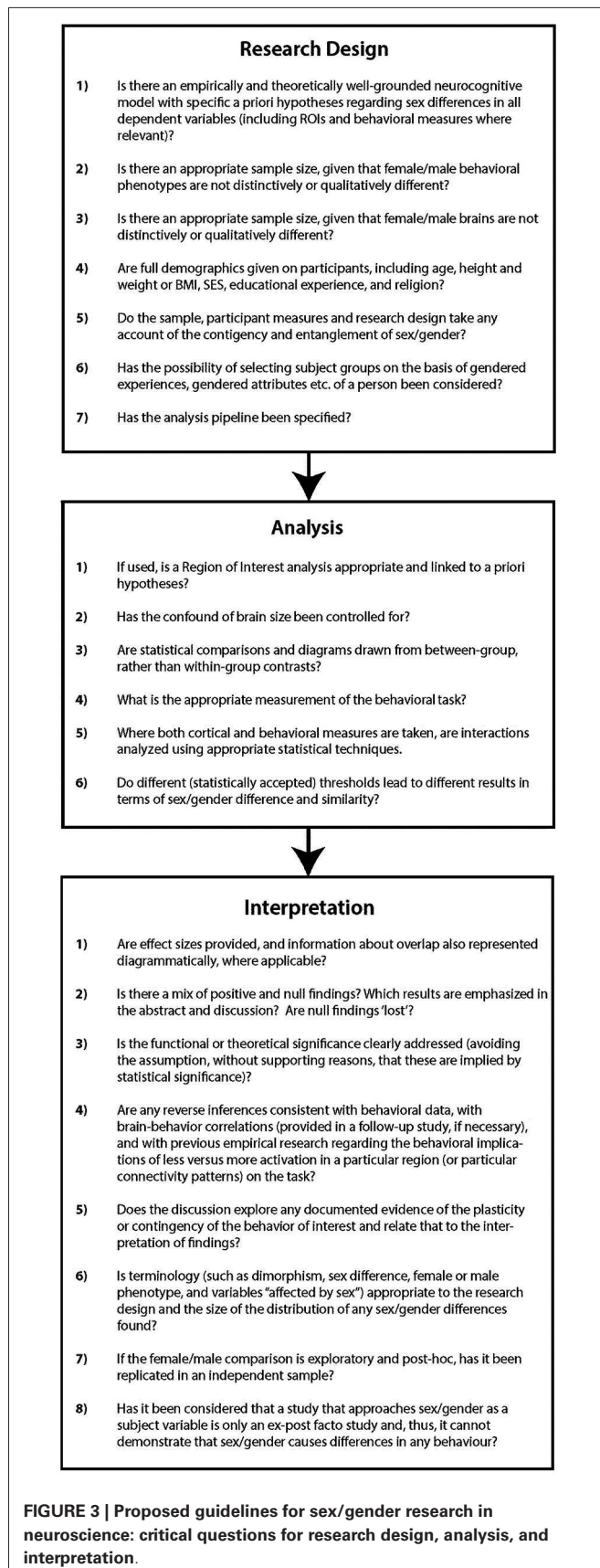
While the case for these two proposals is being made for behavioral science as a whole, the next two suggestions are more specific to sex/gender research, and arise out of the ease of default testing for sex/gender differences *post hoc*. One consequence of this is that the domain-general publication bias towards positive findings in behavioral science (Simmons et al., 2011; Fanelli, 2012; Yong, 2012) is greatly exacerbated in sex/gender research (e.g., Maccoby and Jacklin, 1974). Reviews of sex/gender NI research have demonstrated that this is a field that is indeed vulnerable to an overemphasis on positive findings and “loss” of null results (Bishop and Wahlsten, 1997; Fausto-Sterling, 2000; Kaiser et al., 2007; Fine, 2013a; see **Figure 2**). The first proposal is for the institutionalization of sex/gender similarity as well as difference in databases, to make it more likely that null findings are both recorded and identifiable. The second proposal is for editors of NI journals to request that sex/gender differences are replicated in an independent sample (obviously with discretion, depending on the rigor of the initial findings), to reduce the littering of the scientific literature with false-positive results.

Although, de facto, all research areas will wish to follow best practice guidelines, it is particularly important that the sex/gender NI research community is aware of the potential social significance of their findings (Roy, 2012; Schmitz, 2012). As reviewed elsewhere (e.g., Fine, 2012; Fine and Fidler, 2014), Choudhury et al. have argued that the representation of “brain facts” in the media, policy, and lay perceptions influence society in ways that can affect the very mental phenomena under investigation

(Choudhury et al., 2009). This is illustrated in the upper part of **Figure 1**, whereby the result of the experiment itself, through its popularization, becomes part of gender socialization, and thus the experiment becomes entangled with the phenomenon of interest. With respect to NI research, this feedback effect may be enhanced by the popular and powerful impact of “brain facts” (Weisberg et al., 2008). The original finding of persuasive power of brain images (McCabe and Castel, 2008) has been disputed both qualitatively (Farah and Hook, 2013) and quantitatively in a recent meta-analysis (Michael et al., 2013). However, “brain facts”, regardless of the presence or absence of brain images, may enhance how satisfactory or valuable lay people judge scientific explanations of psychological phenomena to be (Morton et al., 2006; Weisberg et al., 2008; Michael et al., 2013). Gender essentialist thinking has been associated with a range of negative psychological consequences, including greater endorsement of gender stereotypes both in relation to self (Coleman and Hong, 2008) and others (Martin and Parker, 1995; Brescoll and LaFrance, 2004), stereotype threat effects (Dar-Nimrod and Heine, 2006; Thoman et al., 2008), greater acceptance of sexism, and increased tolerance for the status quo (Morton et al., 2009). This is in line with what Hacking (1995, p. 351) has described as “looping” or “feedback effects in cognition and culture”, whereby the causal understanding of a particular group changes the very character of the group, leading to further change in causal understanding. In other words, the outputs of sex/gender NI can affect the very object of their investigation, putting a particular responsibility on scientists to follow good practice guidelines for research. By taking steps to avoid false positives, to avoid the use of stereotypical reverse inferences, to give equal weight to sex/gender similarities as well as differences and to acknowledge the dynamic and entangled aspect of sex/gender variables, with research findings only representing a static “snapshot” in time, scientists can do much to avoid the undesirable consequences outlined above (see also Fine et al., 2013).

CONCLUSION

We have outlined above the consequences for NI sex/gender research design, analytical protocols, and data interpretation of the four key principles of overlap, mosaicism, contingency, and entanglement and have summarized the consequences of these as a set of guidelines. These key principles and recommendations could also inform editorial boards and journal reviewers, as well as those who view, communicate, and interpret such research. In **Figure 3**, we offer a set of guidelines for the assessment of NI sex/gender research in order to assure that such research has addressed these implications (or, indeed, can). NI research is costly, time-consuming, and labor intensive. If it is to be applied in the field of sex/gender research then attention to the issues discussed here could reduce the incidence of under-informed research designs with consequent lack of reliable findings and/or waste of potentially valuable datasets. Changes to current research practices should result in a greater contribution to an understanding of the interaction between the neurobiology of the individual and the environment in which s/he develops and functions.



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Using evolutionary theory to enhance the brain imaging paradigm

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In recent years, there seems to be no preference, choice, emotion, thought, or behavior that has escaped the scrutiny of a neuroimaging machine. Scanning the brain allegedly reveals insights into the foundations of morality (Greene et al., 2001), altruism (Tankersley et al., 2007), sense of humor (Bartolo et al., 2006) and even religious beliefs and God (Kapogiannis et al., 2009), to name just a few of the disparate topics that have been studied. As neuroimaging studies become increasingly popular, a growing number of researchers in the business disciplines are applying such techniques within their areas of interest. In such works, researchers look at and map the parts of the brain that are involved in processing decisions, preferences, and choices. Studies range from predicting future sales of popular songs based on how certain areas in the brain were activated on a sample of individuals prior to a song's release (Berns and Moore, 2012), how advertisements engage different parts of the brain (Cook et al., 2011), and how arbitrary prices of wine alter the reward activities in an area of the brain associated with pleasure (Plassmann et al., 2008).

The modus operandi of most imaging procedures, such as fMRI, is to track blood oxygenation in the brain with the underlying assumption that as blood flows to a region, the more neurons are activated in this area. The idea behind such studies is not only to locate the exact area in the brain where information is processed, but also to have insights into people's true thoughts and preferences, since individuals cannot control their brain activity and are not always consciously aware of their

thought processes. There is a prevailing view that by looking at individuals' brain activation patterns, we could unveil their latent desires. Ariely and Berns (2010) discuss this premise skeptically, specifically in the marketing discipline, where there is a nagging fear that by looking at people's brains, marketers would be able to predict individuals' penchants for certain products, future acquisitions and needs, and hence manipulate customers to take advantage of those desires.

This fear is probably unwarranted and stems from what Rozenblit and Keil (2002) describe as "the illusion of explanatory depth," namely to exhibit overconfidence in one's ability to offer veridical explanations about natural phenomena when one's true knowledge is tentative at best. Neuroimaging scholars are especially susceptible to such biases. The striking colorful brain photos and associated technical jargon have a persuasive effect on researchers and lay person alike (McCabe and Castel, 2008; Trout, 2008; Weisberg et al., 2008), but this should not blind us to some of the shortcomings of the paradigm including the likelihood of reporting spurious correlations (Vul et al., 2009) and false positives such as the infamous case of the neuronal activation patterns "found" in a dead Atlantic salmon (Bennett et al., 2010). Next we detail some of the problems in neuroimaging research that need to be taken into account, and offer a theoretical framework that might be helpful in better interpreting the reaped results.

There are several practical problems associated with the neuroimaging paradigm. Imaging studies are typically conducted in artificial settings where

subjects are physically constrained within a narrow and claustrophobic device which may lead to a selection bias. The contrived laboratory environments lack ecological validity and as such it is unclear whether the neuronal activation patterns would be the same were participants making real and consequential choices. To make an actual moral choice in real life differs from having to imagine making a hypothetical one whilst lying down in a machine. Brain scans are also quite costly and thus sample sizes are typically quite small, yielding low statistical power, a possible overestimation of effects sizes, or the failure to detect true effects when they indeed exist (Button et al., 2013). Underpowered studies are hard to replicate and they often lead to selection biases in published results. Such studies can either report bogus results or can lead to the file drawer effect (e.g., unpublished positive results that did not reach significant levels due to small samples). These problems are relatively easy to fix with more rigorous study designs that include adequate sample sizes and transparency regarding power calculations.

A more fundamental problem in neuroimaging studies is the inability to identify the exact area in the brain responsible for a given cognitive process. The brain, which consumes roughly 20% of all energy in our body, is responsible for monitoring and managing every human activity, and is built in a complex network where different modules work simultaneously for almost any task (see Pinker, 1997). At any moment, multiple areas are activated concurrently, and it is not easy to pinpoint the one region that is responsible

for a certain thought or desire, if one such place even exists. Neuroimaging studies are adept at illuminating areas in the brain that are associated with certain behaviors, thoughts, or preferences, but interpreting which functions these areas serve based on the images is difficult and typically cannot be derived directly from such images. Moreover, highlighted areas in the brain do not exclude the possibility that other parts of it are also involved, as these parts may already be activated but not show additional activity with the new task (Lee et al., 2012). That said, recent studies have documented the ability to classify mental states, namely to accurately map a mental task with a particular activation pattern (Poldrack et al., 2009).

Locating a neuronal activation pattern in the brain tells us little about the underlying causes that led to the cortical activity in question. To better understand the causal mechanisms that lead individuals to act the way they do, we need a meta-theory one that has the power to explain the ultimate causes of behaviors and preferences and not just help “locate” them in the brain. Evolution is the only scientific theory that could explain the underlying ultimate causes of behaviors and preferences, and the forces that shaped them via natural and sexual selection processes. The ultimate goal of every organism is to survive and reproduce and thus, inquiries into the functionality of the human brain require the evolutionary lens. That said, the great majority of neuroimaging studies fall within the proximate realm (address *how* and *what* factors), and as such they seldom seek to elucidate the Darwinian genesis of neuronal processes (ultimate causation). It is one thing to detail where in the brain emotions such as fear, love, or anger “reside,” but another epistemological lens is needed to understand why humans possess the ability to fear or to love, under what circumstances these emotions are activated, and which evolutionary purpose they serve in terms of an individual’s survival and reproduction outlooks. It is crucial to differentiate between how cognitive processes manifest themselves in the brain at the neural level and the evolutionary pressures leading to the existence of such structures. The identification of neural activities is important and can shed some light on their

purpose, but without recognizing specific evolutionary mechanisms such as natural, sexual, and kin selection, we cannot fully infer why they came to be in the first place (see Senior et al., 2011).

A first step toward Darwinizing the brain imaging paradigm would be to make greater use of evolutionarily meaningful stimuli and tasks (photos of a juicy burger or a sexy prospective mate) instead of largely relying on abstract domain-general stimuli and tasks (playing chess or choosing between probabilistic gambles). Moreover, using an evolutionary framework can help generate context-specific stimuli that are differentially relevant to various demographic groups. For example, if we wish to examine how sexual arousal is expressed in the brain, knowing the evolutionary roots of sexual fantasies and how men and women differ in their responses to visual stimuli (Ellis and Symons, 1990) can help in devising experimental tasks that would produce sex-specific arousal (e.g., explicit vs. non-explicit photos). More generally, evolutionary thinking can contribute to neuroimaging research by invoking domain-specific processes that map onto key basal Darwinian modules including survival, mating, kin selection, and reciprocity (Platek et al., 2007; Saad, 2007, 2011).

The examination of the four Darwinian modules has yielded new insights when applied to neuroimaging research. In a study pertaining to the survival module, the mere exposure to pictures of highly caloric food produced brain activation in areas associated with taste and rewards, similar to ones that are triggered in response to real food (Simmons et al., 2005). Of relevance to the mating module, researchers found that when faces of attractive women are presented to men, these activate reward systems in the brain that had previously been identified as responsible for other powerful rewards such as drugs and money (Aharon et al., 2001). Using kin selection principles, Platek and Kemp (2009) showed how different parts of the medial substrates in the brain are activated in response to faces of kin, non-kin friends, and strangers. This makes evolutionary sense since facial categorization and the ability to distinguish between kin and non-kin have important

consequences for survival (differentiating a friend from a foe) and reproduction (avoiding incest with a family member). More generally, the ability to recognize human faces is itself adaptive. Using an evolutionary perspective, researchers have shown that the medial frontal cortex was much more activated when making a decision about whether to trust another person, but not when interacting with an avatar (Riedl et al., 2014). Lastly, various works have explored neural processes associated with the reciprocity module including identifying specific areas in the brain that are activated during moral dilemmas that require cooperation (Singer et al., 2004) and detecting cheaters (Stone et al., 2002).

Ultimately, the exploration of evolved domain-specific modules (rather than domain-general cognitive processes) via the use of ecologically relevant stimuli and tasks will yield a consilient brain atlas. Furthermore, it will likely reduce the “fishing expedition for statistical significance” feel of many neuroimaging studies, by permitting for more ecologically relevant study designs and by facilitating the positing of *a priori* hypotheses.

Given the apparent methodological sophistication of the brain imaging paradigm, neuroscientists are particularly prone to what the Darwinian philosopher Daniel Dennett referred to as “greedy reductionism” (Dennett, 1995). Endless studies are conducted void of any organizing theory or guiding *a priori* hypotheses. Rather, the sophisticated methodology drives the epistemological engine. In a survey of 50 neuroimaging studies only 42% (21 papers) included *a priori* hypotheses (Garcia and Saad, 2008). Of these, 15 were evolutionary based and 6 were non-evolutionary based. Most striking is the fact that only 17 of the 50 papers took an evolutionary approach in the first place, meaning that 88.2% of the evolutionary papers posited *a priori* hypotheses, where only 18.2% of the non-evolutionary papers used such hypotheses. In other words, an evolutionary framework is much more likely to generate *a priori* hypotheses that can be tested using imaging devices, where non-evolutionary approaches produce many more *ad-hoc* and *post-hoc* explanations. Thus, a parsimonious and integrative framework

such as evolutionary theory serves as a safeguard of the scientific method.

While some have described the neuroimaging paradigm as the new phrenology (Uttal, 2001), we do not share such a pessimistic outlook. Neuroscience is still a nascent and rapidly developing field, and some of the criticism is overstated (Farah, 2014). Recently, the United States and the European Union announced two ambitious projects: the BRAIN Initiative and the Human Brain Project. Key objectives include mapping the brain as well as creating a full simulation of it, which could not only help us in better understanding the human mind but also could help in combatting various brain and mental illnesses. Similar to previously innovative technologies such as the telescope and the microscope, brain imaging machines are merely tools that need to be used within a specific meta-theory. The evolutionary framework could provide a good starting point as an overarching theory to better organize and fully understand the ultimate mechanisms that drive our behaviors, emotions, and thoughts, as seen in such lively brain images.

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A sociogenomic perspective on neuroscience in organizational behavior

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We critically examine the current biological models of individual organizational behavior, with particular emphasis on the roles of genetics and the brain. We demonstrate how approaches to biology in the organizational sciences assume that biological systems are simultaneously causal and essentially static; that genotypes exert constant effects. In contrast, we present a sociogenomic approach to organizational research, which could provide a meta-theoretical framework for understanding organizational behavior. Sociogenomics is an interactionist approach that derives power from its ability to explain how genes and environment operate. The key insight is that both genes and the environment operate by modifying gene expression. This leads to a conception of genetic and environmental effects that is fundamentally dynamic, rather than the static view of classical biometric approaches. We review biometric research within organizational behavior, and contrast these interpretations with a sociogenomic view. We provide a review of gene expression mechanisms that help explain the dynamism observed in individual organizational behavior, particularly factors associated with gene expression in the brain. Finally, we discuss the ethics of genomic and neuroscientific findings for practicing managers and discuss whether it is possible to practically apply these findings in management.

Keywords: behavioral genetics, epigenetics, leadership, personality, adult development, evolutionary psychology, organizational behavior

It seems that we have a fascination with the brain. In *The psychopath inside*, neuroscientist James Fallon describes his discovery that scans of his own brain showed patterns of activation indicating potential psychopathy (Fallon, 2013), evocatively described as similar to scans of convicted killers. Fallon describes the neuroanatomical features associated with the constellation of behavioral tendencies that make up psychopathy, including impulsivity and lowered empathy, as well as their genetic and epigenetic correlates. This description almost immediately gives rise to questions of how determined a complex behavioral phenomenon, such as psychopathy, is by its biological foundations (see Stromberg, 2013, for a discussion of the book). Psychopathy—the tendency to be impulsive, manipulative, anti-social, and to lack fear and empathy (e.g., Hare, 1985, 1999)—is of increasing interest in the organizational sciences (e.g., Spain et al., 2014), because it can help explain phenomena such as supervisors who behave in an abusive manner toward their subordinates (cf., Krasikova et al., 2013), *managerial derailment*, the phenomenon of seemingly promising managers who become decidedly ineffective, usually due to interpersonal problems (Leslie and Van Velsor, 1996; cf., Harms et al., 2011), and *counterproductive work behaviors*, or those times when employees engage in activities such as stealing from the company, sabotage, or interpersonal aggression at work (O’Boyle et al., 2011). If organizational scientists could reliably identify psychopaths from objective indicators, such as functional magnetic resonance imaging scans of their brains or

genetic tests, they may be able to design interventions that could help remediate a great deal of suffering in work organizations.

It is, however, unlikely that we can make such identifications reliably. The question posed above, how determined are complex social behaviors by their biological foundations, remains. For instance, consider the case of James Fallon above. He describes himself as a “prosocial psychopath,” and attributes his relatively benign, if competitive, behavior to growing up in a loving family (Stromberg, 2013): he has psychopathy “in his genes,” but it is not so clearly expressed in his behavior.

Additionally, there are many reasons why, even if we could make such identifications, we would not want to use this in the day-to-day practice of management. For instance, genetic screening or brain imaging could be expected to lead to a form of “genetic discrimination.” Such discrimination may be problematic for ethical reasons, and practically, as long as the biological indicators measured are weakly predictive of behavior. For instance, in the United States, the Genetic Information Nondiscrimination Act of 2008 (GINA) Title II prevents employers (and some other non-employment agencies) from requiring or requesting genetic information as a condition of employment (www.genome.gov/10002077). In spite of such legislative barriers to direct use of biological research in employment settings, interest among organizational researchers remains high, as evidenced by the forthcoming book edited by Collarelli and Arvey, *The biological foundations of organizational Behavior*.

Arvey and colleagues (Arvey et al. (2014), Arvey and Bouchard, 1994; Ilies et al., 2006) provide detailed summaries of the research on behavioral genetics in organizational behavior. The earliest investigations in behavioral genetics in organizational settings found that heritable, genetic factors accounted for variation in behavioral characteristics related to leadership (e.g., Johnson et al., 1998). More recent studies aim to examine mediators of the genetic effects, or environmental moderators of these effects to examine how inherited factors play a role in becoming a successful leader. We note that much of the organizational research using behavioral genetics has been directed at the question, “are leaders born or made,” that is, whether leadership is substantially heritable or not. Therefore, our review will be focused on leadership phenomena, but not exclusively about them.

The “are leaders born or made” question is an example of a very common question about genetics in the social sciences, which is: what wins, nature or nurture? Unfortunately, this question is effectively a straw man, because human action is the result of *both* nature and nurture (Ridley, 2003; Rutter, 2006)—one may as well ask which contributes more to the area of a rectangle, its length or its width (an analogy attributed to Donald Hebb in many sources, including Meaney, 2004, p. 2). That is, variation in almost every individual difference studied in psychology is partially due to both genetic and environmental effects. This concept has been codified in Turkheimer’s three laws of behavior genetics (Turkheimer, 2000, p. 160):

1. All human behavior traits are heritable (genetic effect),
2. The effect of being raised in the same family (shared environment) is smaller than the effect of genes, and
3. A large percentage of the variation in human behavioral traits is not accounted for by either genes or by shared environment (unique environment),

which together show that genes and experience, especially an individual’s *unique* experience, both play important roles in the development of complex behavioral characteristics. By this logic, leaders are both born *and* made. An additional important point is that it is meaningless to take the slightly more nuanced position of “if both are important, which is more important?” In the current essay, we review the etiology of leadership through the lens of sociogenomics. For these purposes, we consider leadership largely at the level of the individual leader—the individual characteristics and behaviors that allow that individual to emerge, be accepted, and be effective as a leader. However, each stage of this process involves social interactions with other people. We therefore do consider the influence that individuals have on one another. So, while our perspective speaks most directly to behavioral and trait-based approaches to leadership, the overarching perspective has some bearing on interpersonal and dyadic perspectives, as well.

The sociogenomic framework articulates the mechanisms through which genes and environments interact to help shape observed behavioral characteristics. The promise of sociogenomics lays in using the genome—the entirety of an organism’s hereditary characteristics—as the basis for understanding behavior (Robinson, 2004; Robinson et al., 2005; Roberts and

Jackson, 2008), including leadership behavior. This paper argues that such an approach has a great deal to offer to the study of leadership, even for researchers that do not aspire to collect biological data, because the theory has broad impact on basic research questions in leadership. We believe that a sociogenomic perspective can serve as a meta-theoretical backdrop for leadership scholars that could help to integrate many disparate findings.

We contrast the sociogenomic view with three contemporary perspectives on the biological substrate of leadership: 1. The existence of genetic effects indicates that leaders are “born,” not made (e.g., Ilies et al., 2006; De Neve et al., 2012), 2. the proportionally low variance in phenotypes (about 30%) accounted for by genetic factors indicates that leaders are “made,” not born (Avolio, 2005; Avolio et al., 2009), and 3. an interactionist perspective that acknowledges the mutual influence of genetic and environmental factors (e.g., Arvey et al., 2007; Zhang et al., 2009b). Researchers tend to focus on questions driven by the first two positions. For instance, a researcher may be interested in establishing how much of the observed variance in a leadership characteristic—most of this research has focused on attaining a leadership role—is attributable to genetic factors by estimating the heritability coefficient, h^2 (described below). Another researcher may be concerned with showing that some early life experience influences these same leadership characteristics. In contrast, the sociogenomic approach embraces both of these explanations simultaneously.

We also see something like sociogenomics as an effectively necessary component of doing any biological research into human social behavior in the *post-genomic* world (Charney, 2012). That is, many of the assumptions that earlier work in behavioral genetics has rested on have been called into question as a result of findings since the mapping of the human genome in the early part of this century. Most importantly, DNA is a dynamic entity whose structure and function is altered throughout the life-course by other entities such as retrotransposons (mobile DNA elements that “copy-and-paste” themselves into other sections of a person’s DNA sequence; Charney, 2012) and copy number variations (deletion, insertion, and duplication mutations). Further, DNA may not be the only heritable biological element—*epigenetic* information (loosely speaking, information about how the cellular environment regulates the expression of DNA; we will describe epigenetics in more detail below) may also be transgenerationally heritable (Zhang and Meaney, 2010; Charney, 2012). Each of these elements seems to be environmentally responsive, which goes some way to explaining how the environment interacts with the genome to produce behavior.

It is important to clarify from the outset how sociogenomics differs from more traditional interactionist viewpoints; in fact, it is not the case that sociogenomics *is* an interactionist approach. It is, rather, a framework for understanding how gene \times environment interactions operate; for explaining genetic and environmental effects within a common language. That is, sociogenomics *subsumes* interactionist approaches. We believe that the sociogenomic perspective provides a broader view than the basic interactionist perspective allows. Furthermore, the sociogenomic model predicts that both factors, genes and environmental experiences, work in the same way: by influencing

which genes code for proteins at a given moment in time. That is, the sociogenomic approach adds value by explaining that both genes and environments operate on the genome; they both work by affecting gene expression (Robinson, 2004). In the example above, what distinguishes a sociogenomic explanation from other interactionist perspectives is the understanding that both the genetic factors and the early life experiences operate on the genome; they modulate the expression of certain genes. Sociogenomic explanations focus on *how* gene by environment interactions work.

A sociogenomic model of leadership provides an integrative framework for explaining the roles that genetics and environmental factors play in leader behavior. We next provide a brief overview of the methods used in behavioral genetics studies, called biometric models. Then we review the behavioral genetics literature on leadership, and interpret these findings in a standard behavioral genetics way. We then explain how the sociogenomic approach differs from a behavioral genetic approach. Finally, we outline a series of proposals for innovative research in leadership that are suggested by the sociogenomic model. We conclude by examining ethical considerations for practicing managers. We begin by discussing the roles of psychological and biological explanation in the study of leadership and other organizational behavior.

WEAK vs. STRONG BIOLOGISM

Materialism is a basic tenet in much of modern philosophy, and certainly in the sciences (Dennett, 1991). That is, it should be uncontroversial to describe any human behavioral phenomenon as “biological” in the sense that our psychological selves are situated in our bodies, and therefore must run, like software does on a particular piece of hardware, on our brains—our minds live in our brains. This is the position that Turkheimer (1998) called *weak biologism*, and considered it essentially tautological, that this position is a necessary consequence of the materialist point of view. That is, since our behaviors occur through the workings of all of our bodies’ biological (e.g., musculoskeletal, neurological) systems, that there is some psychobiological association is unsurprising. Where there is interest is in the position Turkheimer (1998) called *strong biologism*, that there is a strong association between well-defined biological structures or processes and well-defined human behaviors. That is, strong biologism provides the necessary mechanisms to identify the etiology of a behavioral syndrome.

The conflation of weak and strong biologism has led to much of the confusion, difficulty, and acrimony in the nature-nurture debate (Turkheimer, 1998). We believe that this is also the case in discussions of biological underpinnings in organizational behavior and leadership. For instance, in asking the question, “are leaders born or are they made?” we are implicitly asking a strong biological question—at least when the question is considered in a genetic vs. environmental causation way. That is to say, this question assumes that there is a specific biological etiology for the behavioral syndromes of leadership, a reasonably simple mechanism or set of mechanisms or processes that is localized in the brain, or there simply is not (the former position embodies the conception of leaders being born, the latter, made).

In other words, if this proposition were true, it would be possible to study leadership at the biological level of analysis, and such study would scale directly to the behavioral level. With a phenomenon as complex as leadership, this is unlikely to be the case. Such questions are not answered by examining whether a phenotypic trait is heritable (Kempthorne, 1978; Turkheimer, 1998). Estimated heritability is, however, the mainstay of our knowledge of the biological foundations of complex behavioral phenomena, including leadership and other characteristics of interest in organizational behavior. We next review the basic models of such biometric research, with the intent to make these models completely accessible to non-specialists.

BIOMETRIC MODELING

In order to understand the literature that genetic research in leadership is built on, it is necessary to understand *biometric*, or behavioral genetic, models. The standard model in behavioral genetics is defined by the equation (e.g., Plomin et al., 2001):

$$P = A + C + E \quad (1)$$

with the components of the equation estimated using a sample of identical (*monozygotic*) and fraternal (*dizygotic*) twins. In the equation, *P* is the *phenotypic trait*. Phenotype means that the trait is observed or measured. Examples of phenotypic traits are height, eye color, measured intelligence, or the occupation of a leadership role. The *A*-term refers to the *additive* genetic component. The *C*-term refers to *common environment*, factors that are not genetics that make twins more alike. Typically, these factors are considered related to family upbringing and common schooling or early life experiences shared between twins. The *E*-term represents *unique environment* (confounded with error), or the percentage of variance attributable to experiences that are wholly unique to each individual, and other purely idiosyncratic variance. This model is typically estimated using samples of identical and fraternal twins, though adoption studies are sometimes used. Identical twins share roughly 100% of their genetic material—copy number variations can differ across identical twins, and random mutations can occur during development, but for practical purposes, identical twins share 100% of their genetic material, while fraternal twins are no more similar genetically than any other siblings—sharing on average 50% of their genetic material. Therefore identical twins have perfect genetic correlations, whereas fraternal twins have genetic correlations half as strong. Both types of twins have equally strong common environmental effects, and the unique environmental effect is specific to each individual. This model allows behavioral genetics researchers to estimate the heritability coefficient, h^2 , which is the population-level variance in the phenotypic trait, *P*, that is associated with the variance in genetic material (i.e., Kempthorne, 1978, p. 11): $h^2 = \text{Var}(A)/\text{Var}(P)$. It is extremely important to note that the h^2 coefficient is a population statistic—it does not apply at the individual level, so it should never be interpreted that an h^2 of 0.50 means that half of an individual’s trait level is genetic. The statistic only indexes the population’s proportion of phenotypic variance attributable to genotypic variance.

BEHAVIORAL GENETICS IN ORGANIZATIONAL BEHAVIOR AND LEADERSHIP

Several studies have investigated the heritability of leadership styles and occupancy of leadership roles (such as supervisor or manager). For instance, Johnson et al. (1998) examined the heritability of self-reported scores on the Multidimensional Leadership Questionnaire (MLQ; Bass and Avolio, 1991). They found a heritability coefficient of 49% for transactional leadership style, and a heritability coefficient of 59% for transformational style. Again, these findings do not mean that half of any one person's score on transformational or transactional leadership is attributable to their specific genetic makeup. These findings also do not imply heritability such that leadership is, "like father, like son," as heritability estimates do not ensure large correlations across generations (Jackson et al., 2011). More importantly, these findings *absolutely do not* suggest that leadership cannot be taught, as heritability does not imply immutability. Instead, these findings only imply that identical twins are more similar on the transformational and transactional leadership scales than fraternal twins due to inherited genetic factors.

Extending these findings within the same sample of twins, Johnson et al. (2001) examined the genetic correlations between transformational and transactional leadership styles, again measured with the MLQ, and the five factor model of personality (Goldberg, 1993). Such a design allows the researcher to determine how much of the correlation between two measured variables is determined by shared genetic causes. For example, we might estimate how much of the observed relationship between the personality trait extraversion and transformational leadership is a result of these two characteristics sharing common genetic causes. These researchers found substantial genetic correlations between transactional leadership and Conscientiousness, Extraversion, and Agreeableness (-0.49 , -0.46 , and -0.23). Similarly, transformational leadership was strongly genetically correlated with Conscientiousness, Extraversion, and Openness to Experience (0.58 , 0.23 , and 0.56). The pattern, but not the strength, of relationships was the same for both phenotypic and genotypic correlations.

Again, these correlations are at the genetic level, so it is likely that transactional leadership shares some of its underlying genetic substrate with Conscientiousness, Extraversion, and Agreeableness, while transformational leadership shares genetic substrates with Conscientiousness, Extraversion, and Openness. Specifically, based on this study, transformational leadership appears to have genetic causes in common with Conscientiousness, Extraversion, and Openness. One possible avenue for future research that these findings suggest is that any physiological system that is implicated in one of these personality traits may be a candidate for study with leadership style. For instance, the serotonin system has been implicated in self-control or impulsivity (Carver et al., 2008), so it appears relevant to conscientiousness. Therefore, it is a reasonable neurological system to study in relation to rated transformational and transactional leadership.

In a study of leadership emergence, as defined by the attainment of leadership roles such as supervisor or manager, Ilies et al. (2004) meta-analytically estimated the percentage of variance in

leader emergence attributable to genetic factors, as mediated by personality traits. The results of this meta-analysis provided 17% as a lower-bound estimate of the heritability of leader emergence. This meta-analysis also provided evidence that personality traits mediate the influence of genes on leader emergence, such that genes \rightarrow personality \rightarrow leader emergence, as causal structure consistent with the "leaders are born" thesis (see Figure 2 and related discussion below).

In a twin study, Arvey et al. (2006) found that 30% of the variance in leadership role occupancy was explained by genetic factors, with the rest explained by non-shared environmental factors. Additionally, genetic factors accounted for substantial amounts of variance in personality traits, though there was no evidence that these personality traits mediated the genetic influence on leader role occupancy. In other words, both personality traits and leader role occupancy had heritable components, but there was no evidence in this study that the genetic effect on leadership was mediated by personality.

Additional evidence was provided by Arvey et al. (2007), who found that 32% of the variance in leader role occupancy was attributable to genetic factors. This study also tested whether developmental factors, specifically formal work experience and family experience, accounted for variance in leader role occupancy. These experiential variables both had significant zero-order correlations with leader role occupancy, but when the genetic factors were controlled for, only the work experiences factor remained associated with leader role occupancy. In other words, family experiences no longer count when genetics are controlled for, but on-the-job work experiences still independently contribute to leader role attainment.

None of these studies found that leadership, however defined, is entirely explained by genetic factors, leaving a lot of room for environmental factors as explanations. Still, leadership, however defined, has been found to have substantial genetic component with around 30–60% of the variance explained by genetic factors. The fact that a sizable amount of variance is explained by genetic factors is consistent with a "Leaders are born" approach. On the other hand, around 40–60% of the variance in self-reported leadership style and 70% of the variance in leader role occupancy was not explained by genetic factors, consistent with a "leaders are made" explanation. That work experiences contributed, independently of genetic factors, to attaining a leadership role (explaining 17% of the variance in leader role occupancy; Arvey et al., 2007), offers support for the "made" interpretation.

Additionally, Avolio et al. (2009) reported findings that after controlling for genetic effects, there were still significant effects on leader role occupancy for authoritative parenting and rule-breaking behaviors in childhood. Further, Ilies et al. (2006) reported the results of an unpublished study by Arvey et al. (2004) that found experiencing leadership roles in high school moderated the genetic effect on work leadership. These findings raise the possibility that the heritability of work leadership may be affected by environmental variables, in this particular case, earlier investment in leadership roles (Avolio, 1994). In addition, Zhang et al. (2009b) found in a sample of male twins that growing up in an enriched environment (as indicated by family socioeconomic status, perceived parental support, and reported conflict

with parents) significantly moderated the heritability of leader role occupancy. Specifically, higher levels of enrichment were associated with lower heritability estimates.

The previous finding is very similar to the evidence that the heritability of cognitive ability is moderated by socioeconomic status (Turkheimer et al., 2003). Specifically, at low levels of SES, 60% of the variance in measured cognitive ability is attributable to shared environment, with almost no genetic component. At high levels of SES, the results are almost exactly the reverse, with the genetic component taking over. Taking these findings together appears to show that the enrichment of the environment that a person grows up in is an important moderator of genetic effects on a wide range of variables, including leadership style.

This latter set of findings demonstrates that, while there is a genetic component to leadership, the environment clearly has a role to play. So, the simple question of whether leaders are born or made has a very simple answer: Yes, leaders are both born *and* made. The question now shifts; was Avolio (2005) correct in emphasizing *made* over *born* in leadership development? We address this more nuanced question by examining traditional biological models of traits with a sociogenomic approach, and considering the implications of each viewpoint on the evidence thus far.

A SOCIOGENOMIC PERSPECTIVE

Recent advances in biology show that the “born, not made” viewpoint cannot be entirely correct (e.g., Robinson, 2004; Robinson et al., 2005; Roberts and Jackson, 2008), for any behavioral domain. That is, “When it comes to behavior, we have moved beyond genetic determinism. Our genes do not lock us into certain ways of acting; rather, genetic influences complicated and mutable and are only one of many factors affecting behavior,” (Jasny et al., 2008). The perspective we call *sociogenomic* rests on two main findings and one fundamental assumption. The assumption is taken from a sociobiological perspective of evolution (e.g., Wilson, 1975), that genes and evolutionary forces influence behavior. This is necessarily true for any heritable behavior with implications for survival or reproductive success, even a given effect is small (Penke et al., 2007). This applies to animals that live in social groups with cooperation and competition as necessary ingredients for survival and success, such as human beings. Leadership, in particular, may be an important evolutionary context (Van Vugt, 2006; Van Vugt et al., 2008).

For instance, consider leadership as an example of social rank. Rank in social hierarchies is very important to social functioning in several primate species. For instance, young adult male chimpanzees spend tremendous amounts of time and effort in attempts to ascend the social ladder to attain alpha male status (Wrangham and Peterson, 1998) and low rank in the social hierarchy has severe negative implications for stress and health in savannah baboons (Sapolsky, 2001, 2005). Such studies provide a useful context for considering leadership behavior. Our distant primate cousins may shed light on aspects of social behavior, stripped of human cultural context, that are shrouded in complexity for humans. Such comparative approaches may aid

us in understanding the origins and functions of leadership in our evolutionary past. Similar, though non-identical, evolutionary pressures are likely to have shaped such behaviors in the great apes.

Such observations about social rank in primate species become important when we consider the first finding of importance to the sociogenomic approach—that the genome is highly conserved across species. Because of this, we can learn a great deal about human behavior from animal models, a point we return to shortly. There has already been some effort along these lines in personality psychology (e.g., Gosling, 2001, 2008; King et al., 2005; Mehta and Gosling, 2006). We believe that a great deal can be learned regarding human leadership and influence processes by examining these processes in other species, and some compelling work has already been done (e.g., de Waal, 2000; Arvey et al., 2014). Furthermore, animal models can provide extraordinary isolation of variables. By studying leadership in chimpanzees we can see the political process stripped of the artifacts of human cultures and language.

Sociogenomics provides a deep reason for examining behavior comparatively: due to the conservation of the genome, behavior syndromes in multiple species probably share genetic determinants and molecular pathways (e.g., Donaldson and Young, 2008). Work that might not be possible with human subjects may be possible using animal models. That is, using current technology, barring post-mortem autopsies, it is not possible to examine gene expression levels in the human brain, but the relevant molecular pathways may be examined in surrogate animals, such as rats and mice.

The second finding is even more relevant in comparison to other contemporary models of the genetic determinants of behavior. The effects of genes are dynamic in their transactions with the environment: genes in themselves *do not determine* behaviors, thoughts, or feelings. Genes code for proteins, period. They do not directly encode behavior; rather, genes are expressed via the proteins for which they code. The general process is as follows: genes are transcribed into RNA sequences that are then translated into polypeptides, and these finally form proteins. The amount, location, and timing of the production of proteins are contingent on the cellular environment. The cellular environment is influenced by the external environment at every step of the above process. The processes of gene expression link the influence of DNA with the environment (Robinson, 2004). This is in contrast to the “genes as distal causes” approach outlined in Figure 1. Unlike Nicholson’s (1998) admonishments that leader characteristics are fundamentally innate, but can be moderated by the situation, a sociogenomicist realizes that genes may also moderate responses to the environment. That is to say, the environment may have a direct effect on behavior, and genes may modulate that environmental effect. Genes can be both causal drivers that the environment constrains, but it is also possible for the environment to be the causal driver that genes serve to constrain (cf., Robinson et al., 2008).

GENE EXPRESSION

We first note that gene expression is a complex phenomenon: we will often discuss “which genes are expressed,” but this is

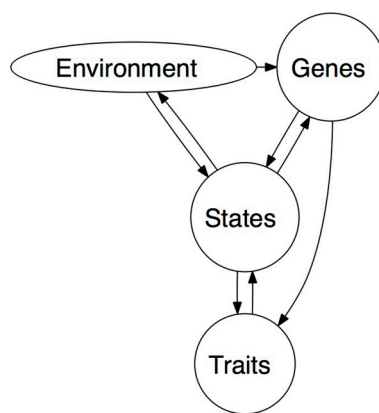


FIGURE 1 | Sociogenomic model of traits (adapted from Roberts and Jackson, 2008).

short hand for the degree to which genes are expressed. When it comes to behaviors such as leadership or job performance, the differences we discuss are more typically quantitative rather than qualitative. The location (in the brain) of the gene being expressed or the degree of expression are the key features¹. There are two major mechanisms that account for differences in gene expression. The first mechanism is differences in genetics between people, which are consistent with the “Leaders are born” (nature) position. The second mechanism is that gene expression can be influenced by variations in environmental conditions, consistent with the position that “Leaders are made” (nurture). Both of these mechanisms may result in different levels of gene expression, meaning that both affect which proteins are being synthesized in the person at any given time, and most importantly meaning that both can affect the neurobiology associated with leadership behaviors and traits.

These two mechanisms are so tightly intertwined that it is absolutely untenable to frame the question whether leaders are born vs. made, or even to simply assert that they are born and made. A dichotomous viewpoint is demonstrably false. Both the genetic mechanism and the environmental mechanism operate on the same substrate: the genome itself. We cannot emphasize this point strongly enough. Environments wield their influence by affecting the production of proteins—gene expression. Both are capable of influencing gene expression and both can affect brain functioning similarly. We believe that nature and nurture should be viewed not as two distinct processes but merely two sides of a coin (Robinson, 2004; Balaban, 2006; Roberts and Jackson, 2008). For instance, consider the study of genetics and social environment by Zhang et al. (2009b). The genetic influence on leader role occupancy is strongest in low socioeconomic strata and weakest for those brought up in highly enriched environments. Genetic differences may predispose someone to be a good leader but a certain environment may squash this or a person born with unfavorable genetic polymorphisms may live in an enriched environment and become successful. The key issue in sociogenomics

is how genes and environmental experiences combine together in their effects.

Think of social status as an environmental variable. Social status can have profound physiological effects. As an example, consider the orangutan. Dominant males have pronounced secondary sexual characteristics, but subordinate adult males have their development arrested in a “subadult” state (Maggioncalda et al., 2002). This is not just a chronological phase in their development; should the dominant male be removed from power, the subordinate males will develop secondary sexual characteristics. Note that the subordinate males are not truly juvenile; they are fertile and can reproduce, generally by forcing intercourse with females when the dominant male is absent (Sapolsky, 2005). In this case, an environmental variable, social status, greatly affects a physiological mechanism—physical maturity.

In a similar vein, Roberts and Jackson (2008) describe a particularly dramatic example of the impact of the environment on gene expression: the life course of the blue-headed wrasse, a tropical reef fish (e.g., Stearns, 1992). The males are large and bright blue, while the females are small and dull brown. Males tend to collect a harem of females whom they protect and mate with. When a predator eats the male, the females do not search out a new male. One of them instead transforms into a male overnight. This effect is genetically mediated, but it is accurate to say that an environmental condition, loss of the harem’s male, causes the sex of the fish to change. That is, an environmental event induces a change in gene expression, which then results in profound physical and behavioral changes.

Further examples of genetic and environmental forces working together can be drawn from the lives of honeybees. Worker bees begin life as caretakers of the hive but eventually become food gatherers (Robinson, 2004). This change is associated with changes in the expression of more than 2000 genes (Whitfield et al., 2003). Changes in the *for* gene are associated with shifts in the environment. For instance, when there is a shortage of food gatherers, the *for* gene becomes expressed and a cascade of changes occur that transition the worker into a food gatherer (Ben-Sharar et al., 2002). The gene is similar across all bees, but the influence of the gene for a particular bee is contingent on the state of the particular bee’s environment—the conditions of its hive.

Such changes in gene expression that are not dependent on the DNA sequence itself are called *epigenetic* effects (Zhang and Meaney, 2010). Such effects occur as a result of various mechanisms, but the most well understood is DNA methylation. Methylation stops the transcription of a gene, halting production of the protein that gene codes for. Strands of DNA can continue to be methylated across time, demonstrating how an environmental effect continues to effect expression even after the environment is removed.

Such epigenetic effects can manifest in very subtle ways. For instance, rat pups that have been licked more by their mothers handle stress better than pups that have not been licked, but that licking behavior is itself heritable. So, it is unclear whether the response to stress in rat pups is directly heritable or if it is environmentally mediated by this licking behavior (Weaver et al., 2004)—the genetic and environmental effects are observationally

¹ We thank an anonymous reviewer for clarifying this point to us.

confounded. Examining the mechanisms of gene expression clarifies this problem, however: maternal licking behavior affects methylation that in turn affects expression of the glucocorticoid receptor gene. Rats with greater activity in the glucocorticoid receptors are better able to tolerate stress. This means that the observed individual differences in rat stress response were not directly attributable to genetics, but via the epigenetic modification of gene expression due to methylation (Weaver et al., 2004). The effect of the gene is contingent on environmental factors.

There is some early evidence for such epigenetic effects in humans. For instance, methylation patterns between identical twins are highly, but not perfectly correlated (Mill et al., 2005). Identical twins share 100% of their genes, but this finding indicates that some life event(s) altered gene expression in the twins studied. This finding has been replicated, and it has been shown that the degree of epigenetic dissimilarity was correlated with the age of the twins and the amount of time the twins had spent together (Fraga et al., 2005). Older twins and twins who spent more time apart had greater differences in methylation patterns. Even for identical twins, who share exactly the same genetic material, external events are capable of changing the way these genes are expressed. DNA is not the only causal driver of gene expression; the environment can play an important role.

A sociogenomic leadership theory that embraces gene-environment interplay points to new avenues of research. For instance, consider the Avolio et al. (2009) study of the effects of authoritative parenting and rule-breaking behavior on leader role occupancy. A sociogenomic leadership researcher would be interested in the mechanisms by which authoritative parenting operates on rule-breaking behavior and leader emergence. Like the rat pups above, are certain gene sequences silenced by authoritative parenting? What mechanisms might drive these findings? Parenting style may set limits on the environments that a child is able to enter. This would be a case of the effect being entirely environmentally mediated, whereas the example of the rat pups is genetically mediated, but either mechanism is possible.

While it is not yet possible to study gene expression directly in living humans, studies of gene-environment interactions suggest that these contingencies may exist. Most behavioral genetic studies in psychology find that somewhere around half of the variance in phenotypes is genetic and the other half is mostly attributable to unique environmental effects (there is often some small amount of variance attributable to common environment found, but see Turkheimer's second law above). Such findings are often built around an improperly specified model: one that does not explicitly account for the environment (e.g., Brofenbrenner and Ceci, 1994). When the environment is explicitly taken in to account, the findings can be markedly different. The heritability estimates are moderated by the environmental effects, such that heritability can be higher or lower as a function of some environmental variable, such as the effects of socioeconomic status on the heritability of intelligence discussed above (Turkheimer et al., 2003). For instance, the heritability of negative emotionality decreases and the effect of *shared* environment

increases at higher levels of parental conflict (Krueger et al., 2008).

Such findings from the personality psychology literature may help to put results such as Zhang et al. (2009a,b) into context. Recall that the genetic effect on leadership role occupancy was moderated by level of social enrichment. The sociogenomic approach leads to questions about how these effects occur. What mechanisms get under the skin, transmitting environmental effects to the genome? Roberts and Jackson (2008) presented a schematic model for a sociogenomic personality psychology. **Figure 1** presents a modified version of this model. We consider all major facets of the model to be latent variables; we assume that even biological substrates will be measured with some error. What is important to note in this model is the direction of the arrows. The environment may act directly upon the biological substrates, through epigenetic mechanisms and gross insults (toxins, brain parasites, iron damping rods through the face), but the biological substrates act on the environment indirectly by way of traits and, most proximally, states. Environments may also act indirectly on the biological substrates via experienced psychological states. For example, the structure of the brain is reconfigured under long-term stress; the medial prefrontal cortex and hippocampus atrophy and the orbitofrontal cortex and basolateral amygdala expand (McEwen et al., 2006).

We argue that leadership style is essentially a trait, a pattern of behaviors that is relatively stable across time and situations. Individual leadership behavioral episodes, such as influencing a particular follower are states (cf., Fleeson, 2001; Beal et al., 2005; Fleeson and Leicht, 2006). Traits and the environment both affect states, and states act on the physiological substrates, which in turn influence trait levels. For example, individuals told to pose in powerful ways have been shown to experience elevated levels of testosterone and decreases in cortisol levels which, in turn, impacts their decision-making and risk-tolerance (Carney et al., 2010).

The key behavioral component of this model is the state: individual behavioral episodes. The individual engages in behaviors that set goals, build relationships, express trust in subordinates, initiate structure, and so on. These behavioral episodes are determined by environmental constraints (e.g., department policy, requests from senior management, compensation structure) and by traits (e.g., need for power, need for affiliation, dominance, sociability, attachment style, propensity to trust). From the standpoint of developing leaders, these episodes are key. Like stress remodeling the brain as described above, how can leader development interventions be constructed to redesign the neural architecture of the leader? We see the point of leader development interventions as using the environment to induce states that ultimately alter trait levels.

We believe that the key difference between the current models of biology employed by leadership researchers and the sociogenomic perspective is one of generativity. The sociogenomic perspective, as outlined above and summarized in **Figure 1** provides direction to research investigating the genetic and environmental effects in leadership. We outline a few key areas for emergent scholarship below. Work under current models is effectively descriptive, documenting genetic

and environmental effects. The unifying functional framework provided by sociogenomics presents many opportunities for exploration.

RECONSIDERING THE RECTANGLE: BORN AND MADE

The current approaches to the biology underlying psychological characteristics seem to view genetics as an unchanging causal force on behavior. In such conceptualizations, consequential social phenomena, such as leader effectiveness, lie at the end of a causal chain begun with the biological substrates underlying personality traits (e.g., McCrae and Costa, 1996; cf. McCrae, 2010). While other stages in the causal chain are seen as subject to environmental pressures, these biological substrates are not. DNA is the core of these structures, and is seen as an immutable influence on phenotypic traits throughout the lifespan. The assumption is that, as genetic polymorphisms do not change, the effects of DNA on behavior should be constant, therefore any changes in phenotype are caused by genes (McCrae, 2010).

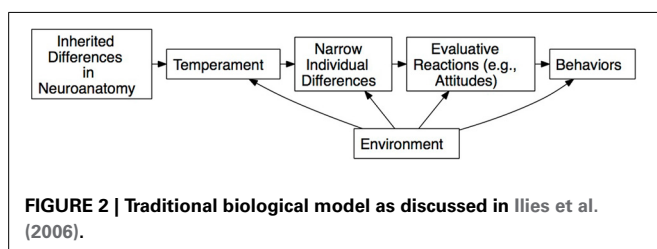
Ilies et al. (2006) employed similar reasoning in their argument that causality flows from genetic factors through large, heterogeneous traits to narrower traits to behavior. **Figure 2** presents a “born not made” model of leadership, adapted from Roberts and Jackson (2008). This model remains current in biological thinking throughout the social and organizational sciences. The origins of this perspective lie in Eysenck’s (1967) views on personality and intelligence, which have been very influential on biological thinking in psychology. The details of specific biological models vary, but the take-home point regarding models of this form is this: causal flow is always from the biological substrate to the behavioral or social outcomes (e.g., McCrae and Costa, 1995, 1996; DeYoung, 2010). This point of view seems well represented in organizational research, with a model like this implicit in Ilies et al.’s (2006) review, and the explicit argument in Antonakis et al. (2010) that personality traits can be used as instrumental variables in many settings in organizational research, because their levels are set exogenously by genes. According to this theoretical point-of-view, the environment is generally viewed as capable of modulating anything causally downstream from the functional neuroanatomy, but does not generally impact genetic or physiological systems, barring gross injury (such as the well-known fable of Phineas Gage).

Nicholson (1998) provides a fairly clear summary of this viewpoint. He describes three hypothetical children from a hypothetical family, each with a radically different temperament: the first is introverted and grows up to be a research scientist, the second is talkative and grows up to be a salesperson, the last is even-tempered and grows up to be a schoolteacher. Nicholson

states, “Evolutionary psychology tells us that each one of these individuals was living out his biogenetic destiny.” Personality dispositions are described as hardwired. Leadership skills can be taught, but the “passion to lead” is an innate difference (cf. Doh, 2003). Nicholson points out that possessing this genetic endowment may not always lead to successful leadership, though, as situational characteristics may necessitate some other set of traits. From this perspective, the biological component of behavior—the disposition—simply *is*, and is effectively immutable; situational characteristics merely determine whether expressing that disposition is effective vs. ineffective. That is, genes are the causal drivers and the environment acts only in modifying the effectiveness of genetically caused preferences.

How should the behavioral genetic evidence discussed above be interpreted under this perspective? The key to understanding this perspective is that physiological systems are given causal primacy over psychological mechanisms. This is the approach adopted in some quarters of personality psychology, with the implication that genetic polymorphisms manifest themselves in specific neuroanatomical structures which in turn give rise to largely static psychological characteristics (McCrae and Costa, 1995, 1996; DeYoung, 2010). Advocates of this viewpoint usually argue that since the genetic polymorphisms are invariant and, barring gross injury, so are the neuroanatomical structures and their concomitant temperaments/traits. The environment is essentially restricted to affecting what McCrae and Costa refer to as *characteristic adaptations*, the learned habits that individuals develop to express their native traits in acceptable or functional ways within their environment.

The “Leaders are BORN” view tends to force such dichotomous thinking, however (and so does the “Leaders are MADE” perspective). If the genetic polymorphisms one is born with are invariant over the life course and they guide the development of the neural architecture we think with, how can it be otherwise? Researchers operating within this framework have a tendency to demonstrate that a genetic component exists for leadership (e.g., Johnson et al., 1998) or to statistically control for genetics in order to more purely estimate the environmental effects of interest (Avolio et al., 2009). The next section argues that this point avoids addressing the true complexity of the relationship between genetics and experiences as causal agents. Studies such as Avolio et al. (2009) demonstrate a conceptual weakness in other interactionist perspectives, relative to the sociogenomic outlook. Statistically controlling for a genetic effect while estimating the environmental effect separates two inseparable things—remember both genes and environment operate through mechanisms of gene expression—and assumes that the genetic effect is invariant over time. These traditional interactionist studies ask the aforementioned question, “which contributes more to the area of a rectangle, its length or its width?” Like Nicholson (2005), we believe that a *truly interactionist* perspective is needed, but we believe that a sociogenomic approach—where both genes and environment are truly causal mechanisms—provides that perspective. Specifically, recent evidence indicates the epigenetic mechanisms are active throughout the life-course (Zhang and Meaney, 2010; Charney, 2012). It is possible that these mechanisms are responsible for various aspects of development and behavioral plasticity.



WHAT CAN ORGANIZATION STUDIES SCHOLARS LEARN FROM THE SOCIOGENOMIC PERSPECTIVE?

The major take home messages from the sociogenomic perspective are quite broad. Sociogenomics provides a meta-theoretical framework that can assist leadership scholars in framing and interpreting new and existing research. This framing is achieved by recognizing the deep interdependence of genes and the environment in facilitating behavior. To explore this interdependence, we propose three platforms of research informed by the sociogenomic perspective.

PROPOSAL 1: CONDUCT CROSS-SPECIES STUDIES OF SOCIAL INFLUENCE PROCESSES

Recall that one of the foundational points of the sociogenomic perspective is the conservation of the genome. One main point is that the behavioral syndrome we call leadership has direct analogs in other species, and that the chemical pathways that lead to the syndrome are likely to be the same, whether the subjects of study are people, primates, or stickleback fish. Additionally, even simple species, such as nematodes, fruit flies, and honeybees, display interesting social behavior that have human analogs (Sokolowski, 2010). Roberts and Jackson (2008) pointed out that a sociogenomic personality psychology would be a comparative psychology from the start. This point is also true of a sociogenomic leadership theory. This can be a challenge because of the definition of leadership in many areas of biology—for instance, in behavioral ecology, leadership is often being the individual who selects which direction the group will move in most frequently (cf., Van Vugt, 2006), though this may provide some insight into humanity's evolutionary past.

To use this proposition, organizational researchers who embrace the sociogenomic model would first investigate how the behavioral syndromes associated with leadership roles are manifested in other species. For instance, the political rivalries and power plays within a colony of chimpanzees may inform research on power and status motives in human leaders or the process of coalition building in human work teams (de Waal, 2000). With this suggestion, we do not just mean to address neurobiological systems. Animal models may allow us to formulate tighter hypotheses about important experiences and environments. By examining the more visible social and power relations in animal models, we may have a better idea of whether important experiences or developmental environments occur early or later in life, whether those experiences involve peers, and the degree to which a formative experience can shape an individual. Social experiments that may be difficult or unethical with human participants might be possible. For instance, what happens both socially and neurobiologically when an individual at the top of a hierarchy in a particular context is moved into a new context? Are they still “a leader”; how is their neurobiology affected?

Such a lack of normal social context for leadership using animal models may disconcert many organizational scientists. We do not suggest that *normative* findings will be discovered from cross-species research; to expect so would mean we have committed the naturalistic fallacy—“that which is, must be good.” We suggest, instead, that such research can open up a very clear view of the neurochemical mechanisms that drive certain

aspects of leadership-relevant behavioral syndromes. This, in turn, may provide deeper insights into the psychological mechanisms that constitute leadership. Additionally, the insights gained from understanding animal nature may have direct practical implications, for the opposite reason of the naturalistic fallacy. These insights may help us to understand how humans *want* to behave, contrary to organizational and societal expectations (e.g., de Waal, 2000; Van Vugt and Ahuja, 2011).

PROPOSAL 2: INCREASE PRECISION AND SPECIFICITY IN MEASURING ORGANIZATIONAL BEHAVIOR CONSTRUCTS

Part of the problem in asking strong biologicistic questions about leadership is that leadership, as a set of phenomena, is likely too complex to submit to localization in specific neural structures or processes. A sociogenomic approach to leadership would thrive on detailed, specific measurements of its constructs and the differences between them. There are two major reasons for this. The first is that it is necessary to clearly understand the phenotype in order to progress in understanding the genotype—and its transactions with the environment. Measurement is, unfortunately, not a particular strength of current leadership research, and is weak in much of organizational behavior. The proliferation of constructs in leadership theory, with little clear evidence for their distinctiveness makes this point problematic: what are the important, distinct behavioral syndromes that sociogenomic researchers should be investigating? For instance, it has been shown that satisfaction with one's job has a heritable component (Arvey et al., 1989). That such attitudes are heritable has sometimes been explained by the heritability of more general personality traits (e.g., Olson et al., 2001), but is that argument fully consistent with a sociogenomic analysis (cf., Roberts and Jackson, 2008)?

In leadership research, specifically, another rationale for improved psychometrics in organizational behavior is that precise measurement would allow the community of leadership researchers to build up a well-specified nomological network to enable understanding of how, why, and when good leaders emerge and how they behave while holding their leadership roles. That is to say, what are the biological and psychological factors that predict “leadership”—before the putative leader is even thrust into any leadership role? Measurement in the field of leadership must be put on firmer psychometric grounding. Leadership scholars may need to invite assistance from psychometricians to achieve this goal. Even with such assistance, confronting biological systems may require further refinement of measures.

For example, serotonin functioning is implicated in dominance behavior in chimpanzees, and treatments with the serotonin precursor tryptophan increase dominance in everyday social interactions in humans (Moskowitz et al., 2001). In particular, to understand the role played by serotonin, one needs to differentiate between two modes of self-regulation. In the first mode, individuals engage in quick, affect-laden responses built upon approach and avoidance emotions (e.g., joy vs. fear). The second mode is an effortful control system that can serve to guide voluntary behavior or to inhibit inappropriate responses. The second mode is capable of overriding the first mode. Essentially, at

any given time, any given human is working in one of two ways: a highly emotional, reactive mode or a deliberative, thoughtful mode. Carver et al. (2008) argued that the serotonin system facilitates greater effortful control.

Using such a highly specific, detailed formulation of the constructs allows considerable insight into the serotonergic system and its associated behavior syndromes. Depression reflects the combination of low activation in both the approach system and the effortful control system. Similarly, the construct *impulsivity* confounds high activation in the approach system with low effortful control. Since serotonin facilitates effortful control, it therefore affects a wide range of seemingly unrelated psychological domains, such as depression, angry hostility, and impulsivity.

Current assessment of leadership is frankly weak from a biologically informed perspective. Behavioral syndromes such as transformational, transactional, or authentic leadership are probably too coarse (see Avolio and Gardner, 2005) to be diagnostic of the physiological systems at play. We do not mean to single out these constructs as being the only ones in the leadership literature that are too broad to aid in building biological theories of leadership. It is unlikely many of the leadership measures in current widespread use would be sufficiently precise for such purposes.

To reiterate, there are multiple ways to think about leadership. In this essay, we have approached leadership in a behavioral or trait-like manner. That is, that a leadership style is a pattern of behaviors exhibited by an individual in a formal or informal leadership role that is fairly stable (in contrast to, say, emotions) across time and situations². We wish to be clear that we are not indicating that leadership *per se* is a trait, but that a variety of leadership constructs, such as leadership style, can be approached in the same manner as other individual differences.

Beyond the previous considerations, the individual's physiology has implications for any conceptualization of leadership, and the measurement systems used should incorporate those considerations. As an example, consider the serotonergic system. It is implicated in dominance, and dominance appears important to attain and maintain status. Now, we are left with a host of research questions regarding the role the serotonin system plays in dominance and status attainment. For example, how does variability in serotonergic functioning affect leader emergence? Does attaining leadership status, in turn, affect the serotonergic system (a responsive effect; Roberts and Caspi, 2003)? Different social settings are likely to allow only some dominance displays—what role does serotonin play in navigating this social milieu?

A connected point that is important here is that multiple methods should be used to investigate the biological underpinnings of leadership behavior. Hormonal assays can be used

to study the roles that stress and sex hormones play in various leadership-relevant interpersonal interactions. For instance, recent work shows that while member testosterone, as measured with saliva swabs, does not predict member status within the group, mismatches between testosterone levels and member status in group settings negatively impact the group's collective efficacy (Zyphur et al., 2009). There are also indirect measures of testosterone level that can predict leadership-relevant qualities. Facial masculinity, a signal of testosterone, is associated with rank both at US Military Academy at West Point and late-career rank (Mueller and Mazur, 1996). Depth of voice, another indicator of testosterone, is a robust signal of dominance (Wolff and Puts, 2010).

We also think that brain-imaging work can be helpful in clarifying the meaning of leadership constructs. Use of brain imaging methods is tightly tied to our concerns regarding the specificity of measurement systems employed in leadership research. For instance, is it meaningful to ask, what are the neural correlates of transformational leadership? As an example, it has been suggested that neuronal coherence (an index of communication between areas in the brain) in the right frontal cortex may be associated with visionary communication (Waldman et al., 2011). Perhaps more meaningful is to narrow this question down to deal with the construct of "charisma" (Gardner and Avolio, 1998). The point remains that constructs must be sufficiently well defined so as to permit investigation of their neural substrates. Additionally, we can ask this question in two ways. First, on the leader side, which neural mechanisms are involved in the kinds of idealized influence tactics that constitute charismatic leadership? Secondly, on the follower side, which mechanisms do those influence tactics engage?

Finally, finer measurement of leadership constructs would increase the utility of molecular genetic studies. For instance, consider the measurement of power motivation, which has been argued is extremely important to the acquisition of leader status (Nicholson, 1998; Pfeffer, 2010). Power motivation can be measured using an approach motivation framework, desire for power, or using an avoidance motivation framing, fear of power (Harms and Roberts, 2006; Harms et al., 2007). Using these approaches may help to clarify the role of the neurophysiological systems in understanding leadership phenomena, and help to direct attention to candidate genes (such as dopamine receptor and serotonin transporter genes). The molecular genetic approach is open to criticism, in that the results are notoriously difficult to replicate—but the original research should be done so that issues of replication can even be addressed.

PROPOSAL 3: IDENTIFY KEY CONTEXTS AND TIMING FOR ADULT DEVELOPMENT AT WORK

The key insights from a cross-species, sociogenomic view of leadership demonstrate how critical particular environmental experiences can be for profound behavioral—and sometimes physical—change. Avolio (2005) discussed the tension between the "born" and "made" perspectives in the development of leaders. The premise is that the genetic endowment an individual has is a starting point. The stream of events and situations a person experiences is what develops the individual as a leader. The

²Alternative views of leadership may conceive of leadership as a social process centered around influence or as a relationship. However, we believe that the most popular operationalizations of leadership (i.e., self- and other-reports of typical behaviors) are consistent with a trait-like perspective of leadership, where traits are considered as typical levels of behavior that persist over time and situations, but are flexible and develop over time, rather than being static (Roberts, 2006).

key insight from sociogenomics is that, even for highly heritable traits, those traits are still open to environmental influence. Again, heritability does not reflect the degree to which an attribute is “set in stone” and does not necessarily act as a constraint on the amount of influence that environment *can* have on shaping leadership. That is, no matter how high the heritability there is still a possibility for environmental interventions. Thus the question becomes, what are the situations (occurrences, times of life, and so on) that will allow a person to develop into a leader and are there interventions that can lead to better leadership?

A sociogenomic leadership approach would help to develop a science of leader development in two key ways: to help understand what contexts are developmentally important and when they can be expected to occur (cf., Day et al., 2009). For instance, it is appropriate to question what the evolutionarily appropriate contexts for leader development are. Hogan (2007) has argued that in the work context, individuals must balance two fundamental motives: getting ahead and getting along. Hogan argues that these motives are products of our evolutionary history as social animals. Entry into the organization can be viewed as entry into a social hierarchy, and many of the situations that follow can be viewed through the lens of attempts to attain and maintain status within the hierarchy. Again, comparative study of other primates or traditional social groups (e.g., hunter-gatherers) could help us understand these contexts.

What if it is possible to design interventions that counteract or decrease the phenotypic variance attributable to genes (similar to the Turkheimer SES and IQ studies mentioned above)? For example, consider the US Military Academy at West Point. West Point has a strict organizational hierarchy, with cadets attaining various ranks that mirror the active duty Army. Additionally, West Point has the explicit goal of *developing* cadets into military leaders, and uses a variety of formal and informal developmental interventions to do so, including 360 feedback mechanisms. There are individual differences in the developmental trajectories for cadets for scores on those 360 instruments (Harms et al., 2011), indicating that some cadets are more successful at navigating this formal hierarchy. A sociogenomic approach to such a study would attempt to capture the psychological, physical, and political tools that cadets use to navigate the organizational hierarchy, and how those tools relate to leader competencies across time. For instance, do leadership skills enable ascent in the organization, or does role attainment facilitate skill development? Another key question is how do experiences in the organization get translated into trait-like leadership competencies; what behavioral episodes are key?

As a further example, can traumatic experiences catalyze the development of leadership within a person, such that a person experiencing traumatic events becomes more resilient and more capable of exerting leadership (e.g., Avolio, 2005)? A sociogenomic researcher might ask which genes are expressed (or suppressed) when trauma occurs? What is the biochemical pathway such trauma induces—does the expression of these genes trigger a cascade of expressions in other genes that influence activity in multiple areas of the brain? For instance, trauma is implicated in a number of negative behavioral syndromes, such as

antisocial personality disorder and depression (Caspi et al., 2002, 2003). What are the physiological differences that allow some individuals to use traumatic events to catalyze their leader development, as opposed to sinking into violence or despair? What interventions can alter the individual's reaction to the traumatic event? Can we identify the molecular pathways such an intervention would engage? How does the whole process play out? Understanding the biological mechanisms that mediate the effects of trauma and recovery will help design more effective interventions. Based on the model in **Figure 1**, it is clear that because psychological states mediate the influence of the environment on both the biological substrate and leadership-relevant traits, it is likely that effective leadership interventions should be sustained over longer periods of time. For instance, the West Point study by Harms et al. (2011) found development on leadership competencies persisted over a period of 2 years.

Furthermore, the existing evidence from behavioral genetic studies shows that a considerable amount of variance in leadership outcomes is unexplained. Unique environmental factors explain most of the variance in leader role occupancy, but only a fraction of this variance has been explained by measured life experiences (Arvey et al., 2007). How might experiences with authority, early leadership roles, responsibility in fraternal, social, or civic organizations, and other life experiences shape the states that individuals experience? How do those states affect gene expression and neural architecture? Is it possible to use animal or ethological models to identify important roles and timing for leader development experiences? We focus above on leader development, but it seems clear that the roles, demands, and general characteristics of an individual's job impacts his or her personality development (e.g., Roberts, 2006). If personality is important to a wide variety of on-the-job behaviors, then this development will have important consequences of our understanding of the relationship between genetic, neurological, and behavioral variables in organizational settings.

PROPOSAL 4: CLOSER INTEGRATION WITH EVOLUTIONARY PSYCHOLOGY

Up until this point, we have largely ignored the other main biological research tradition in behavioral science: evolutionary psychology. One reason is that, until relatively recently evolutionary psychology has focused on species-general adaptations (i.e., mechanisms or structures that do not vary over individuals in a population; e.g., Tooby and Cosmides, 1990; cf., Penke, 2010), and such universal features are less generally relevant in organizational contexts: understanding them could help design very general aspects of the work environment (e.g., safety, compensation systems), but are less helpful in selecting, training, motivating, or leading individuals at work. More recently, though, researchers have begun to integrate evolutionary psychology with research on individual differences (e.g., Penke, 2010; Buss and Penke, 2014). Such efforts revolve around understanding individual genetic variation and its impacts on behavioral characteristics. We have argued throughout this essay that sociogenomics is an effective meta-theoretical framework for studying psychological, behavioral, and neuroscientific phenomena in organizations; evolution (and, by extension, evolutionary psychology) is *the*

meta-theory that the sociogenomic framework plugs into (cf., Buss, 1995).

Evolutionary theory also provides a variety of conceptual tools that can aid researchers in analyzing problems and behaviors, such as life history theory and costly-signaling theory, to name just two (Buss and Penke, 2014). Consider life history theory, as an example. Individuals have limited time and energy to devote to their various pursuits, and so face trade-offs when investing these resources in any particular activity. Life history theory provides a broad framework for analyzing these choices (Kaplan and Gangestad, 2005). For example, an individual male may invest efforts into securing a leadership position at work to increase his status and compensation, in order to secure a desirable mate and provide resources for future offspring, helping to solve the two major problems of *reproduction* and *parenting* (cf., Buss and Penke, 2014). Thinking about the action *acquiring a leadership position* in this way could help to better understand the motivations and cognitive processes the individual has, opening this action up to greater theoretical elaboration.

Further, evolutionary theory can help to provide implementation guidelines for our previous proposals. Specifically, consider our discussion of *identifying key contexts and timing for leader development* above. Such contexts are situations, in the classical person-situation debate sense (cf., Mischel, 1968). Important situations are defined by the adaptive problems that obtain within their boundaries (Buss and Penke, 2014). A relevant context for leadership development may be a child's first day of school, for instance: his or her first exposure to a prominent status hierarchy with authority figures (i.e., teachers, administrators) who are not the child's parents. While we focus here on the first day of school, it is the experience of the status hierarchy that defines the *evolutionarily* important context.

ETHICAL CONSIDERATIONS

In some ways, genetic or other physiological screening in organizations is similar to the psychological and physical testing already used for selection among applicants (cf., Guion, 1998). The measures used in those settings, such as cognitive ability tests, personality assessments, and tests of physical strength, dexterity or endurance are imperfect indicators of the underlying psychological or physical entity (cf., Lord and Novick, 1968). They are also imperfect predictors of future behavior at work. Often, however, the results of these measures are imbued with a certain physical, biological interpretation: that is, a person's levels of some personality trait, like conscientiousness—the tendency to be neat, orderly, punctual, achievement-oriented (cf., Barrick and Mount, 1991)—is set by the person's genes (e.g., Antonakis et al., 2010). If that viewpoint held, then direct assessments of the genes or neuroanatomical structure that serve as the biological foundation of conscientiousness would be just as appropriate.

One of the major purposes of this review has been to demonstrate *why* that view has flaws. Possessing a particular genetic polymorphism seems unlikely to be enough to determine an individual's standing on a trait as complex as conscientiousness (or any other complex behavior). The genes a person possesses may express themselves differently (or not at all) conditional on the environment. Further, environmental changes may impact the

individual's psychological states, which could then affect gene expression and remodel the person's neuroanatomy (cf., Roberts, 2006; Roberts and Jackson, 2008). When these possibilities are taken into account, it seems unwise to simply examine an individual's current biology and make strong behavioral predictions based on it.

Let us return to the example from the beginning, of the “psychopath” neuroscientist, James Fallon. If we lived in a world with rigid genetic or neuropsychological screening, he would perhaps never have been admitted to graduate school to earn a Ph.D. We would then not have his example to illuminate the possibility that our genes are not our destiny, that an individual whose genes appear to code for psychopathy, and whose neurological functioning bears this out, can be a successful scientist with a close family. Under the sociogenomic framework, there is a complex path from the particular variant of a gene that an individual possesses and the behaviors they are likely to exhibit; as a result, it seems to us that organizational interventions based on genetic or neurological information are a long way from being tools in the practicing manager's kit.

CONCLUSION

This paper is meant to incorporate theoretical insights from molecular biology within leadership research, using a framework that has been profitable to understand social behavior across species, time and outcomes (Robinson, 2004; Robinson et al., 2008; Bell and Robinson, 2011). Certainly, we do not cover every aspect of this theory, nor can this be considered the final word on the topic. We mean to contrast static thinking regarding the influence of both traits and genetics with the highly transactional view of the gene-environment interplay provided by the sociogenomic perspective. That is, to say that a characteristic is genetic is not to say that it is unchanging; there is a fundamental interplay between genes and the environment throughout the life course. Our genetic material does not make our destiny; it does not have a simple direct influence on phenotypic behavior. Sociogenomics encourages leadership researchers to focus on functional questions: what mechanisms facilitate leader emergence? What psychological adaptations facilitate effective leadership? What are the physiological substrates of leadership constructs?

Further, sociogenomics urges leadership researchers to attend to the evolutionary context in which leadership emerged: this may provide key insights into how these functional mechanisms operate within modern organizational contexts. For instance, how is social status attained within an organization, and which mechanisms facilitate its attainment? A sociogenomic leadership theory would provide a modern biological framework for interpreting genetic research in leadership by encouraging detailed research questions regarding the mechanisms underlying genetic and environmental effects found in contemporary behavioral genetic studies.

Recent interest in and efforts to incorporate biological reasoning into management and leadership seem to point to a bright future. To this end, we have borrowed and elaborated on a theoretical model from biology. This is a model that has some traction in disciplines that have close ties to leadership theory,

most notably personality psychology. We advocate a move to a sociogenomic leadership theory. The perspective offered by this model shows us that DNA is not always the causal driver of behavior. Environmental conditions interact with genes to build the biological architecture upon which behavior plays itself out.

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A face for all seasons: searching for context-specific leadership traits and discovering a general preference for perceived health

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Previous research indicates that followers tend to contingently match particular leader qualities to evolutionarily consistent situations requiring collective action (i.e., context-specific cognitive leadership prototypes) and information processing undergoes categorization which ranks certain qualities as first-order context-general and others as second-order context-specific. To further investigate this contingent categorization phenomenon we examined the “attractiveness halo”—a first-order facial cue which significantly biases leadership preferences. While controlling for facial attractiveness, we independently manipulated the underlying facial cues of health and intelligence and then primed participants with four distinct organizational dynamics requiring leadership (i.e., competition vs. cooperation between groups and exploratory change vs. stable exploitation). It was expected that the differing requirements of the four dynamics would contingently select for relatively healthier- or intelligent-looking leaders. We found perceived facial intelligence to be a second-order context-specific trait—for instance, in times requiring a leader to address between-group cooperation—whereas perceived health is significantly preferred across all contexts (i.e., a first-order trait). The results also indicate that facial health positively affects perceived masculinity while facial intelligence negatively affects perceived masculinity, which may partially explain leader choice in some of the environmental contexts. The limitations and a number of implications regarding leadership biases are discussed.

Keywords: leadership, prototypes, contingency, categorization, face perception, attractiveness, health, intelligence

INTRODUCTION

Investigating evolved cognitive mechanisms mediating the connection between environmental triggers and leadership emergence is a burgeoning field that works to add a biologically inspired expansion to traditional models of contingent and implicit leadership (e.g., Fiedler, 1964; Lord et al., 1982; Spisak et al., 2012). Such research helps to clarify leadership biases and their potential impact on everything from voting behavior and CEO succession outcomes to informal leadership emergence in local networks. The underlying psychological mechanisms facilitating this emergence have been referred to as context-specific cognitive leadership prototypes (Spisak et al., 2011).

Such psychological adaptations are arguably part of the human evolutionary trajectory toward increasingly complex social group strategies as a means to maintain and increase fitness in competitive environments (e.g., Couzin et al., 2005). As groups grow in size and complexity, costly risks arise in the form of reoccurring coordination problems which select for adaptive solutions—including leadership (Van Vugt et al., 2008). Indeed, leadership has been observed across cultures (Brown, 1991) and emerges

with minimal conscious effort (De Cremer and Van Vugt, 2002). Collective action challenges benefiting from such a social adaptation includes the successful management of competition and cooperation between groups. Poor coordination during competition can lead to failure in the presence of a *raiding* out-group whereas the ability to effectively cooperate between groups can, in *trading* situations, reduce the costs of conflict and increase success. Further, research on modern organizational behavior has demonstrated that management efforts to correctly orient a team either toward competition or cooperation depending on the task can have a significant impact on performance (Beersma et al., 2003). Thus, these “raiding vs. trading” dynamics were (and are) powerful forces in the adaptive landscape of group behavior (e.g., Wrangham and Peterson, 1996; Bowles, 2009; Van Vugt, 2009).

There is also the need to effectively divide the investment of time and energy between finding new resources vs. extracting rewards from existing resources—known as the “Exploration-Exploitation Dilemma” in the organizational science literature (March, 1991) and related to ecological theories such as “Optimal Foraging Theory” (MacArthur and Pianka, 1966). A balance

needs to be made where a group must not over-exploit for fear of becoming obsolete relative to more exploratory groups. On the other hand, a group must work to competitively capitalize on an established resource before shifting to more exploratory alternatives. Effectively managing the exploration-exploitation dilemma subsequently increases (or decreases) group success—be it migratory decisions about food or executive strategies in free markets. As with raiding vs. trading, the pressures of exploration vs. exploitation appear to have also had an impact on human evolution. Specific neural mechanisms, occupying distinct substrates, exist for processing information regarding this dilemma (e.g., Daw et al., 2006). Cohen et al. (2007), for instance, report that this neuromodularity reacts to estimates of uncertainty and expected utility (i.e., fundamental aspects of the exploration-exploitation dilemma). Relatedly, McDermott et al. (2008) connects this underlying evolved logic of optimal foraging to the well-established decision-making assumptions of prospect theory (Kahneman and Tversky, 1979). Such evidence points to cognitive systems which have been selected for to solve reoccurring problems associated with exploring new alternatives vs. exploiting an established option.

It is argued that (1) leadership (i.e., the ability to influence others and act as a focal point of coordinated behavior to achieve group objectives; e.g., Yukl, 2006) is an adaptation to manage challenges associated with exploration vs. exploitation and competition vs. cooperation and that (2) dealing with these distinct “fitness-relevant” coordination problems over time has selected for contingent leadership prototypes to aid in the swift endorsement of appropriate context-specific leaders (see Spisak et al., 2011). Leadership increases the efficiency and effectiveness of collective action and taking too long to coordinate or following the wrong leader can severely hinder the fitness-enhancing value of a social group strategy (Van Vugt et al., 2008). The skills required to dominate competitors, for example, can be a hindrance when attempting to create and maintain cooperation between groups. In a contemporary context, this inability to correctly assign leadership may be one of the reasons why researchers find that approximately half of all mergers and acquisitions fail (Cartwright and Schoenberg, 2006). Some organizations may simply take a “one size fits all” approach to leadership and dominant agents maintain their hierarchical authority when more prosocial leadership should be allowed to emerge.

Research on shared leadership, where distributing leadership across a number of individuals can significantly enhance group performance (e.g., Carson et al., 2007), provides a clear connection between repetitive organizational challenges and evolved leader prototypes. Here we aim to understand how evolution may have shaped our implicit preferences for shared leadership. Specifically, we are investigating cognitive associations between the evolutionarily consistent coordination pressures mentioned above and contingent leader qualities which may have been selected for as part of human followership psychology. Such efforts advance our understanding of contingent decision-making which consequently helps to maximize the benefits of shared leadership (i.e., selecting the right leader for the situation as opposed to one size fits all).

To understand this cognitive process one must first consider how such contingencies are executed to produce leadership emergence. A prominent cue for this purpose is the human face, which provides a wealth of information about an individual, including information about character traits and genetic fitness (Bruce and Young, 2012). We more specifically know that individuals can assess leadership success of political candidates better than chance by mere exposure to their photograph (Todorov et al., 2005), and children as young as 5 years old can replicate this outcome (Antonakis and Dalgas, 2009). The latter sample of children (who are void of political experience) suggests that such judgments have less to do with social stereotypes of politicians and more to do with a deeper cognitive bias triggered by information embedded in the face.

The face stores a significant amount of useable data for context-specific leadership decision-making. Qualities such as facial femininity or perceived age can have a significant impact on who followers endorse as a leader in different situations because these visual signals can serve as a proxy for latent behavioral potential (e.g., Little et al., 2007). Estrogen levels, for example, are positively associated with both perceived facial femininity (Smith et al., 2006) as well as nurturing and affiliative behaviors (i.e., tending and befriending; Taylor et al., 2000) suggesting that the human face can serve as a reliable cue when selecting context-specific leaders (e.g., feminine face = tending and befriending = peace leader). Followers also seem to use a categorization approach with multiple levels of discrimination (see Spisak et al., 2012). Followers decide whether in the first-order a person looks like a leader in general and in the second-order relies on context-specific cues for decision-making (e.g., feminine face = peace leader).

A first-order facial cue that appears to generally (and positively) influence the perception of others is attractiveness—known as the “attractiveness halo” (see Moore et al., 2011). Included in this positive halo is leadership endorsement (Verhulst et al., 2010) and it is therefore important to accurately assess how this biasing process favoring attractive leaders operates. Employing a contingent categorization approach provides a useful framework for further clarification. The reason being is that attractiveness is associated with perceived facial health and perceived facial intelligence (see Zebrowitz and Rhodes, 2004) both of which have been argued to be important traits for leadership (e.g., Antonakis et al., 2009; Björklund et al., 2013). Thus, we can split apart the first-order attractiveness halo and search for context-specific second-order effects of health and intelligence, thereby expanding the boundary of understanding for both leadership categorization and context-specific cognitive prototyping.

This approach generates a number of relevant questions regarding implicit leadership processes. For instance, based on an implicit match between contextual requirements and distinct qualities associated with cues of intelligence and health, will leaders who look relatively more intelligent be favored in situations where experience or knowledge is more important and will group members be more likely to follow healthier-looking leaders in physically demanding circumstances? In addition, given that these cognitive contingencies would have developed over the course of human evolution, will they still hold in modern

organizational settings? Signals of health are perhaps exceptionally important in dynamics which traditionally required a leader to exert an increased amount of physical energy such as during intergroup conflict. However, modern competition does *not* necessarily require physical action. That said, it appears that despite such discrepancies competitive environments in business still tend to select for individuals high in risk-taking and testosterone (Sapienza et al., 2008) indicating that the underlying contingency logic and associated leadership prototypes of these coordination challenges remain intact.

In the current paper we work to further our understanding of leadership by activating contemporary versions of the coordination problems described above (i.e., competition vs. cooperation and exploration vs. exploitation) and pairing these group challenges with faces of potential leaders where first-order attractiveness is controlled for and the subcomponents of health and intelligence are independently manipulated. It is clear that over the course of human evolution, the aggressive nature of *competition* had a significant physical component (e.g., Keeley, 1996) and we therefore expect followers to contingently prefer healthier-looking leaders over intelligent-looking leaders. Conversely, maintaining prosocial *cooperation* between groups through tending and befriending strategies such as trust building and empathy is mentally taxing—demanding *both* cognitive and emotional processing (Penner et al., 2005). Thus, in cooperative between-group situations, it is expected that followers will contingently prefer intelligent-looking leaders over healthier-looking leaders. As for exploration vs. exploitation, it is first important to note that the cognitive adaptations driving our exploratory vs. exploitative decision-making are relatively understudied (Cohen et al., 2007) and it is therefore important to approach cautiously. In groups, *exploration* of new resource opportunities traditionally required relatively increased physical output (MacArthur and Pianka, 1966) and as a result we predict that healthier-looking leaders will be preferred. However, ensuring a group stabilizes and maintains consistent exploitation of an established resource requires the utilization of existing knowledge and past experience (e.g., crystallized intelligence; Cattell, 1987) relative to physical ability and we expect intelligent-looking leaders to contingently match this situation. Finally, followers likely prefer leaders to be *both* healthy and intelligent, but by separating these subcomponents one can better understand what is driving the attractiveness halo in leadership decisions and more accurately model its impact on leadership emergence in diverse situations.

MATERIALS AND METHODS

PARTICIPANTS

One hundred and 48 participants (79 males, 69 females, $M_{\text{age}} = 33.1$, $SD = 11.8$) completed an online experiment for financial compensation. The experiment was made using Qualtrics and distributed to Mturk users with Crowdfunder. The original dataset consisted of 191 participants. We deleted participants who did not complete the experiment, participants who failed a simple reading test (“This question tests whether you are reading the questions and answers. Please answer 3”), and participants who failed more than 1 out of 4 manipulation checks (manipulation checks tested

whether participants could identify which scenario they had just answered questions on).

PROCEDURE

The procedure for the experiment consisted of three separate tasks. First, the facial stimuli used for testing were created. Second, business scenarios based on the coordination problems mentioned above were developed. These materials were then combined to run the experiment. Finally, the created faces were rated by two samples on perceived health, intelligence, masculinity, and attractiveness.

Health and intelligence face morph materials

Stimuli were created using Psychomorph (Tiddeman et al., 2001), custom built software for the graphical manipulation of facial photographs. First, we created four base identities, each by combining three individual faces of undergraduate white men who were all clean shaven and had no glasses or visible jewelry. We combined faces such that both perceived intelligence and attractiveness were matched, based on previous ratings of the individual faces ($N = 14$ raters). This procedure ensured that differences between stimuli in perceived health and intelligence were driven exclusively by our transforms and not by idiosyncratic differences between stimuli.

Next, each identity was transformed in apparent intelligence. To this end, high and low apparent intelligence prototypes were created as described in Moore et al. (2011). Briefly, these prototypes were created by regressing ratings of attractiveness, masculinity, health, and perceived age against ratings of perceived intelligence. The faces with the largest positive and negative residuals (i.e., those who were rated as looking much more or less intelligent than predicted by their age, attractiveness, masculinity, and health) were “averaged” using Psychomorph software to create composite high and low perceived intelligence faces. Subsequently, each base identity was transformed in face shape by $\pm 50\%$ of the linear shape difference between the high intelligence and low intelligence prototype, yielding 2 versions of each identity: one high intelligence version and one low intelligence version. Moderate manipulations of the two versions (i.e., high and low intelligence) were also created by reducing the transform to $\pm 25\%$.

Third, we next transformed both the high and low intelligence versions of each identity to be high or low on apparent health. To this end, we manipulated the skin areas of each face to appear lower or higher in carotenoid-associated skin coloration, observed following increased fruit and vegetable consumption (see Whitehead et al., 2012) and reliably perceived as healthy looking (e.g., Stephen et al., 2009). To simulate an increase in health appearance we added 4.35 units of yellowness (b^* in the CIELab color space, see Stephen et al., 2009 for details), subtracted 1.1 units of lightness (L^*) and added 1.4 units of redness (a^*) to all faces. To simulate a decrease in healthy appearance, the reverse manipulation was performed. The levels of positive transform were derived from a previous study, which indicated that on average, this amount of color change was applied to Caucasian faces to make them appear most healthy (see Lefevre et al., 2013). In addition, we created a moderate health transform version, so as

to ensure that the transform would be more closely aligned in magnitude with the two levels of the intelligence transform. To this end, we halved the amount of color added and subtracted, in other words, we added 2.18 units of b^* , subtracted 0.55 units of L^* and added 0.7 units of a^* to each face to create the medium level healthy face. The medium level unhealthy face was created by reversing this manipulation.

To sum up the procedure, facial shape was first adjusted to alter perceptions of intelligence, creating high intelligence (Hi) and low intelligence (Li) versions of the base faces. Next, the coloration of Hi and Li facial images were manipulated to create high health (Hh) and low health (Lh) version. This process yielded four face types (i.e., HiHh, LiLh, HiLh, and LiHh; **Figure 1**). To examine possible thresholds for perceiving difference between health and intelligence we also created medium and strong versions of the four face types by adjusting the transform percentages. Images were then cropped to the outer boundaries of the face. The transforms thus created a total of 32 faces. Four different male composite base faces, of which each had four health/intelligence versions (HiHh, LiLh, HiLh, and LiHh), all of which had a 25% and a 50% transform version ($4 * 4 * 2 = 32$).

Experimental procedure

The next step was to pair the face types with business scenarios based on the four coordination dynamics identified in the introduction (i.e., competition, cooperation, exploration, and exploitation; see Supplemental Materials for the scenarios). The objective was to investigate which subcomponent of attractiveness

(i.e., health or intelligence) would be preferred in each coordination dynamic. To accomplish this, each scenario was presented one at a time with one male base face in all possible paired combinations of the four face types presented below, six combinations in total (e.g., HiHh vs. LiLh, HiLh vs. LiHh). We counterbalanced which male base face was paired with which scenario, and also counterbalanced the order in which the different scenarios and different male base faces were presented. Per scenario, participants thus chose their preferred leader out of two faces (both coming from the same base face but transformed differently) six times. Each participants made 24 (6 combinations * 4 scenarios) leadership decisions, either with a transform level of 25%, or a transform level of 50% (transform level varied between subjects).

The scenario appeared at the top of the screen and the participant was presented with the first pair of faces and asked to vote for the face they would prefer as a leader for the depicted scenario (i.e., forced-choice pairing). Once a decision was made, the next face pair would appear below the scenario and the participant would make another leader choice. This procedure continued until all six paired face combinations had been displayed with the scenario. Then the scenario would switch and the procedure would repeat until a decision for all face combinations were made for all four scenarios. Scenarios, face pairings, and side of the monitor where the face appeared were randomized to control for order effects. Scenario and assigned faces were randomized to control for idiosyncratic effects of any one particular face paired with any one scenario. Following the leadership selection task, participants explicitly rated the faces on perceived health, intelligence, attractiveness, and masculinity (e.g., “This person looks attractive,” 1 = *strongly disagree*, 10 = *strongly agree*). The experimental design was approved by the ethics committee at the VU University Amsterdam. Before the experiment informed consent was obtained and following the tasks participants were thanked and debriefed.

RESULTS

RATINGS OF HEALTH, INTELLIGENCE, AND ATTRACTIVENESS

In order to get some insight into how the faces were perceived, we had all faces rated on health, intelligence, masculinity, and attractiveness, by two samples. All ratings were performed on a scale ranging from 1 (*strongly disagree*) to 10 (*strongly agree*). The first sample ($N = 105$, 69 female/36 male, $M_{age} = 36.46$, $SD_{age} = 12.69$) collected via MTurk performed the face ratings separately before we conducted the actual main study, and thus did not complete any other parts of the experiment (i.e., they did not choose leaders for different scenarios). This first sample originally consisted of 118 participants—those who failed a reading test or a manipulation check (“What gender were faces in this experiment?”) were deleted from the dataset. The second sample consisted of the 148 participants of the actual experiment (who performed the ratings after they had completed the leadership selection task in all four scenarios).

Tables 1, 2 summarize the mean ratings of health, intelligence, attractiveness, and masculinity per manipulation. The ratings in the high health columns of **Tables 1, 2** are the average ratings of perceived health of the two face types with high health transforms (i.e., HiHh and LiHh), while the ratings in the low health

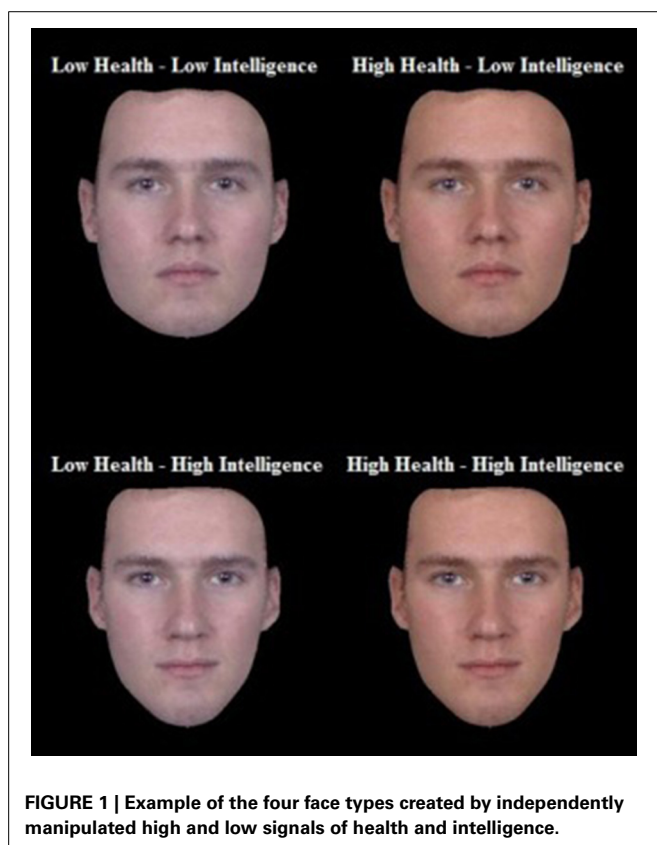


FIGURE 1 | Example of the four face types created by independently manipulated high and low signals of health and intelligence.

Table 1 | Sample 1 (*N* = 105) Ratings of high health vs. low health faces, and ratings of high intelligence vs. low intelligence faces—Means, SDs, *t*-tests, and Cohen's *D*s.

	High Health	Low Health	Difference
Health	6.56 (1.77)	6.28 (1.81)	$t = 3.81, p < 0.001^*, d = 0.37$
Intelligence	6.09 (1.57)	5.88 (1.61)	$t = 4.08, p < 0.001^*, d = 0.40$
Attractiveness	5.34 (1.84)	5.10 (1.91)	$t = 3.53, p = 0.001^*, d = 0.34$
Masculinity	6.60 (1.98)	6.41 (2.13)	$t = 2.91, p = 0.004^*, d = 0.28$

	High Intelligence	Low Intelligence	Difference
Health	6.54 (1.72)	6.30 (1.88)	$t = 2.89, p = 0.005^*, d = 0.45$
Intelligence	6.17 (1.57)	5.80 (1.66)	$t = 4.62, p < 0.001^*, d = 0.28$
Attractiveness	5.36 (1.86)	5.07 (1.92)	$t = 3.51, p = 0.001^*, d = 0.34$
Masculinity	6.41 (2.06)	6.60 (2.07)	$t = -2.35, p = 0.020, d = -0.23$

**p* remains <0.05 after adjusting for multiple comparisons (Bonferroni correction).

columns are the average ratings of perceived health of the two face types with low health transforms (i.e., LiLh and HiLh). The same goes for the high and low intelligence columns—under high intelligence are the average ratings from the two transforms of the high intelligence faces (i.e., HiHh and HiLh), and under low intelligence are the average ratings from the two transforms of the low intelligent faces (i.e., LiLh and LiHi). These scores are the average of the 25% and 50% transforms—if the main analysis shows that transform strength affects how our manipulations influence leader selection, we planned to revisit the ratings separately for the 25% and the 50% transforms. The ratings show that the high health faces are indeed perceived healthier than the low health faces, and that the high intelligence faces are seen as higher in intelligence than the low intelligence faces, as the manipulations intended. However, other cues are also affected by the health and intelligence manipulations. For instance, participants rate the high health and high intelligence faces higher on attractiveness than the low health and low intelligence faces. Additionally, the high health faces are perceived as more masculine than the low health faces, whereas intelligence has the opposite effect—the low intelligent faces are seen as more masculine than the high intelligent faces. Most effects of the health and intelligence manipulations on ratings are of small to medium size (as denoted by Cohen's *D*), with a notable exception of a larger effect of the health manipulation on perceived health in the second sample. A preference for a high health face over a low health face, and a preference for a high intelligence face over a low intelligence face, may thus be explained by a combination of subjective perceptions of health, intelligence, masculinity, and attractiveness.

Table 2 | Sample 2 (*N* = 148) Ratings of high health vs. low health faces, and ratings of high intelligence vs. low intelligence faces—Means, SDs, *t*-tests, and Cohen's *D*s.

	High Health	Low Health	Difference
Health	7.37 (1.59)	6.49 (2.01)	$t = 8.17, p < 0.001^*, d = 0.67$
Intelligence	7.00 (1.65)	6.81 (1.77)	$t = 2.47, p = 0.015, d = 0.20$
Attractiveness	6.14 (2.01)	5.63 (2.15)	$t = 5.95, p < 0.001^*, d = 0.30$
Masculinity	7.34 (1.76)	7.03 (1.95)	$t = 3.84, p < 0.001^*, d = 0.32$

	High Intelligence	Low Intelligence	Difference
Health	7.15 (1.75)	6.70 (1.99)	$t = 3.34, p = 0.001^*, d = 0.27$
Intelligence	7.09 (1.80)	6.71 (1.79)	$t = 3.13, p = 0.002^*, d = 0.26$
Attractiveness	6.15 (2.18)	5.63 (2.20)	$t = 3.69, p < 0.001^*, d = 0.30$
Masculinity	6.98 (1.97)	7.39 (1.96)	$t = -3.11, p = 0.002^*, d = -0.26$

**p* remains <0.05 after adjusting for multiple comparisons (Bonferroni correction).

It is also interesting to consider the different perceptions of the two opposed-combination faces, i.e., the low intelligence but high health face (LiHh), and the high intelligence but low health face (HiLh). First, the high health but low intelligence face is perceived as more masculine in both samples [sample 1 – $t_{(104)} = 3.60, p < 0.001, d = 0.35$, sample 2 – $t_{(147)} = 4.91, p < 0.001, d = 0.40$]. Second, while the low health but high intelligence face is rated more intelligent than the low intelligence but high health face in both samples [sample 1 – $t_{(104)} = -2.03, p = 0.045, d = -0.20$, sample 2 – $t_{(147)} = -1.22, p = 0.225, d = -0.10$], the difference is only significant in the first sample. Third, the high health but low intelligence face is rated more healthy in the second sample, but there is no difference in ratings between the two face types concerning health ratings in the first sample [sample 1 – $t_{(104)} = 0.35, p = 0.730, d = 0.03$, sample 2 – $t_{(146)} = 2.42, p = 0.017, d = 0.20$]. Finally, there is no difference in perceived attractiveness between the high health but low intelligence face, and the low health but high intelligence face (sample 1 and 2 – $t < 1, p = \text{ns}$). A preference for one of these opposed-combination face types over the other will thus not be driven by a difference in attractiveness, but may be guided by perceptions of health, intelligence, and masculinity.

PREDICTING LEADER SELECTION BY HEALTH AND INTELLIGENCE

To analyze the data we utilized a version of the Bradley-Terry Model which uses a log-linear approach to account for the dependence between multiple paired comparisons from a given set of objects (Dittrich et al., 2002). This statistical technique allowed us to analyze voting preferences for each face-type separately (i.e.,

HiHh, LiLh, HiLh, and LiHh) while accounting for the interdependency of multiple paired comparisons within participants. Subsequently, we were able to generate a 2×2 design to investigate main effects of intelligence (high vs. low) and health (high vs. low). We combined the 25% and 50% transforms for the analyses, with the plan to revisit the two transform levels separately should the analysis show that transform level affects results.

On average (taken across all 4 scenarios), health had a significant positive effect on leader selection [Wald $\chi^2_{(df=1)} = 136.30, p < 0.001$], as did intelligence [Wald $\chi^2_{(df=1)} = 26.51, p < 0.001$]. There were no significant main effects of participant gender [Wald $\chi^2_{(df=1)} = 2.587, p = 0.108$], scenario [Wald $\chi^2_{(df=1)} = 0.005, p > 0.999$], or manipulation strength [Wald $\chi^2_{(df=1)} = 0.015, p = 0.901$] on leader selection.

Health was a significant predictor of leadership ratings in all four scenarios; in cooperation [Wald $\chi^2_{(df=1)} = 22.01, p < 0.001$], competition [Wald $\chi^2_{(df=1)} = 38.00, p < 0.001$], exploration [Wald $\chi^2_{(df=1)} = 32.42, p < 0.001$], and exploitation [Wald $\chi^2_{(df=1)} = 36.10, p < 0.001$]. On the other hand, intelligence led to an increase in leader selection in the exploration condition [Wald $\chi^2_{(df=1)} = 24.06, p < 0.001$], along with an increase in the cooperation condition [Wald $\chi^2_{(df=1)} = 19.24, p < 0.001$], but had no positive effect on leader selection in the competition [Wald $\chi^2_{(df=1)} = 0.18, p = 0.674$] or exploitation conditions [Wald $\chi^2_{(df=1)} = 0.73, p = 0.434$]. Overall, health thus had a positive effect on leader selection in all four scenarios, while intelligence only showed this effect in the exploration and cooperation conditions.

Because we summed across the medium and strong manipulation in the above analyses, we wanted to make sure that there were no interactions of manipulation strength with intelligence or health on leader selection; a significant interaction would imply we need to look at the medium and strong manipulation conditions separately. We performed another analysis across all 4 scenarios together, adding the interaction terms (manipulation strength * intelligence, and manipulation strength * health) to the model. There was no significant interaction between health and manipulation strength on leader selection [Wald $\chi^2_{(df=1)} = 0.019, p = 0.890$], and no interaction between intelligence and manipulation strength on leader selection [Wald $\chi^2_{(df=1)} = 1.089, p = 0.297$].

Health vs. intelligence

We then wanted to see whether one cue had a stronger effect on decision making than the other. Health was the stronger predictor for the exploration scenario [$t_{(148)} = 2.241, p = 0.013$], the exploitation scenario [$t_{(148)} = 4.336, p < 0.001$], and the

competitive scenario [$t_{(148)} = 5.099, p < 0.001$]. There was no significant difference in predictor strength between health and intelligence in the cooperation scenario. [$t_{(148)} = 1.306, p = 0.192$]. Finally, health had an overall stronger effect on leadership ratings than intelligence [$t_{(148)} = 7.027, p < 0.001$].

Comparing predictors across scenarios

We next tested whether health and intelligence had a stronger effect in one scenario relative to another. We were interested in two particular comparisons: the effects of health and intelligence in the competitive vs. the cooperative scenario—tested by combining the data of these two scenarios and testing the interaction between health/intelligence and scenario on leader selection—and the effects of health and intelligence in the exploration vs. exploitation scenario—again, tested by combining the data of these two other scenarios and testing the interaction between health/intelligence and scenario on leader selection. As expected, intelligence was a stronger predictor in the cooperation scenario than in the competition scenario [Wald $\chi^2_{(df=1)} = 18.796, p < 0.001$]. However, contrary to expectations, intelligence was a stronger predictor in the exploration scenario than in the exploitation scenario [Wald $\chi^2_{(df=1)} = 12.154, p < 0.001$]. Results also showed that health was an equally strong predictor in the cooperation vs. the competition scenario [Wald $\chi^2_{(df=1)} = 1.213, p = 0.271$], and also did not differ in strength in the exploration vs. the exploitation scenario [Wald $\chi^2_{(df=1)} = 0.382, p = 0.537$].

Table 3 gives an overview of how often participants chose a high health face over a low health face, and how often participants chose a high intelligent face over a low intelligent face, across all trials. In line with the main results, these percentages show that while there are some scenarios where high intelligence faces are only favored slightly above chance (i.e., competition and exploitation), the high health faces are always preferred well above chance.

DISCUSSION

To summarize, health and intelligence both influenced leader selection, but the health cue (facial color) was clearly more influential than the intelligence cue (facial structure) in our scenarios. Health was an influential cue across all scenarios, while intelligence only had an effect in half of the presented scenarios. Overall, health was a significantly stronger predictor of leader selection than intelligence, except for in the cooperation context, where intelligence and health were predictors of similar strength. Our results indicate a stronger general preference for health vs. intelligence when selecting leaders across context.

As for our hypotheses, we found mixed support. In leader selection, cues of intelligence, as expected, were preferred more often in cooperation vs. competition whereas perceived health

Table 3 | Percentages of choices for high health faces over low health faces and choices for high intelligence faces over low intelligence faces.

	Overall (%)	Competition (%)	Cooperation (%)	Exploration (%)	Exploitation (%)
High Health wins from Low Health	69.4	68.7	67.3	71.9	69.8
High Intelligence wins from Low Intelligence	63.8	53.7	70.1	73.1	58.0

was significantly favored across all four coordination problems. As for exploration vs. exploitation, to date, it has had limited research attention in the behavioral and brain sciences (Cohen et al., 2007) and future research may provide insights into whether our initial predictions regarding prototypical contingencies are accurate. Overall, our findings suggest that although intelligence may be important for leadership in certain circumstances, health (represented by facial coloration based on increased carotenoid pigmentation) appears to dominate decision making in all contexts of leadership. In terms of categorization, this means that leaders relatively high in perceived intelligence have a second-order, contextually-bound advantage—such as in times requiring between-group cooperation—whereas healthier-looking leaders perhaps have a context-general, first-order advantage across a diverse landscape of leadership situations. This aligns with recent work suggesting that the activation of “disease concerns” in the environment exacerbates the voting tendency to prefer attractive political candidates. Attractiveness is in part driven by cues to health and healthy leaders are likely to be exceptionally important when disease threatens the viability of the group (White et al., 2013). Adding to this, our data indicates that with or without specific pathogen threats health is generally an important factor when selecting leaders.

While the facial health and intelligence manipulations predictably affected participants’ ratings of perceived health and intelligence, it is important to note that the manipulations also affected perceptions on other dimensions, such as attractiveness and masculinity. It is apparent from our results that our transforms did change perceptions of attractiveness. However, this was the objective of our research (i.e., to assess which specific dimensions of attractiveness affect leadership perception). We also note in our results that perceptions of attractiveness did *not* significantly differ between high intelligence but low health and low intelligence but high health faces (i.e., HiLh vs. LiHh). Furthermore, while our transforms did also affect perceived masculinity this effect likely does not entirely explain our main effects of health and intelligence on leadership choice for the following reason: Increased health and increased intelligence positively affected leadership perceptions; however, masculinity ratings increased in the high health transform but *decreased* in the high intelligence transform. Also, while we can conclude from our data that increased facial carotenoid pigmentation—a marker for physical health—increases whether someone is preferred as a leader, we have to be more careful with drawing strong conclusions about how facial intelligence affects leader preference. Whereas facial coloration is an objective cue for health, our intelligence manipulation is based on subjective perceptions of low and high intelligence. This subjective intelligence transform may actually be a reflection of other objective cues which were more salient to the participants such as, in this case, facial masculinity (i.e., our low intelligence faces may actually have more masculine features than the high intelligence faces). Thus a better understanding of the relationship between facial masculinity and perceived intelligence is an important next step for drawing a sound conclusion about facial intelligence and leadership preferences.

The ratings of faces high in one positive cue but low in another positive cue—i.e., HiLh vs. LiHh—have additional implications.

The ratings from two separate samples suggest that picking up on a high health cue (facial coloration) seems more difficult when the facial structure is characteristic of low intelligence, and vice versa, picking up on cues for high intelligence seems more difficult when there is a clear competing cue for low health. However, when a face has low intelligence combined with high health facial coloration, perceptions of masculinity are particularly enhanced. These results demonstrate how a facial cue can have different effects when combined with other cues, and that novel perceptions may arise from a specific combination of cues—an interesting avenue for future research.

Like much previous research, our results demonstrate that morphological cues can guide decision making when it comes to leadership. From an organizational science perspective, this means that, for instance, leadership succession planning, external hiring of managers and executives, and general willingness to follow a leader are likely biased by a variety of such cues. We must then account for these biases and work with or around such cognitive shortcuts. As an example, a relatively healthy-looking leader may have a better chance of gaining sufficient levels of followership investment to initiate change. On the other hand, a potential leader who looks relatively less healthy may be overlooked even if they are better suited for the job—the difference between emergence and effectiveness.

There are also a number of limitations to the current study that deserves mentioning. First, leadership selection for the exploration-exploitation dilemma needs further development. Continued effort is necessary to identify and match the contingent leadership traits associated with both exploration and exploitation. Second, intelligence is a somewhat broad concept. The difference between fluid and crystallized intelligence (i.e., the ability to develop novel solutions to novel problems vs. the ability to use acquired knowledge, skills, and experience; e.g., Cattell, 1987) are perhaps best suited for exploration vs. exploitation, respectively. Future work should investigate perceptual differences between these types of intelligence. Existing research on the developmental differences between fluid vs. crystallized intelligence (e.g., Horn and Cattell, 1967) suggests that facial cues of age may serve as a proxy when perceptually attributing these two types of intelligence (i.e., young = fluid and old = crystallized) and, as a consequence, this could create a contingent match between young exploration leaders and old exploitation leaders. Further use of the contingent categorization approach can provide a framework for constructing a network of first- and second-order cues and how they shift in importance across context. Finally, the scenarios used in this study, designed to represent situations characterized by cooperation, competition, exploration, or exploitation, had some specific details which may have affected decision making. For instance, the between group competition scenario may have elicited a particularly individual-level focus (the situation concerned everyone, but “especially you”), while the between group cooperation scenario may have also enhanced stronger feelings of group identification (the focus here is on “your colleagues,” and not on “especially you”) due to wording of the scenarios. Replication of our main results with different scenarios is necessary to test how robust these results are.

A modern version of implicit leadership categorization that contingently considers the dynamics of fitness-relevant situations is an effective approach for understanding why certain leaders emerge when they do. Our results demonstrate that when one attempts to split apart perceived facial attractiveness into second-order categories they immediately discover a general preference for health, characterized by facial coloration, when selecting leaders. Thus health is a first-order categorization variable that initially biases us to perceive a potential candidate as a leader in general or *not*. This adds an attractive twist to research on beauty and its impact on followers.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://www.frontiersin.org/journal/10.3389/fnhum.2014.00792/abstract>

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A case for neuroscience in mathematics education

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Mathematics lies at the heart of science and technology impacting on the economic performance of societies since ancient times (OECD, 2010). At the level of individuals too, the development of mathematical proficiency appears correlated with individual development and career prospects across a wide range of professions (RAND Mathematics Study Panel and Loewenberg Ball, 2003). It does not come as a surprise to realize that mathematics education traces back several thousand years. However, still very little is known about the fundamental principles of how individuals learn mathematics and at which age education should start. The issue is far from trivial as it is commonly assumed that mathematics is a special subject area perhaps requiring specific motivation, interest and teaching methods in order to be learned efficiently (National Council of Teachers of Mathematics, 2000). Here, we are attempting to make a case for neuroscience methodology as a modern tool capable of contributing to the debate, where a special but not exclusive emphasis is on brain development. Note that for the purpose of this opinion paper, neuroscience is essentially equated with magnetic resonance imaging (MRI), as MRI based approaches currently constitute mainstream research in this field of study according to our understanding.

Developmental studies are increasing our understanding of maturational changes in the human brain (Blakemore, 2012). In particular, structural MRI studies reveal an increase in white matter volume during childhood and adolescence suggesting an increase of connectivity in the developing brain (Giedd and

Rapoport, 2010). Interestingly, gray matter volume is characterized by an inverted-U shaped curve peaking at different age in different brain regions (Giedd et al., 1999), which suggests a non-linear, heterogeneous trajectory where proficiencies mature at different times and speeds dependent on which brain regions are most important for a given skill. For example, it is commonly agreed that the intuitive sense of number or quantity is an early ability that can be observed already in infants and that can predict mathematical proficiency later in life (Starr et al., 2013).

In addition to structural studies, functional neuroimaging provides further insight relevant to mathematics education. For example, a developmental functional MRI study of mental arithmetic has shown that the pattern of brain activation changes with student age (Rivera et al., 2005). Importantly, these age-related changes were associated with functional maturation rather than alterations in gray matter density. Moreover, functional studies can help to elucidate the role of specific brain regions in mathematical processing. For example, it has been suggested that the intuitive understanding of quantities is associated with activity in the intra-parietal sulcus (Dehaene, 1997) and, more generally, parietal cortices that are involved in various mathematical tasks from number comparison to complex processing such as proportional and deductive reasoning (e.g., Kroger et al., 2008; Vecchiato et al., 2013). However, additional studies are needed to establish links between development of brain structures and their functional maturation.

Many neuroimaging studies have focused on development of arithmetic skills in children and adults (for a review see Zamarian et al., 2009). Again, different parts of the parietal cortex, such as bilateral intra-parietal sulcus and left angular gyrus, are shown to have a crucial role in mental calculations (e.g., De Smedt et al., 2011; Grabner et al., 2013). In contrast, other brain areas appear to mature relatively late, such as prefrontal association areas thought to be involved in mathematical cognition and other higher-order processes developing throughout childhood and adolescence (Blakemore, 2012). Such insight might shed some light on the transition from concrete arithmetic to the symbolic language of algebra, where students have to develop abstract reasoning skills that enable them to generalize, model, and analyze mathematical equations and theorems (e.g., Qin et al., 2004; Lee et al., 2007; Anderson et al., 2012).

Ultimately, mathematical proficiency will require the coordinated action of many brain regions as exemplified by an influential model of algebraic equation solving (Anderson et al., 2008). Based largely on functional MRI studies of brain activation, the model stipulates distinguishable functional modules that map onto anatomically separate brain regions. For example, a visual module that extracts information about the equation is associated with the fusiform gyrus. An imagery module holding a representation of the equation and performing transformations on the equation is located in posterior parietal cortices. A module responsible for retrieval of previously learned algebraic rules is associated with the left prefrontal cortex. Such models are

important as they help to devise methods to track mental states in individuals solving algebraic equations (Anderson et al., 2012). Thus, neuroscience could conceivably help to better understand the relationship between biological brain development and the development of the human capacity for mathematical cognition mediated by educational experience (Royer, 2003).

More specifically, longitudinal studies of changes in brain activation with practice in equation solving (Qin et al., 2004) confirm what educators have known since ancient times—continued exercise in problem solving is very important. This is non-trivial as such studies offer independent insight about the time needed for practice to yield robust effects on brain activity. In principle, such changes in brain activity can be used to compare different teaching methods at the neuronal level. For example, a study investigating the neuronal correlates of algebraic problem solving by two different methods that are taught in schools in Singapore (Lee et al., 2007) suggested that the more symbol oriented a method was, the higher was the load on the attention system of the brain, which might help to explain why symbolic manipulations are usually considered difficult.

In this context, a number of neuroimaging and neuropsychology studies have demonstrated that the relationship between number and space processing is reflected in the organization of parietal circuits assumed to be associated with these skills (Hubbard et al., 2005). Thus, a better understanding of number and space processing in the brain might conceivably yield guidelines informing teachers how to develop both concepts in parallel. Developing skills in parallel might go further than numbers and space, as there is emerging evidence that pattern recognition that is important in algebraic reasoning (Susac et al., 2014) is closely related to visual attention and visual brain regions (Anderson et al., 2008).

Research efforts have also focused on dyscalculia, a specific learning difficulty in understanding numbers and operations with numbers. Mathematics teachers and parents should be aware that the prevalence of developmental dyscalculia is about 5–7% (Butterworth et al.,

2011). Only joint effort of mathematics educators and neuroscientists can lead to better understanding of developmental trajectories of dyscalculia and possible positive effects of early diagnosis and interventions. There is growing evidence that insight gained from neuroscience can inform computer-assisted interventions. For example, neuroscience based computer games have been shown to improve the number comparison ability in children with low numeracy skills (Wilson et al., 2006; Räsänen et al., 2009).

In particular, The Number Race is an adaptive software program designed for teaching number sense to young children aged 4–8. It trains children on the entertaining numerical comparison task developing counting and simple arithmetic skills (1-digit addition and subtraction). It is designed to strengthen links between symbolic and non-symbolic representations of number (concrete sets, digits, and number words). Attention and motivation of children is maintained by adjusting the level of task difficulty so that the success rate stays at around 75%. The rewarding environment may help with other problems, which can be associated with dyscalculia such as attention deficit and hyperactivity disorder (ADHD). Moreover, The Number Race and similar computer-assisted interventions can advance mathematics learning and achievement also in typically developing children (Griffin, 2004).

This game is based on current understanding of the neural circuits involved in numerical cognition, in particular the parietal cortices (Dehaene et al., 2003). However, a caveat is in order. A recent review revealed that only 3 out of 20 mathematics intervention software packages reported the use of neuroscience research as a tool in intervention development (Kroeger et al., 2012). Moreover, the majority of programs reviewed (15/20) lacked any empirical validation, preventing teachers from making informed decision on implementation of such programs in the classroom. Evidently, further empirical, peer-reviewed research is needed to evaluate existing software packages and to guide further developments.

There are challenges. From the early days of educational neuroscience, there have been skeptical views on the possibility

of direct classroom application of neuroscientific data (as a “bridge too far” in the words of Bruer, 1997). The increasing public visibility of neuroscience has led to what some scholars call neuromyths, i.e., certain beliefs turned into facts because of having been expressed ever so often through virtually all communication channels, such as the view that some people are left-brained and some are right-brained, or that humans use only 10 percent of their brains. Worryingly, unsubstantiated, neuromyth based teaching and learning methods are in use or have been advertised to teachers and education professionals (Goswami, 2006). This reinforces the notion that insight obtained from high-quality neuroscience must be presented in a non-specialists form to mathematics educators, parents, and politicians so that informed decisions on educational issues can be made (building “bridges over troubled waters” in the words of Ansari and Coch, 2006).

In summary, we are inclined to argue that neuroscience can eventually impact on mathematics education by providing hints as to (a) what mathematics curriculum should be provided at which age, (b) which skills should be developed in parallel, and (c) how to reliably assess the effects of early diagnosis and interventions in the case of specific learning disabilities. Research on the timing of maturation of brain areas involved in mathematical cognition appears particularly important as some economic models propose that earlier economic investment in education, i.e., in preschool programs, always lead to larger economic return than later investments (Cunha and Heckman, 2007). There is neuroscientific evidence, however, that indicates continuing development of executive functions throughout childhood and adolescence. Thus, educational policy makers should be aware of the current neuroscience findings when deciding on the timing of educational investment (Howard-Jones et al., 2012).

We believe that neuroscience will not and should not obviate behavioral and psychometric studies that provide independent insight facilitating the development of new experimental paradigms for neuroimaging studies. One should be clear that neuroscience findings have not made it directly into the mathematics classroom

at present. However, this should not deter research and we would like to urge investigators not only to continue but also to extend their study of educational neuroscience. Groundbreaking thoughts take time to mature and to find direct applications, as in the case of Carnot's thermal efficiency theorem. As Carnot's work set up a framework for design of more efficient engines that were constructed decades later, neuroscience research today is setting the scene for future developments in mathematics education.

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The role of attachment styles in regulating the effects of dopamine on the behavior of salespersons

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Two classic strategic orientations have been found to pervade the behavior of modern salespersons: a sales orientation (SO) where salespersons use deception or guile to get customers to buy even if they do not need a product, and a customer orientation (CO) where salespersons first attempt to discover the customer's needs and adjust their product and selling approach to meet those needs. Study 1 replicates recent research and finds that the Taq A1 variant of the *DRD2* gene is not related to either sales or CO, whereas the 7-repeat variant of the *DRD4* gene is related to CO but not SO. Study 2 investigates gene \times phenotype explanations of orientation of salespersons, drawing upon recent research in molecular genetics and biological/psychological attachment theory. The findings show that attachment style regulates the effects of *DRD2* on CO, such that greater avoidant attachment styles lead to higher CO for persons with the A2/A2 variant but neither the A1/A2 nor A1/A1 variants. Likewise, attachment style regulates the effects of *DRD4* on CO, such that greater avoidant attachment styles lead to higher CO for persons with the 7-repeat variant but not other variants. No effects were found on a SO, and secure and anxious attachment styles did not function as moderators.

Keywords: attachment styles, *DRD2*, *DRD4*, customer orientation, sales professionals

INTRODUCTION

Organizations are especially interesting social environments as they differ from everyday social groups such as found in family life, friendship, or hobby clubs. Within organizations, people undertake both long and short-term strategies to fit into their group and interact with others outside their group to meet the needs of their organization. Consistent with the emerging organizational cognitive neuroscience (OCN) framework (Senior et al., 2011), we seek to understand the biological processes—hard-wired neurological and endocrine processes conserved over millions of years in different species—that might help us understand how people operate in organizations, particularly those whose job requires them to deal with others outside their organization to meet their organization's mission. Specifically, we seek to explain the strategic orientation that salespersons take in their relationship with customers. Two fundamental, recently studied orientations are the sales orientation (SO) and customer orientation (CO) (Bagozzi et al., 2012). A SO involves the use of deception and guile by a salesperson to get customers to buy even if they do not need a product. A CO characterizes a salesperson's attempts to first discover the customer's needs and then adjust their product and selling approach to meet those needs. Sometimes the terms hard and soft selling are used to describe these orientations, where the latter generally leads to long-term relationships, whereas the former, given its one-sided exploitive nature, is typically short-lived.

Hard-wired neurological and endocrine processes, which undergird phenotypical selling and COs, provide ultimate explanations that define evolutionary fit outcomes. In developing our

hypotheses and interpreting findings, which entail cross-level gene and phenotype descriptions, we draw upon molecular genetics research to ground our studies. Our approach is guided by two aims recently recommended in the literature, namely, (1) to replicate recent findings so as to show the relevance of candidate genes and set up the need to explore gene-phenotype interactions to explain strategic orientations of salespersons on the job (Munafò et al., 2008), and (2) to give special attention to definition and measurement of explanatory phenotypes and develop a theory accounting for how they moderate the effects of candidate genes on strategic orientations (Munafò et al., 2008).

Originally introduced in 1982 (Saxe and Weitz, 1982), the concepts of sales and COs and their measurement have found currency across many studies, where more than 30,000 salespeople have been investigated (Franke and Park, 2006). Nearly all of this research has been conducted at the psychological level of investigation, with self-reports as measures of independent and dependent variables. The sole exception appeared in a recent study by Bagozzi et al. (2012) (Study 2), where the *DRD2* A1 was found to be marginally associated with a SO ($p = 0.07$), and the *DRD4* 7R⁺ allele was found to be significantly associated with a CO ($p = 0.04$). The rationale for the former finding was that salespeople carrying the A1 variant should have a reduced response to dopamine, seek greater stimulation, and favor greater immediate gratification than carriers of the other variants, and therefore should be inclined to press customers into yielding without fully taking into account their needs. In contrast, the rationale for the latter finding was that salespeople carrying the 7R⁺ variant should be more curious and open to opportunity

recognition, greater risk takers, and more inclined to search for unique needs of customers and put greater effort into finding and constructing a mutually beneficial match between buyer and seller.

A shortcoming of the study by Bagozzi et al. (2012) is that finding the main effects of candidate genes might occur by chance and reflect a false-positive outcome. To guard against prematurely placing too much credence on the findings in Bagozzi et al. (2012), it would be advisable to conduct replications on different subjects operating in different organizational environments. Further, discovery of the effects for individual candidate genes may be unrealistic in that factors other than genes may be of equal or greater importance or may be conditional on when and how genes function, if they function at all, in real-world job environments under naturalistic conditions. Therefore, our second aim is to develop a meaningful phenotype to explore a plausible gene \times phenotype interaction effect on salesperson job orientation in the field. The phenotype chosen was the biological/psychological theory of attachment.

The OCN perspective seeks to uncover the role of higher-order psychological concepts in translational research by explicating hard-wired biological mechanisms and in doing so deepen and even change the measurement and functioning of these concepts (Senior et al., 2011). The challenge with developing strong hypotheses is that most studies in genetics are more on patients and less on healthy people, let alone people who operate in professional settings. In this regard, the *DRD2* ("reward or reinforcement gene") and *DRD4* ("impulsive gene") are known as risk genes, meaning that they are linked with such non-desirable phenotypes as addiction or impulsivity (e.g., Noble, 2000; Eisenberg et al., 2007; Green et al., 2008). Given the differential sensitivity hypothesis, which suggests that in different environments a particular gene might have opposite effects (Belsky et al., 2009), carriers of certain alleles of the *DRD2* or *DRD4* might actually thrive in certain environments, rather than necessarily exhibit the risk factors associated with clinical populations. Such a perspective might help us make better predictions and lead to better understanding of phenotypes and their effects. In what follows we explore the pathways in which *DRD2* and *DRD4* are expressed, and we investigate how polymorphisms of these genes regulate these pathways differently under the differential influence of the attachment phenotype.

Consequently, we investigate the moderating role of attachment, where we also examine a type of differential sensitivity and challenge the received view in the literature. Attachment theory arose out of clinical and cross-cultural research by Bowlby (1988) and Ainsworth (1991). A central claim is that young children develop stereotypical interpersonal styles because of relationships with early caregivers, typically the mother. Three distinct patterns tend to develop: anxious, avoidant, and secure. The anxious style is marked by the tendency to seek support from an attachment figure, to worry about being rejected, to harbor doubts about one's self-efficacy, to have low self-esteem, to crave attention and closeness, to feel vulnerable and helpless, and to possess a negative self-model, while being generally positive toward others because of a desire for support and protection. The avoidant style is characterized by a low need to feel close to others, a tendency to

seek independence and self-reliance, and a propensity to focus on positive features of the self and downplay negative ones to build a positive self-model, while being dismissive or mistrustful of others. The secure style is distinguished by a positive self-image and relative openness and trust in relationships with others. Considerable evidence shows that attachment styles formed early in life persist to influence adult behavior (Mikulincer and Shaver, 2007).

Recent research with adults finds that the secure attachment style is the most functional across a wide variety of relationships. For example, consumer behavior research finds that people with secure, as opposed to anxious or avoidant, attachment styles form positive relationships and experience positive outcomes in service settings (e.g., Mende and Bolton, 2011). Research with employees in organizations shows that workers with avoidant and anxious attachment styles are less supportive in helping colleagues (Geller and Bamberger, 2009). We would argue, consistent with research with adults in family and romantic relationships (e.g., Mikulincer and Shaver, 2003, 2007), that the secure attachment style should be functional in everyday consumer behavior because consumers seek to find products that meet personal needs, and initial openness and trust when facing sellers should be conducive to meeting personal needs, whereas anxious or avoidant styles would interfere with the discovery of desired requisites. Likewise, within organizational boundaries, workers function best when cooperation and trust flourish and they strive to fit in and work together on common goals. Here a secure attachment style should promote such endeavors, whereas anxious and avoidant styles should interfere or lead to disharmony.

In contrast to research with consumers and workers *within* organizations, and opposite to predictions of attachment theory in romantic and family contexts, we argue that the secure attachment style will not be more functional than other attachment styles for salespersons, but rather the avoidant style will be most conducive to successful exchanges. This seeming paradox is based on the contingent role that the attachment phenotype plays in the unique context of business-to-business selling. Salespersons in such contexts function in decidedly *inter*-organizational environments where they venture away from the home organization to negotiate deals inside the buyer's organization. This not only weakens felt normative and peer pressure from the home organization, but exposes the seller to greater pressure from buyers in a more vulnerable setting, and leads to an interpersonal environment with more uncertainty, ambiguity, and tension than typically found in intra-organizational or personal relationships. Somewhat similar psychological tensions occur for ambassadors, diplomats, and inter-mediators in government and similar settings.

In a business-to-business context, informal norms and company policies by both seller and buyer firms typically caution, and even dictate and sanction, against the development of intimate or overly personal relationships (Anderson and Jap, 2005). Rather, buyer and seller are required to conform to professional rules of decorum and propriety. Codes of conduct and ethical guidelines govern personal involvement, fraternization, leaking of corporate information, and standards of behavior. Coupled with legal and moral issues concerning sexual harassment, bribery, kickbacks,

and related topics, such work guidelines place real restrictions on the nature of social contact between sales representatives and buyers and color transactions. In addition, sales representatives operate as organization-boundary spanners and engage in such proactive behaviors as seeking new customers and making autonomous decisions when negotiating prices, especially in business-to-business contexts, all of which require sales representatives with an ability to behave efficaciously during interactions with customers (Crant, 1995).

These norms and expectations lead us to propose that avoidant styles are particularly suited for sales representatives in such relationships in business-to-business contexts. It is fruitful to conceive of attachment styles as working cognitive models on how one regards others and the self in social relationships in terms of the support one can give or get in times of need. Attachment styles are mental representations of person-person transactions that motivate one to seek protection or help from others in interpersonal relationships, to the extent that there is a threat or danger (Mikulincer and Shaver, 2003, 2007). Research shows that persons with avoidant attachment style prefer to hold a certain emotional distance from interaction partners to be able to keep the initiative and behave proactively (see Mikulincer and Shaver, 2003; Ein-Dor et al., 2010). Arguably, in common business-to-business settings, policies, and norms require that sales representatives uncover the needs of customers, offer solutions, and achieve commercial results. At the same time, persons with avoidant styles tend to be self-reliant (see Mikulincer and Shaver, 2003; Richards and Schat, 2011), which is a useful trait in sales representatives who operate in demanding inter-firm environments and are often physically away from both the home organization and its social support. Although some people are both high in avoidance and anxiety (termed in the literature, “fearful avoidance”), Mikulincer and Shaver (2003, p. 70) note that such persons are “less likely to arise in normal samples of college students and community adults” and are more common “in samples of abused or clinical samples.” Thus, the avoidant attachment style, where social anxiety is not a deficit, is consistent with modern characterizations of business relationships. Successful business-to-business sales representatives need to be sufficiently independent and detached, self-reliant, and not deterred by anticipatory anxiety to function well in such contexts (which tends to occur when representatives ask commitments of customers or when they have to close a deal; Vinchur et al., 1998; Richards and Schat, 2011). These conditions fit the avoidant attachment style well.

The secure attachment style is less conducive to the demands on sales representatives in business-to-business contexts. Researchers characterize the secure style as one where the person exhibits “comfort with closeness” and intimacy (Mikulincer and Shaver, 2003, p. 9). Such an orientation is not largely an asset in formal business relationships because buyers and sellers realize that there is potential for tension between the goals of buyer and seller organizations. Also, give and take are integral parts of the relationship, as both parties are required to meet the requisites of their home firms, which often do not fully coincide with the other firm’s. Intimacy or comfort with closeness may even interfere with interactions in some business relationships. In addition, it is possible for employees to be too

secure and not motivated as much by “the hunger to make a sale” or “the fear of failure,” whereas a person who is avoidant in orientation is more likely to be more motivated. The avoidant style places emphasis on business goals, not personal relationship ones, *per se*, although goals can be met mutually in business-to-business contexts, and thereby promoted largely when a CO vs. a SO is pursued. This is especially salient in inter-organization relationships.

The anxious attachment style also seems not to fit business-to-business settings as well as the avoidant style. Preoccupation with the fear of rejection or failure to make a sale, or “a strong need for closeness, [and] worries about relationships,” as found for anxious attachment style persons (Mikulincer and Shaver, 2003, p. 69; see also Ein-Dor et al., 2010, p. 134), would seem to lead sales representatives to work too hard to elicit immediate support and even affection from customers, which draws attention away from exploring via conversation the needs of buyers and then presenting a commercially viable solution to meet those needs and close the sale. The avoidant style should entail less disruptive and more realistic coping with fear or anxiety (e.g., Ein-Dor et al., 2010, p. 134; Richards and Schat, 2011).

The avoidant attachment style thus seems to strike a balance between the secure and anxious styles. To the extent that avoidant attached salespeople remain self-confident, they should abstain from relying too much on trust in others, meaning that they will retain a certain amount of self-reliance, spontaneity, and initiative to make sure customers understand offers and respond accordingly. The avoidant attachment style salesperson is therefore neither too secure nor too anxious but rather reflects a realization that selling to business customers is more rooted in a rational or professional relationship than a personal one *per se*.

In sum, we hypothesize that the avoidant attachment style, but not the anxious or secure, should function as the best moderator of the effects of the *DRD2* and *DRD4* genes on CO. How this happens also invokes differential sensitivity.

GENETIC STUDY 1

The two genes, *DRD2* and *DRD4*, although often perceived as risk genes, might turn out to be functional in a selling context (Goodman, 2008; Tripp and Wickens, 2009). Both genes code for receptors for dopamine (a catecholamine), which is known to modulate synaptic transmission, especially in the cortex and striatum (Tritsch and Sabatini, 2012). Specifically, *DRD2* is mainly expressed in the ventral striatum and thus affects instrumental learning and conditioning, whereas the *DRD4* is mostly expressed in the prefrontal cortex (PFC) and affects how people process information and engage in self-regulation. These mechanisms for dopamine (D) modulation are vast, operating in pre-synapsis neurotransmitter release (e.g., vesicular release machinery), in post-synapsis detection of neurotransmitter detection (e.g., modulating membrane insertion), and synaptic integration and excitability (e.g., modulating ion channels) (Tritsch and Sabatini, 2012). Therefore, as Green et al. (2008) suggest, it is too simplistic to relate a specific gene polymorphism to a specific region of the brain, given the huge connectivity between the brain nuclei but also the great complexity of neuromodulation. Rather than one or a small number of regions

of the brain involved, it is more realistic to expect many regions to be engaged in a complex system of interactions.

Here we mainly focus on the differential roles of the D1-like (D1 and D5) and D2-like (D2, D3, and D4) receptors in the intercellular integration within post-synapse areas. The D2-like receptors compared to the D1-like type receptors have a higher affinity for dopamine (10 to 100-fold greater for the D3 and even more greater for the D4) (Tritsch and Sabatini, 2012). A key for both cognition and reward system functioning is the D1/D2 ratio (dual state model). Here, the D1 receptor plays a gating role by controlling the threshold of significance above which information must pass before it can be admitted to working memory (achieving stabilization), and the D2 signals the presence of information (mostly reward based information) that allows the PFC network to respond to this new information by updating its working memory system (achieving flexibility) (Seamans and Yang, 2004; Savitz et al., 2006). The D1/D2 ratio regulation implies that D1-like receptors are bound to *stimulatory* G proteins (hence called G protein-coupled receptors) that energize adenylyl cyclase, and this activates the production of cyclic adenosine monophosphate (cAMP), and thus activation of protein kinase A (PKA). PKA mediates the phosphorylation and regulates the function of a wide area of cellular substrates such as K⁺, Na⁺ and Ca⁺, glutamate, GABA receptors, and transcription factors. D2-like receptors bind to *inhibitory* G proteins that hinder adenylyl cyclase and thus reduce the production of cAMP, which prevents cAMP activation of PKA and also reduces N-methyl-D-aspartate (NMDA) receptor activation and GABA-ergic inhibition (Seamans and Yang, 2004; Tritsch and Sabatini, 2012).

Dopamine levels have an effect on the D1/D2 ratio, but this effect is different in the PFC (slow modulation) compared to the striatum (reinforcing brief activity), thus complicating the ability to make clear conjectures (Tripp and Wickens, 2009). The striatum and PFC are mutually interconnected, as well as to the dopamine system, and thus stimulation by dopamine affects both reward seeking and planning, which is why dopamine levels have an inverted U curve effect on cognitive performance; both low and high levels of dopamine fail to affect cognitive performance, but intermediate levels effect cognitive performance strongly. This is because the striatum is activated more intensely by dopamine and (due to its connection with the PFC) leads to reductions in flexibility of switching costs, at least under some conditions such as in planning (Aarts et al., 2011).

For cognitive processes, when dopamine levels are high (low), there is a higher (lower) D1/D2 ratio, which due to cAMP activation and its intracellular chain reaction affects the excitatory release of glutamate from pyramidal cells of the PFC. Consequently, there is stronger excitatory signaling and better inhibition of noise due to distraction in the environment (in other words, more focus occurs). Higher PFC activation also feeds back to the striatum and allows for better regulation of striatal impulses (needed for self-regulation and inhibition). However, higher dopamine levels in the striatum have a different effect: activation in the striatum helps a person respond flexibly to environmental cues, especially for what is desired (routines and wanting). However, when strongly activated, the striatum might

predispose a person to respond inflexibly to the environment as routine responding takes over (Aarts et al., 2011). In short, strong striatum activation might compromise cognitive flexibility or raise switching costs. We expect that the two candidate genes (*DRD2* and *DRD4*) will affect the D1/D2 ratio and thus have an impact on cognitive and reward processes. Somewhat similar outcomes happen with the *COMT* gene where Met carriers experience lower ability of enzyme breakdown of dopamine, and thus dopamine levels remain high, and a higher D1/D2 ratio occurs resulting in greater cAMP activation, higher glutamate levels, and greater cognitive focus, at the cost of more rigid behavior.

The *DRD4* gene (D2-like), located on chromosome 11p15.5, codes for the dopamine D4 receptor and includes in exon III a 48-bp variable number of tandem repeats (VNTR) polymorphism, which contains 2–11 repeats. This VNTR is located in a region that encodes the supposed third cytoplasmic loop of the receptor that couples to inhibiting G proteins, which reduce the production of cAMP, and thus inhibits the chain reaction in the neuron (Wang et al., 2004; Barnes et al., 2011). Carriers of the *DRD4* 7⁺ repeat (7R⁺) variant of this polymorphism in the *DRD4* gene experience reduced ability to blunt cAMP signaling in neurons (Asghari et al., 1995; Oak et al., 2000), compared to 7R⁻ carriers (both in the pre- and post-synapsis), and thus are less able to play an inhibitory role, so undergo higher glutamate activation. Due to the fact that *DRD4* is mainly expressed in the PFC, there is more cognitive elaboration and higher alertness for what might be new. This leads to the following cognitive and behavioral effects: the dopamine system switches too quickly from a tonic to a phasic state (higher sensitivity to reward salience) (Grace, 1991), and this makes the person more open to experience; indeed Munafò et al. (2008) showed that carriers of the *DRD4* 7R⁺ were more likely to show approach-related personality traits (especially novelty-seeking). Carriers of the *DRD4* 7R⁺ are less able to maintain cognitive self-control than non-carriers and thus are more vulnerable to distracting information, which if occurring in a sales conversation might consist in lost information that is relevant, such as happens with non-verbal signals. Similarly, carriers of the *DRD4* 7R⁺ are less able to self-regulate and have difficulties post-poning gratification, making them vulnerable to committing more impulsive behaviors (Munafò et al., 2008).

Successful selling requires salespeople to look for opportunities displayed implicitly in interpersonal encounters (e.g., being sensitive to implicit meaning and non-verbal communication) and explicitly by customers (e.g., voicing needs, objections). Salespeople who are carriers of the *DRD4* 7R⁺ might be more likely to respond to these changes and thus better sense opportunities than non-carriers.

The *DRD2* gene, located on chromosome 11q22-q23 (region rs 180049), codes for the dopamine receptor D2, and includes exon 8 of the *ANKK1* gene (Ritchie and Noble, 2003). *DRD2* is especially active in the ventral striatum, and it is the most widely expressed D receptor in the brain (Tritsch and Sabatini, 2012). Carriers of the *DRD2* Taq A1 experience a reduction in both pre and post-synaptic D2 sites, which results in increased dopamine release. More dopamine means that there is a greater activation of neurons in the striatum (Laakso et al., 2005). As dopamine levels rise, so will activation of the striatum (the D1/D2 ratio changes

accordingly, and the consequent intracellular cascade will occur). Due to the connection with the PFC, this might affect flexibility in cognitive tasks and produce a concave U effect. Optimal levels of dopamine might result in optimal cognitive performance, but too much dopamine results in lower cognitive performance. For example, Stelzel et al. (2010) found that carriers of *DRD2* Taq A1, were less proficient in adjusting their behavior based on feedback about earlier performance (but not when they engaged in a novel cognitive task). In addition, because the striatum (especially the NAcc) has the most D2-like receptors, there is also a higher probability that carriers have greater wanting and reward dependency (Trifilieff et al., 2013). Thus, they might be more motivated and willing to put pressure on customers due to their stronger wanting. Considering the facets of a SO described above, carriers of the *DRD2* Taq A1 might engage more frequently in a SO.

MATERIALS AND METHODS STUDY 1

SUBJECTS

A total of 64 salespeople, all working in business-to-business environments, were asked to participate in a study involving DNA analysis. They came from the following industries: 4% came from automotive, 3% from food and beverage, 15% from banking, 3% from utilities, 9% from manufacturing, 23% from professional services, 7% from pharmaceuticals, 2% from telecom, 5% from logistics, 20% from IT, 3% from retailing, and 6% from other industries. Respondents answered an online questionnaire containing CO and SO questions from the SOCO scale (Saxe and Weitz, 1982), identical to those used in the study by Bagozzi et al. (2012) (see **Table 1**). The response format was a 7-point disagree-agree Likert format. However, one item from the CO and two items from the SO were deleted because they

Table 1 | Customer orientation and sales orientation scales (see Bagozzi et al., 2012).

CUSTOMER ORIENTATION (CO)	
1	I try to get customers to discuss their needs with me.
2	I try to find out what kind of product would be most helpful to a customer.*
3	I try to bring a customer with a problem together with a product that helps him solve the problem.
4	I try to give customers an accurate expectation of what the product will do for them.
5	I try to figure out what a customer's needs are.
SALES ORIENTATION (SO)	
1	I try to sell a customer all I can convince him to buy, even if I think it is more than a wise customer would buy.
2	I try to sell as much as I can rather than satisfy a customer.
3	If I am not sure a product is right for a customer, I will still apply pressure to get him to buy.*
4	I paint too rosy a picture of my products, to make them sound as good as possible.*
5	It is necessary to stretch the truth in describing a product to a customer.

*These items had low factor loadings, so all analysis were done twice: once with the original full scales above, and one with the full scales above, and once with the full scales with these items removed (see **Tables 2, 3**).

loaded too low on their respective factors, based on exploratory factor analysis. Nevertheless, since one aim of our study is to replicate the original findings of Bagozzi et al. (2012), we will report results for the SO and CO scores on the scales from the current study, as well as the original scales as used by Bagozzi et al. (2012). The alpha of the (4-item) CO scale from this study was 0.71 (5-item Bagozzi et al., scale = 0.60). The alpha of the (3-item) SO scale was 0.76 (5-item Bagozzi et al., scale = 0.82).

PROCEDURES AND STATISTICAL ANALYSES

We followed recommended practice to gather DNA data and analysis, and allele frequencies analysis using the Hardy-Weinberg Equilibrium. We use parametric *t*-tests for tests of equality of means on the CO scale and SO scale and *DRD2/DRD4* polymorphisms of participants.

RESULTS

Tables 2, 3 present the findings. The results for *DRD2* show that neither CO ($t = -0.69, p = 0.91$; $t = -0.85, p = 0.87$) nor SO ($t = -0.31, p = 0.77$; $t = -0.38, p = 0.70$), differ significantly between the A1 and no-A1 variants. By contrast, for *DRD4*, 7R⁺ carriers have significantly higher means than non-carriers on CO ($t = 2.37, p = 0.02$; $t = 2.60, p = 0.01$), but no differences were found on SO ($t = -0.11, p = 0.91$; $t = -0.50, p = 0.62$).

Table 2 | *DRD2* Taq A1 *t*-tests for equality of means.

	Group	Mean	<i>t</i> -test (two-sided)	<i>p</i> -value
Customer orientation	No A1	6.33	-0.69	0.91
	A1	6.42		
Customer orientation (Bagozzi et al., 2012)	No A1	6.15	-0.85	0.87
	A1	6.26		
Sales orientation	No A1	5.33	-0.31	0.77
	A1	5.42		
Sales orientation (Bagozzi et al., 2012)	No A1	5.42	-0.38	0.70
	A1	5.31		

Table 3 | *DRD4* 48 bp VNTR *t*-tests for equality of means.

	Group	Mean	<i>t</i> -test (two-sided) ^a	<i>p</i> -value
Customer orientation	NO 7R	6.26	-2.37	0.02
	7R	6.59		
Customer orientation (Bagozzi et al., 2012)	No 7R	6.09	-2.60	0.01
	7R	6.42		
Sales orientation	No 7R	5.35	-0.11	0.9
	7R	5.38		
Sales orientation (Bagozzi et al., 2012)	No 7R	5.34	-0.50	0.62
	7R	5.49		

^aBold values are significant at a 5% significance level.

DISCUSSION

Molecular genetics has the potential to inform organizational theory about key phenotypes from a biological perspective. However, to have a significant impact both in predicting and understanding behavioral tendencies or traits, findings between variants of specific genes and phenotypes should be replicated using different independent samples. We replicated recent findings concerning the relationship between the *DRD4* and *DRD2* genes and CO and SO, respectively (Bagozzi et al., 2012). In particular, consistent with Bagozzi et al. (2012), we found that salespeople carrying the 7R⁺ variant of the *DRD4* gene have a higher propensity to engage in CO. In contrast, no relationship between the variants of the *DRD2* genes and SO was found. It must be noted, however, that in Bagozzi et al. (2012) the association between *DRD2* A1 and SO was only marginally significant ($p = 0.07$).

Our findings show a clear impact of genes on SO, which goes beyond the scope of behavioral genetics. We would like to point out that such replications of candidate gene studies are rare, and indeed failures to replicate are the norm (e.g., Seabrook and Avison, 2010). One group of researchers (Chanoock et al., 2007, p. 655) characterizes the published literature in this regard as “a plethora of questionable genotype-phenotype associations, replication of which has often failed in independent studies.” The latter authors maintain that “the challenge will be to separate true associations from the blizzard of false positives attained through attempts to replicate positive findings in subsequent studies” (p. 655).

GENE × ENVIRONMENT INTERACTION

Our aim in Study 2 is to develop a theoretical basis for hypothesizing the conditions for the effect of key dopamine genes in an organizational context by specifying a particular gene-environment (phenotype) interaction. Since the molecular genetics approach more directly reflects how the brain functions (in this case the dopamine system), we are able to better understand how actions are initiated and maintained. These molecular mechanisms potentially contribute to our understanding of the phenotype, since they offer an additional explanation as to how our brain influences our behavioral tendencies. Specifically, salespeople's curiosity and eagerness to understand customers' needs involve regulation of the dopamine system known to be involved in novelty-seeking and the related motivational processes reviewed above, as governed by attachment style individual differences.

Attachment systems imply double-sided mechanisms: people, when anxious, seek proximity with others but also need to *feel secure in relationships*, such that they can further broaden and build behavioral repertoires in different social environments. Attachment styles develop in young children (Van IJzendoorn, 1995) exploring their environment. They experience fear when confronted with challenging situations, and then seek proximity to attachment figures (such as parents) and, when present/supportive, secure attachment styles evolve such that children comfortably seek and feel support from significant others; especially oxytocin (OT) and dopamine are involved in this (see hereafter). Based on these experiences, children

develop a secure *working model*, developing expectations for predicting future interactions (cognitive schemas) and believing that others will be available and respond empathically if necessary. Children can then co-regulate stress (achieving emotional comfort or “neuroception” of safety) and attain feelings of security, allowing them to broaden their social exploratory behaviors, develop a theory of mind (TOM), de-activate negative expectations and boost their coping skills, such as is reflected in better ability to not get distracted and to conduct cognitive reappraisal (Porges, 2003). Secure attached people also like to give comfort to others (e.g., Mikulincer and Shaver, 2003).

The pleasant feeling that comes from close interaction (social approach) occurs because when children are nurtured by their parents there is a modest increase in dopamine transmission in the NAcc, which activates dopamine receptors D1 and D2, and both influence affection and pleasure and help maintain social bonds. D1 and D2 have different effects on approaching behavior as they have contrasting effects in the intracellular mechanisms: D2-like receptors (expressed in neurons that project from the rostral shell of the nucleus accumbens to the ventral pallidum) are necessary for the formation of a pair bond. Specifically the D2 receptors are bound to inhibitory G proteins, which act to reduce the cAMP, which prevents PKA, and is associated with the facilitation of attachment (primary unconditional rewarding). D1 receptors are bound to stimulatory G proteins, which increases cAMP signaling, which in turn increases PKA, and results in reduced mating partner preferences, but especially reduces the seeking of new partners once a bond has been made. Key is that OT promotes the activation of inhibitory G proteins and down regulates the intracellular cAMP cascade. OT also enhances the hedonic value of social interactions by activating areas rich in dopamine receptors in especially the reward system (which includes the VTA, substantia nigra). OT changes how the dopamine system updates the outcome of actions; it reduces the feelings of risk (reduction in amygdala activation), and this motivates people to undertake social interactions and experience them as intrinsically rewarding. In other words, for many people, especially stable-attached persons, social interaction with significant others is intrinsically rewarding.

There is now evidence that secure interactions entail long-term changes in the brain: secure attached people have greater gray matter reward volume in the reward network and interconnected regions such as hypothalamus or orbito frontal cortex (OFC) (e.g., the ventral striatum is differentially activated in secure mothers when they see their own babies smiling or crying, Strathearn et al., 2009). In addition, secure mothers also experience increased gray matter volume in the amygdala, the longer the post-partum period; in other words, it shows that they have a greater affective vigilance for their own children compared to other children. Secure mothers also have greater gray matter volume in areas related to TOM processes, such as the PFC, STS, and fusiform gyrus, and higher BOLD (blood-oxygen-level dependent) signal responses when hearing babies, which shows that as they interact with people they constantly improve their TOM network.

When attachment figures are not reliably available or supportive (e.g., caregivers behave unpredictably or do not provide support), a healthy sense of security is not attained, and secondary strategies of affect regulation come into play. Two internal working models emerge: avoidant and anxious.

Avoidant people do not have a healthy approaching system and have reduced, or lack, reward-related activity during positive social situations; e.g., avoidant attached individuals rate positive social information as less arousing (e.g., avoidant mothers had low activation of the ventral striatum and VTA) or do not experience positive social interaction as intrinsically rewarding compared to secure mothers, as they deactivate the attachment system and therefore do not seek to approach people (Vrtička and Vuilleumier, 2012, p. 6). Avoidant people are more concerned with self-preservation, have a positive self-model, show distrust to a partner's goodwill, and strive to maintain independence. Strong self-reliance often develops. Besides experiencing relatively low feelings of pleasure in social interaction, avoidant attached people may exhibit ill-functioning emotional coping styles: avoidant attached people de-emphasize threats and tend to cope without help or support from others; e.g., when rejected they have a decreased activation of the anterior insula and dACC (DeWall et al., 2012), which indicates a blunted response to social negative contexts (or a lower need to feel included). The problem is that this blunting might not work when pressure is high. For example, Vrtička et al. (2012) show that when emotional regulation strategies are constrained, avoidant attached persons have higher amygdala responses to emotional stimuli.

Anxious people develop vigilance reactions: they hyperactivate the attachment system when stress occurs resulting in an inability to handle threats autonomously. Anxious people tend to exaggerate threats. For example, Vrtička et al. (2008) show that the amygdala was selectively activated when angry faces were presented as negative feedback after giving incorrect responses; this leads to heightened distress and higher emotionality. This amygdala activation shows that anxious persons experience heightened distress in situations of personal failure or social disapproval. Equally, when people are excluded from others in the Cyberball paradigm, they show increased activation of the anterior insula and dACC, which means that they are sensitive to rejection (Eisenberger et al., 2003). They become very emotional, and despite feeling that others are inconsistent and not trustworthy, they attempt to gain protection and support. Anxious people also worry that partners will not be available in times of need and attempt to gain partner attention, care, or even love. Feelings of intense dependence and clinginess may emerge.

While most research shows that insecure people might not be strong in relationship building, there is now evidence from animal research and human research in organizations that insecure attached agents are actually very productive to fit. Beery and Francis (2011) show that rats when raised in insecure conditions (low licking and grooming) actually performed better on individual cognitive tasks than rats raised in secure conditions (high licking and grooming). In addition, school children with parents who did not look after them well, actually helped children in

school better than children raised with parents who cared well for them (Obradović et al., 2010). Therefore, we are now looking for different sorts of events to substantiate this.

Beery and Francis (2011) suggest that stressful experiences in mice do not inevitably lead to dysregulation of stress reactivity and that increases in stress reactivity (caused by early life stress due to poor maternal care) are not necessarily dysfunctional. Beery and Francis introduce the concept of stress inoculation, meaning that changes in the HPA axis and reward system to stress learned in early maternal care might actually be beneficial within certain contexts; e.g., rats subjected to stress conditions exhibited less emotionality (Levine, 1962) and demonstrated efficient neuro-endocrine responses. Confirming the effects of susceptibility to environmental influences, stress reactivity to environmental cues can lead to greater responsiveness to stimulating environments in certain contexts.

Ein-Dor et al. (2010) speak about the paradox of attachment, by which they mean that many insecure people can actually perform well at certain tasks. Using an experimental design in which fire suddenly broke out, Ein-Dor et al. found that anxious people first noted the fire, whereas avoidant people were the first to take flight, and secure people followed the avoidant attached people in fleeing. Hence, there is evidence for concluding that in certain situations insecure attached persons might perform well and outperform secure attached persons.

HYPOTHESES

DRD2 moderation

We propose that the effects of variants of the *DRD2* dopamine receptor gene on CO will depend on the degree of avoidance attachment style. Specifically, we hypothesize the greater the avoidance attachment style, the greater the CO for carriers of the A2, A2 allele but not either the A1, A1 or A1, A2 alleles. Carriers of the A2, A2 allele vs. the other alleles are less distracted by intrusive or anxious thoughts (stemming from rumination and anticipated rejection by customers or worry that the customer will think that one is unattractive or less competent) and should therefore be more focused on the needs of customers, listen attentively, and respond to changing interpersonal give and take. In contrast, carriers of the A1, A1, or A1, A2 allele should be more rigid in their thinking and engage inflexibly in stereotypical behavior patterns (van Holstein et al., 2011). In other words, expected higher switching costs for carriers of the A2, A2 allele, compared to carriers of the A1, A2 or A1, A2 alleles, should be associated with greater focus and persistence, when salespersons interact with customers, which fosters the ability to adjust product/service offerings and one's communications to customers. Carriers of the A1, A1 and A1, A2 alleles, compared to carriers of the A2, A2 allele, should not only be more susceptible to distraction but also more impatient and unfocused.

DRD4 moderation

The *DRD4* dopamine receptor gene exists in variants that affect receptor activation by the dopamine neurotransmitter. Specifically, carriers of the 7R allele (7R⁺), vs. non-carriers, have been found to engage in more risk taking (Dreber et al., 2009),

novelty-seeking (e.g., Ebstein et al., 1996; cf., Munafo et al., 2008), and opportunity recognition during customer interactions (see Study 1 in the current paper; Bagozzi et al., 2012). Work to date has focused largely on the main effects of these gene variants, but we examine their modulating effects on the impact of the avoidant attachment style on CO. Consequently, we expect an interaction effect: the avoidant attachment style will lead to greater CO in salespeople with the 7R⁺ allele but not for salespeople without it. The rationale is that for sales representatives with the 7R⁺ allele, the greater the inclination to be open to taking risks and pursuing new opportunities, the more an avoidant attachment style will lead to a strong CO. Again, we argue that the avoidant attachment style is manifest in an ability to remain efficacious and goal driven when discussing customer needs, and present appropriate solutions without allowing feelings of rejection to intrude detrimentally and adversely affect one's efforts (see findings in the psychology literature on "suppressing distress-related thoughts," Ein-Dor et al., 2010, p. 134).

MATERIALS AND METHODS STUDY 2

SUBJECTS

Hypotheses were tested on a sample of 73 sales representatives who volunteered for a study of the role of biomarkers in professional relationships. Participants provided written informed consent, and the study was approved by the local research ethics committee. Participants were not told about the aim of the study at the start but were debriefed after completion of the study. All participated in post-graduate executive education programs. All were business-to-business salespeople selling financial services, trucks, IT services, insurance, pharmaceutical drugs, or consulting services. These selling positions require more thorough and repetitive conversations with customers compared to sales interactions with consumers where impulsive buying and transactions play a more important role (e.g., retail sales; door-to-door selling). All were Caucasian, 87% men, 13% women, 49% had a university degree and the rest vocational school diplomas. The average level of selling experience was 6.8 years. All participants donated saliva so that their DNA could be analyzed for the two candidate genes, *DRD4* and *DRD2*.

PROCEDURE

Attachment styles were measured with 12 7-point "does not describe me at all" to "describes me very well" end-points, and "describes me moderately well" as a mid-point (see Table 4). These items were adapted from Professor Phillip R. Shaver's latest scale, which he kindly provided¹. This scale is based on the original in Hazan and Shaver (1987), which was revised by Collins and Read (1990). Note that there are six items for anxious attachment, three for avoidant, and three for secure.

CO was measured with 5 7-point disagree-agree items with the same format used as for the attachment style items. This scale was

developed by Bagozzi et al. (2012) as a subset of Saxe and Weitz's (1982) original scale. Table 1 shows the items.

RESULTS

Two items from the attachment scale were deleted because they loaded too low on their respective factors, based on an exploratory factor analysis (items 6 and 10). Cronbach's alpha reliabilities for the subscales were 0.69 for anxious, 0.81 for avoidant, and 0.67 ($r = 0.51$) for secure. Because all three factors were uncorrelated with each other, and empirical under identification occurred, we could not run a confirmatory factor analysis (CFA) for all three subscales together. A CFA for the anxious and avoidant subscales fit well: $\chi^2_{(19)} = 17.65$, $p = 0.54$, RMSEA = 0.00, NNFI = 1.01, CFI = 1.00, and SRMR = 0.076.

For the CO scale, the CFA model fit well: $\chi^2_{(5)} = 4.65$, $p = 0.44$, RMSEA = 0.00, NNFI = 1.00, CFI = 1.00, and SRMR = 0.036. Cronbach's alpha was 0.77.

Regressions were done according to standard procedures: first, we added the main effects, then the interaction effect. Here we only report the significant main findings. As we have dichotomous and continuous independent variables, we followed Jaccard and Turrisi (2003) to analyze interaction effects and graphically display the findings (see Nieuwenhuis et al., 2011). For the *DRD2* analyses, the two regression equations are, with *DDR2* coded (A1, A1 and A1, A2) = 1 and A2, A2 = 0 in the first regression and the reverse for the second:

Customer orientation =	5.986 (0.098)	+0.204 (0.074)	avoid (0.149)	<i>DRD2</i> (0.109)	-0.248 (0.109)	avoid × <i>DRD2</i> (0.109)
	61.35	2.75	0.930		-2.29	
Customer orientation =	6.124 (0.112)	-0.044 (0.079)	avoid (0.149)	<i>DRD2</i> (0.109)	+0.248 (0.109)	avoid × <i>DRD2</i> (0.109)
	54.68	-0.55	-0.93		2.29	

Table 4 | Attachment style scales.

ANXIOUS	
1	I worry that others won't care about me as much as I care about them.
2	My desire to be very close sometimes scares people away.
3	I need a lot of reassurance that I am loved by my partner.
4	I do not often worry about being abandoned.
5	I find that my close relationships don't want to get as close as I would like.
6	I get frustrated if partners are not available when I need them.
AVOIDANT	
7	I want to get close to others, but I keep pulling back.
8	I am nervous when partners get too close to me.
9	I try to avoid getting too close to others.
SECURE	
10	I usually discuss my problems and concerns with my partner.
11	It helps to turn to my romantic partner in times of need.
12	I turn to my partner for many things, including comfort and reassurance.

¹ Personal communication with Professor Phillip R. Shaver, January 10, 2011.

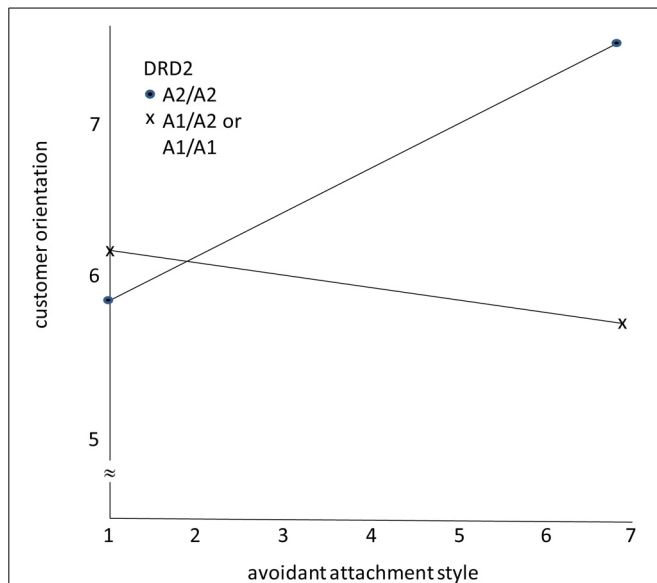


FIGURE 1 | The moderating role of DRD2 gene variants on the effects of avoidant attachment style on customer orientation.

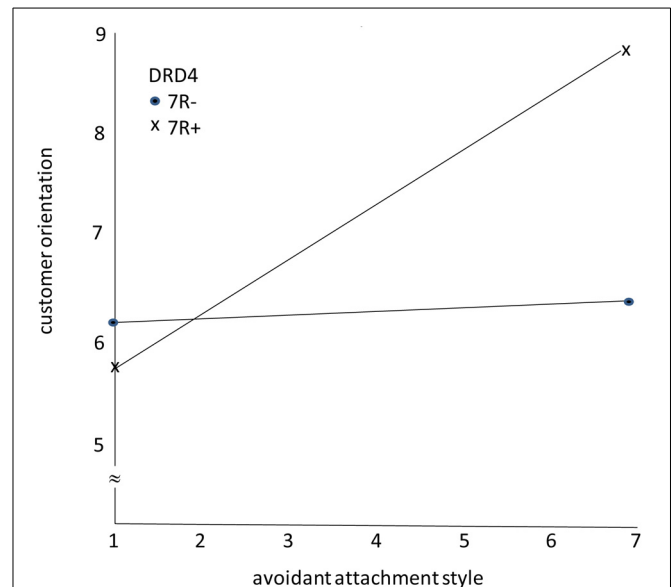


FIGURE 2 | The moderating role of DRD4 gene variants on the effects of avoidant attachment style on customer orientation.

where standard errors are in parentheses and t -values appear below them. This model fit well: $F_{(3, 69)} = 2.73$, $p = 0.05$, $R^2 = 0.11$.

Figure 1 presents the results. As hypothesized, the avoidant attachment style has a positive effect on CO for sales representatives with the A2, A2 variant of the *DRD2* gene. For sales representatives with the A1, A1, and the A1, A2 variants of *DRD2*, the avoidant attachment style has little effect on CO, as predicted.

For the *DRD4* analyses, the two regression equations are, with *DRD4* coded $7R = 0$ and $7R^+ = 1$ in the first regression and the reverse in the second regression:

Customer orientation =	6.116 (0.084)	+0.038 (0.057)	avoid	+0.287 (0.174)	<i>DRD4</i>	−0.395 (0.166)	avoid × <i>DRD4</i>
	72.79	0.67		−1.64		2.38	
Customer orientation =	5.829 (0.153)	−0.433 (0.155)	avoid	−0.287 (0.174)	<i>DRD4</i>	+0.395 (0.166)	avoid × <i>DRD4</i>
	38.11	2.79		1.64		−2.38	

This model fit well: $F_{(3, 69)} = 2.85$, $p = 0.04$, $R^2 = 0.11$.

Figure 2 shows the findings. As predicted, the avoidant attachment style has a positive effect on CO for salespeople with the $7R^+$ variant of the *DRD4* gene. However, for salespeople with the $7R^-$ variant of the *DRD4* gene, the avoidant attachment style had no effect on CO, as expected.

To gain perspective, we also examined the interaction effects on CO of the anxious attachment style with *DRD2* and with *DRD4* polymorphisms, and the interaction effects on CO of the secure attachment style with *DRD2* and with *DRD4*. None of the interactions and none of the main effects were significant in the four regressions.

Also for perspective, we note that CO was not significantly correlated with the anxious attachment style ($r = 0.16$, ns), avoidance attachment style ($r = 0.07$, ns), secure attachment style ($r = 0.11$, ns), *DRD2* ($r = 0.07$, ns), or *DRD4* ($r = 0.07$, ns). Thus, CO was influenced only by the interactions of the avoidance attachment style with *DRD2* and with *DRD4* polymorphisms.

DISCUSSION

As we move into a biology-informed era in social research, researchers will benefit from scrutinizing such higher-order concepts as attitudes, personality traits, and work orientations using lower-order concepts from neuroscience (e.g., Becker et al., 2011; Senior et al., 2011) and molecular genetics. Whereas in our Study 1 we used insights from molecular genetics to replicate previous findings about the association between variations of two candidate genes, namely *DRD2* and *DRD4* (*nature*), in Study 2 we explored how gene activity is affected by interactions with the environment (*nurture*). We investigated this question because we believe that findings from such cross-level studies can enrich theory testing and knowledge development and guide practical decision-making by human resource managers. For customer boundary spanners, a meta-analysis by Ford et al. (1988) investigated how biographical and psychological variables compare in their effects on salesperson's success. Surprisingly, the results seemed to suggest that biographical information predicts performance better than psychological variables (see also Vinchur et al., 1998). Specifically, the findings showed that personal history and family background explained around 5% of the variance in performance and marital status accounted for less than 2%; in comparison, cognitive abilities explained less than 1% and vocational skills less than 1% of performance. Biographical variables, of course, beg the questions what in one's background influences behavior and what the underlying mechanisms are. The

low levels of explained variance for both biographical and psychological variables suggest that the variables function poorly as main effects, and sound theories proposing interactions might be fruitful to explore in a person-by-situation exploration.

More specifically, two problems with such background variables can be identified. First, these variables can be thought to be one-step removed from the origin of salesperson behavior and serve as proxies at best for proximal psychological determinants of behavior. Second, the use of background variables in managerial decision-making risks the stigma of excessive intrusiveness, or even worse, the application of prejudice or profiling due to race, gender, or other categories.

In an effort to elucidate the interplay of *nature* and *nurture* on the etiology of SO, we examined how variants of the *DRD2* and *DRD4* genes moderate the effects of sales representative attachment styles on CO. The findings showed that the avoidant attachment style has a positive effect on CO for sales representatives carrying only *DRD2* A2 alleles, but no effect occur for sales representatives with at least one *DRD2* A1 allele. The avoidant attachment style has been shown to exhibit an orientation of emotional distance, yet a high degree of self-reliance, which seemingly fits expectations in inter-firm business relationships. However, whether, and to what extent, the avoidant style will influence CO apparently depends on the functioning of the dopamine system with regard to goal-directed, motivational, and reward-related behavior.

Carriers of the *DRD2* A1 allele exhibit reduced switching costs compared to carriers of only A2 alleles in intentional cognitive tasks (Stelzel et al., 2010). This should be manifest in greater task focus and persistence by the latter compared to the former, and greater sensitivity to task distracters and greater impatience for the former compared to the latter. The pattern of findings in **Figure 1** is consistent with this interpretation, where we found that greater adherence to an avoidant attachment style leads to a stronger CO for sales representatives with the A2 alleles, whereas sales representatives with at least one A1 allele show no relationship between avoidant style and CO.

Furthermore, carriers of the *DRD4* 7R⁺ allele, vs. the 7R⁻ allele, have been shown to be greater risk takers and have a propensity to seek opportunities while interacting with customers. This, too, appears to regulate the effect of an avoidant attachment style on CO. We speculate that the tension occurring between the need to keep a certain amount of distance between self and customer, and the drive to seek new opportunities leads to a greater application of skills meeting (mutual) needs and greater chance of success.

Additionally, the present research also brings into focus the role in which insecure attachment styles (anxious and avoidant), as opposed to the secure attachment style, play in professional lives. In this regard, Ein-Dor et al. (2010) speak about the attachment paradox. Overall, researchers in psychology (e.g., Shaver and Brennan, 1992) have assumed that people with secure attachment styles fair better than those with insecure ones, with respect to building stable social relationships. The secure style is thought to promote stable relationships with others, because it is believed to increase fitness within the human species. However, when faced with vulnerable relationships or threatening situations, such as in

many inter-firm selling contexts, people with an avoidant attachment style remain self-efficacious and goal driven, and maintain the initiative to seek innovative solutions (Ein-Dor et al., 2010). As Ein-Dor et al. speculate, avoidant attachment styles may be beneficial in certain situations. Our study shows that professional selling in business-to-business markets is such a context. Sales representatives are boundary spanners who work largely autonomously, explore the needs of customers, and shape the way customers view their own problems (Vinchur et al., 1998). They do so while maintaining a professional attitude in the face of conflicts of interest, misunderstandings, and customer resistance. In other words, whereas a secure attachment style might be best for in-group relationships, an avoidant style seems best for ingroup-outgroup relationships.

FUTURE RESEARCH AND PRACTICAL IMPLICATIONS

Our research paves the way for future discoveries. It would be productive to study different phenomena in organization behavior such as job attitudes, social identity, burnout and resilience, and motivation, and explore the role of genetics in combination with environmental factors. Such approaches are challenging, yet they might provide us with more insights into the concepts under study and their effects, which we exemplified in this study. Such insights also allow human resource managers to uncover what biological mechanisms are related to the (higher order) concepts they regularly use.

Elaborating on the study in this paper, we note that sales representatives do not always work alone but often in teams. Would sales teams of people who possess heterogeneous attachment styles function better than those with homogeneous styles? Such teams might contain people who seek psychological comfort (those with anxious attachment styles), sense competitive signals (those with anxious and avoidant attachment styles), and effectively implement interpersonal-change actions (especially those with avoidant attachment styles). As we studied the effects of attachment styles in interaction with genes, such questions are both difficult to ask and difficult to answer.

In terms of task-person fit, what attachment style should be employed by managers that supervise sales representatives with diverse attachment styles? Will managers with secure attachment styles, because they are perceived as open and trusting, attain better results, and can they bring both secure and insecure sales representatives together because they are inclined to promote cooperation, hence enhancing group or team formation and flexibility? Alternatively, could it be that managers with avoidant attachment styles empower their sales representatives because they do not seek unneeded or excessive closeness? Note that our findings showed that attachment styles interacted only with specific genes to influence COs. Holders of other genes might require different leadership strategies or better fit tasks other than boundary spanning roles.

Finally, attachment styles and people's genetic profile are stable and so tend to evoke automatic reactions or predictable tendencies in particular situations. Future research should study how sales representatives self-regulate such automatic tendencies and shape them into productive work orientations. For example, should firms make attachment styles part of awareness

training? If attachment styles interact with genetic abilities, would such knowledge make sales representatives self-conscious of their genetic backgrounds and encourage or discourage adaptive behavior? Our findings invite researchers to explore the consequences of deeper, unconscious biological processes that shape human behavior in diverse organizational contexts.

Genetic data and measures of attachment style, if employed sensitively and applied ethically to hiring, training, and supervisory decisions along with other information, can provide more valid and fair criteria for management than reliance only on background information, interviews, and psychological tests. Of course, any use of such information must be based on validation of their effects on performances in any context, if Equal Employment Opportunity Commission Regulations and anti-discriminatory policies are to be met. Much remains to be done concerning our understanding of the role of genetic factors in organizational behavior. For example, more work is needed into how key genetic variables inter-relate with personality and situational constraints to influence behavior and outcomes. The pursuit of such ends promises to help us understand the “why” of behavior in organizations and provide policy insights.

LIMITATIONS

One shortcoming of our research concerns the construct validity of our phenotype measures for CO, SO, and the three attachment styles. We acknowledge that full analysis of construct validity requires a multitrait, multimethod matrix investigation to assess convergent and discriminant validity. We did not conduct such a study, but some of the features of our approach suggest that construct validity may not be a significant problem. All our measures of variables were drawn from scales used before in a number of studies, thereby receiving some support for validity of measures in different research contexts with different samples. Second, all our measures achieved satisfactory reliabilities, and our factor analyses revealed that convergent and discriminant validity of measures were achieved, albeit with a monomethod approach. Future research could use confirmatory factor analysis in a multimethod design to better establish construct validity (Bagozzi, 2011).

We studied sales representatives to investigate the nature-nurture question related to molecular genetics in organizations. While this context provided initial answers, there are limitations.

First, one can argue that the sample sizes used in this study are small. However, we employed a hypothesis-driven approach, targeting only two genes and based on theory from biology and psychology, which reduces the need for large sample sizes required by exploratory searches across many genes. Importantly, we replicated findings presented by Bagozzi et al. (2012), regarding the association between carrying the *DRD4* 7R⁺ variant and the propensity to engage in customer-oriented selling. Convergent findings by two independent studies with regard to a specific genetic variant are rare in biological research and significantly contribute to the validity of the phenomena under study. Furthermore, the discovery of gene-environment interaction effects is also rarely recounted in the literature. Such interactions require the specification and test of unusual

cross-level hypotheses and when found provide strong evidence for the mechanisms under research. In addition, while the costs of genetic profiling are becoming more feasible, such genetic studies compared to pencil and paper tests are difficult to implement.

Second, the application of molecular genetics research in organization theory and social research contexts would benefit from Genome Wide Association Studies (GWAS). This could uncover a small number of fundamental genes at work in the workplace. The following can be noted in this regard. First, as recommended by Senior et al. (2011) we selected genes for study that have already received some basic research efforts in areas of psychology relevant to our research. Thus, our inquiry was grounded in a specific, well-defined research tradition where in one sense our findings add to this body of knowledge. Second, GWAS require large sample sizes, because they test for up to one million genetic variants at the same time, introducing severe multiple-testing design and statistical issues, and thus significantly increasing the risk for false-positive findings. Finally, in order to build the large cohort that is required to give enough power for GWAS analyses, one needs to study heterogeneous samples, which in our case would mean studying people across many occupational settings and environments and making it difficult to draw conclusions pertaining to the specific work setting we investigated. Given the limited effect sizes that are typically observed in (candidate) gene studies, this might create too much noise in the sample to be able to arrive at valid genetic effects.

Third, we assumed that attachment styles are a reflection of environmental interactions, and therefore are a proxy of the influence of *nurture*, so to speak. However, attachment styles may have genetic association as well (e.g., Gillath et al., 2008). In addition, attachment styles were inferred from questionnaires in our studies, but more objective data could have been used; e.g., observations by clinicians or other experts.

Finally, we used an attachment style questionnaire tailored to how people experience general interpersonal relationships as adults. We could have developed a domain-specific attachment style measure tailored to the organizational context (e.g., Little et al., 2010). However, since we aimed to understand how environment and genes interact to influence behavior, we chose as our measure one that reflects the phenomenon under study in a way that functions during the critical window when one's neurobiological (stress) systems were shaped. This helps tie the findings for the adults under study to the early biological underpinnings and learning that produced the hypothesized consequences on the job.

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A comment on the service-for-prestige theory of leadership

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A commentary on

The evolution of leader-follower reciprocity: the theory of service-for-prestige by Price, M. E., and van Vugt, M. (2014). *Front. Hum. Neurosci.* 8:363. doi: 10.3389/fnhum.2014.00363

Successful collective action often depends on the presence of leaders, who bear greater responsibility than other group members for the logistics of coordination, monitoring of effort, and reward and punishment. Leaders may be expected to shoulder more risk, are vulnerable to retaliation from sanctioned group members, and suffer greater reputational damage from failed collective action. What then motivates individuals to be leaders? From an evolutionary perspective, the answer is not straightforward since most of human history occurred in societies lacking significant disparities in material wealth and institutions that grant leaders coercive power. One possibility is that group members share costs by distributing leadership roles over iterations of collective action. However, this is uncommon where inter-individual differences in leadership ability have an impact on collective action. Whether in small-scale egalitarian societies or large-scale stratified societies, group members typically prefer leaders who are superlative in traits such as physical size, knowledge, and prosociality (von Rueden et al., in press).

Price and van Vugt (2014) offer another theoretical solution: followers reciprocate leaders' services by granting them prestige. As a result of their prestige, leaders receive gifts, coalitional support, deference from competitors, or mating opportunity. I have a minor definitional criticism. I do not see prestige as what is conditionally granted to leaders but rather what leaders

can automatically produce through their actions: a reputation for delivering benefits to others. What Price and van Vugt (2014) note is that the advantages to prestige may accrue principally during times of need, such as during conflict or food shortage, and thus leadership can act as a form of insurance (Boone and Kessler, 1999).

Since the benefits leaders provide are often public goods, the service-for-prestige theory entails that group members can free-ride by (1) not contributing to collective action, (2) not rewarding leaders, and (3) not punishing group members who fail to reward leaders. This is where the service-for-prestige theory makes unique predictions relative to other theories of leadership: followers will experience punitive sentiment toward other group members who fail to reward effective leaders (or followers will experience prosocial sentiment toward group members who criticize ineffective leaders). Price and van Vugt (2014) present an example from the Ecuadorian Amazon (Price, 2003) where group members who lack respect for popular leaders are themselves disrespected. Future work will need to determine whether such punitive sentiment is sufficient to stabilize group member contributions to leaders, in various cultural and organizational contexts.

Theoretical alternatives to service-for-prestige predict that followers do not experience a collective action problem in bestowing benefits on leaders, because leadership produces private goods not subject to free-riding (costly signaling theory), followers' contributions to leaders are a product of group selection, or leaders recoup their costs by receiving greater *direct* benefits from collective action. Examples of the latter include collective actions that produce goods more beneficial to leaders and their kin (Ruttan

and Borgerhoff Mulder, 1999) and leaders who claim a greater share of the spoils (Hooper et al., 2010; Gavrillets and Fortunato, 2014).

As Price and van Vugt (2014) suggest, social neuroscience methods (e.g., identifying the neural correlates of punitive sentiment in public goods games) can help test the explanatory power of the service-for-prestige model against alternative models of leadership. The public goods game has been modified to introduce asymmetries into decision-making over the distribution of public good shares (van der Heijden et al., 2009) or over punishment and reward (O'Gorman et al., 2009). However, caution is required when making inferences from particular experimental games, whose conditions (e.g., player endowments as windfalls) may rarely hold in natural settings or may be interpreted in different ways depending on the cultural context. In highland New Guinea where leaders demonstrated their qualifications via competitive generosity, large offers in the ultimatum game were perceived not as prosocial but as antagonistic (Tracer, 2003).

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Interdisciplinary research is the key

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The organizational sciences are rapidly coming together with neuroscience theory and methods to provide new insights into organizational phenomena (Becker et al., 2011; Senior et al., 2011; Lee et al., 2012), and even the potential development of individuals within organizations (Waldman et al., 2011). A number of challenges become relevant in the pursuit of such an amalgamation, but perhaps the most apparent is the inherent need for interdisciplinary perspectives and research. An overall purpose of this opinion piece is to clarify the importance of interdisciplinary efforts, while at the same time clarifying the challenges to be faced if we are to apply neuroscience to organizations.

Scientists are typically trained and reinforced to work in a unidisciplinary, specialized mode. It really does not matter if we are considering people trained in the so-called “soft” sciences (e.g., psychology), or whether they come from the “hard” sciences (e.g., neuroscience). We are largely groomed and later reinforced to be specialists. I personally was trained in industrial/organizational psychology, a specialized area of the broader field of psychology. When I was undergoing my graduate education, as well as in the years that followed, I never dreamed that I would someday be working with neuroscientists. But it is now happening. In other words, I am conducting interdisciplinary research involving neuroscientists. In so doing, I certainly do not represent the norm among my colleagues. I say this as a professor in a management department of business school. I realize that for many academic psychologists working in psychology departments, the notion of combining psychology and neuroscience has become the norm. Accordingly, much of what I will address

in this opinion piece would not apply to them.

I will address three primary questions in this article. First, what are the institutional and personal impediments that may prevent researchers, especially those in settings such as my own, from engaging in the type of interdisciplinary research that might involve neuroscience? Second, what is the myth vs. reality of the obstacles that might preclude the success of interdisciplinary efforts? Third, what steps can we take to engage in more interdisciplinary research? By addressing these questions, I hope to provide some insight into the issues and benefits of an interdisciplinary approach to neuroscience research. Most of my approach is framed through the perspective of an organizational researcher such as myself, although I conclude with some consideration of why neuroscientists might want to pursue interdisciplinary research that reaches out to the organizational sciences.

INSTITUTIONAL AND PERSONAL IMPEDIMENTS

I first attempted to apply neuroscience to my own area of specialized expertise, leadership in organizations, around 2005. Early on, I made a presentation on the subject and described some recent data collection efforts to my colleagues at Arizona State University. After the presentation was over, one of my colleagues took me aside and said that what I was attempting to do was quite interesting. He also acknowledged that he had never conceived of such possibilities, largely because of the institutional context in which we exist (about which I will say more below). A second colleague who pulled me aside was more cautionary. He essentially acknowledged that what I was doing was innovative, but recommended, “don’t quit your day job.”

In other words, the not-so-subtle message was that such interdisciplinary efforts would not end up being rewarded, and I should just stick with the tried and true of unidisciplinary or specialized research activities. Was he correct?

Before answering that question, let’s consider how interdisciplinary research can exist at different levels or degrees. As a management professor specializing in micro-level, organizational behavior, let’s assume that I want to be more interdisciplinary in my work. I could potentially work on research projects that integrate more macro-level phenomena. Indeed, over the past 20 years I have written on such topics as strategic leadership (e.g., Waldman et al., 2001), corporate social responsibility (e.g., Waldman et al., 2006), and university technology transfer (Siegel et al., 2003). My interdisciplinary work in these areas has brought me together with strategic management and information systems researchers, economists, and financial researchers. The common denominator, however, is that all of this work, and the individuals associated with it, can be placed under the broad umbrella of business-based research. By engaging in interdisciplinary research involving neuroscience, one is “taking a walk on the wild side,” so to speak, and perhaps this is what my colleague was thinking about when he cautioned me to “don’t quit your day job.”

So what exactly are the institutional impediments all about? Many of us conduct our research within the institutional confines of universities and research outlets, specifically journals. Historically, the structure of universities is very segmented or siloed. Even the physical buildings in which our offices are housed tend to maintain this segmentation, e.g., offices for people in a particular department

or disciplinary area are largely in the same location. Perhaps more importantly, our reward systems (e.g., promotion and tenure) tend to reinforce specialization. As an organizational researcher, I have received messages (some subtle, some not so subtle) throughout my career that while some dabbling in other areas might be permissible, I should not stray too far or too much from my own specialization, or else my own tenure, promotion, and reputation could be put at risk. Moreover and relatedly, I have been told that the best journals will not accept highly interdisciplinary research. Below I will attempt to separate the myth from reality with regard to publication issues.

Most of us are keenly aware of the structural or institutional impediments to interdisciplinary research. But perhaps we are not so cognizant of our own personal issues that might preclude us from engaging in such research. We are conditioned early on as graduate students to work on specialized projects. After graduation, we are then encouraged to gradually make a name for ourselves in particular, focused streams of research. Rarely does the thought of interdisciplinary activities take hold. Indeed, the networks that we form, conferences that we attend, and so forth, center around unidisciplinary work. In short, we can get by just fine in our careers without becoming interdisciplinary. So why bother?

SEPARATING MYTH FROM REALITY

Before I provide my take on this question, I first want to separate some myth from reality. The first myth is that researchers from widely disparate disciplines either cannot, or will not, come together to pursue interdisciplinary efforts. As an organizational behaviorist, I will admit to having mixed luck with regard to collaborative relationships with neuroscientists. At times, it has been challenging because of differing goals, perspectives, and the reality that some neuroscientists themselves may not be interested in the pursuit of interdisciplinary research.

But for the most part, I have been able to form beneficial connections with such individuals, and together we have attempted to dispel a second myth. Specifically, there is the myth that top journals in organizational/management

will not accept interdisciplinary research, especially when it crosses such a seemingly huge boundary as the neuroscience realm. This myth personifies the fear that my colleague mentioned back in 2005 when he cautioned me to not quit my day job. The fear was that I simply would not be able to place such research in the top journals in my field. To be sure, at the time, there were no neuroscience-based articles in organizational/management journals. So his conclusion might seem warranted. In addition, interdisciplinary submissions can create difficulties for journal editors, for example, finding suitable reviewers. However, the more entrepreneurially-oriented editors of journals in my field increasingly see the potential value in accepting at least some interdisciplinary articles, including those involving neuroscience concepts and methods. In speaking with editors of journals in my field, they seem keenly aware of how neuroscience is affecting other fields in business. Examples include neuro-economics (e.g., Braeutigam, 2005; Camerer et al., 2005; Kenning and Plassman, 2005) and neuro-marketing (e.g., Lee et al., 2007). So inclusion of neuroscience-based articles is rapidly being viewed as more normal, and less revolutionary. Since 2005, I personally have been able to achieve a least a modicum of success in such publication efforts, largely involving neuroscientists as co-authors (Peterson et al., 2008; Balthazard et al., 2012; Hannah et al., 2013; Waldman et al., 2013). Moreover, it is my experience that grant agencies and foundations increasingly seek interdisciplinary research proposals that involve co-investigators from diverse backgrounds.

STEPS TOWARD BECOMING MORE INTERDISCIPLINARY

The type of interdisciplinary research that I have described here can be framed in terms of the classic approach-avoidance conflict. To a large extent, I have emphasized the salience of the approach aspects that might make a researcher want to proceed with interdisciplinary work, while minimizing potential avoidance reasons for shunning pursuits of this nature. With that said, I fully realize that a key consideration on the avoidance side is the ambiguity inherent in determining when or how to make it happen. In other words,

when and how might one become more interdisciplinary in his/her approach to research, especially with regard to combining neuroscience with fields of study such as the organizational sciences? For individuals whose primary focus is the latter, the first thing that I would caution is to treat the potential integration of neuroscience as more of a personal vision, rather than predominant reality, early on in one's career. In other words, as a doctoral student and in the early portion of one's career, it might be best to focus largely on developing a focused specialization, while at the same time keeping in mind and gradually working toward interdisciplinary possibilities.

Once one has determined to become more interdisciplinary, there are two avenues that might be pursued. First, an individual can simply expand his or her own domain of expertise to include an area such as neuroscience. The obvious limitation of this approach is that we all have time constraints, as well as demands to maintain expertise in our own specialized areas. To some degree, I personally have followed this route. But because of the sheer breadth and complexity of neuroscience, I have chosen a second avenue for approaching neuroscience. Specifically, I have partnered with trained neuroscientists in terms of both publication and grant activities. Indeed, I have found this second avenue to be especially important as a means of providing a better perspective of neuroscience, and to deal with the complexities of actual data collection and analysis processes (e.g., Balthazard et al., 2012). For example, through collaboration with neuroscientists, I have gained a better feel for what "activity" in brain regions may operationally be all about, as well as the potential relevance of both intrinsic and reflexive brain activity to organizational phenomena (Waldman et al., 2013).

CONCLUDING THOUGHTS

Throughout this opinion piece, I have focused on interdisciplinary work from the viewpoint of a non-neuroscientist, such as myself. But what about neuroscientists; what might be their motivation to work with organizational researchers? In my own experience, I have had much more success at connecting with neuroscientists who combine the scientist-practitioner

model, including establishing their own firms to produce applications to such maladies as attention deficit disorder, sleep apnea, and so forth. These individuals have bonafide credentials in terms of their basic understanding of neuroscience theory and methods, but they are also interested in real-world applications. Thus, it is a natural extension of their work to look toward the organizational world to see how their expertise might be applied. In contrast, I have had less luck connecting with “pure” academics, for example, social cognitive neuroscientists who might be working in psychology departments of universities. However, I recognize that there will be more such connections between organizational researchers and basic neuroscience researchers in the future.

In conclusion, it is my hope that this commentary will help to provide some insights into the issues and advantages pertaining to interdisciplinary research in the realm of organizations and neuroscience. There is much potential for research of this nature to address some of the larger problems facing organizations. In turn, by focusing attention on organizational issues, new insights and opportunities may present themselves for neuroscientists.

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Consumer neuroscience to inform consumers—physiological methods to identify attitude formation related to over-consumption and environmental damage

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INTRODUCTION

Climate change, the need for efficient and environment-friendly energy use and health-related issues like obesity and addictions, these three crucial topics build a triad that the global society has extensively been discussing and caring about during the past decades. First, according to the recently published fifth IPCC climate change assessment report (2013), intense weather conditions have been on the rise. These changes will in extreme cases impose life-threatening dangers to some civilizations, but it will mostly influence individual attitudes and decision-making and thus finally modify consumption behavior quite dramatically during the next decades. Second, the European Union is aiming for a 20% cut in Europe's annual primary energy consumption by 2020 (Energy Efficiency Plan, 2011). This government-driven aim does not only affect global industry, but again also the consumption behavior of each individual end-user. Third, according to the World Health Organization (2013), worldwide obesity has nearly doubled since 1980. In fact, 65% of the world's population lives in countries where overweight and obesity kills more people than underweight (World Health Organization, 2013). Given these unpleasant scenarios we need to get active now in order to prevent the worst and to ensure the best possible and highest standards of life across the globe.

TARGETED RESEARCH IS REQUESTED

Fortunately, Horizon 2020, the seventh framework program of the European Commission relates to the abovementioned areas as being important research topics, which need to be investigated more comprehensively until 2020 (European Commission, 2013). However, given their rather global political nature how can reliable respective research be done ideally taking all of these three main concerns into account in one go while at the same time providing useful insight?

Decision-making and attitude formation seem to be the common denominator. What are the true attitudes of an average consumer as the smallest unit in a society? What does a consumer think about his/her individual role within these current dynamics? After all, the actual goal is to understand why one is over-consuming, pursuing an unhealthy lifestyle and wasting household energy, although actually knowing about the negative consequences? Unfortunately, knowing the right questions is not enough, we also need adequate research that provides reliable answers, which let us understand and predict human behavior, particularly consumers' choices. Of course, a lot of research has been done, but traditional research approaches are potentially misleading as highlighted by various studies comparing explicit with implicit responses (Spector, 1994).

WHAT ALTERNATIVE MEASURES DO WE HAVE?

Ultimately, all human behavior is a consequence of both cognitive and affective processing, but only cognitive aspects can be reliably captured through questionnaire-based investigations, while affective processing happens largely outside our awareness (Walla and Panksepp, 2013). Consumer decision-making and attitude formation are strongly engaging affective processing and incomplete understanding and suboptimal investigations might come along with severely negative consequences for the individual as well as for the society and the entire environment. Just to think of one example, when it comes to study the acceptance of new household technologies that are more energy efficient one could get strongly biased and misleading results if only using self-report approaches. Consequently, the potential gap between explicitly stated intention to use power saving household tools and actual future behavior would not help to improve the situation. Especially, topics related to environmental issues are prone to be biased by social desirability and various other often unknown pressures (Glasman and Albarracín, 2006). Similarly, issues related to eating behavior resulting in overweight do rarely have pure cognitive origins, but most commonly are based on emotions grounding on an affectionate and attitude based source. Among

these are emotion regulation, fear and stress (Kemp et al., 2013).

Given this major shortcoming of self-reports in terms of measuring affective processing in the consumer brain, neuroscientific methods are here suggested to provide added value in this respect. However, not all methods from consumer neuroscience are equally suitable. Besides its merits to gather information on fundamental experimental effects, the capabilities of brain imaging techniques like fMRI (functional Magnet Resonance Imaging) to study real consumption behavior are limited. In case one wants to study purchase decisions directly at the point of sale the use of fMRI renders itself impossible. In addition, fMRI is a very expensive technology. Luckily, more affordable while also more reliable methods are available to make the desired progress in studying consumer likes and dislikes, their attitudes and finally to predict their actual behavior. Recent studies that focused on comparisons between explicit and implicit measures of affect as in like and dislike clearly showed that discrepancies between self-reported like and objectively measured like can occur (Geiser and Walla, 2011; Grahl et al., 2012; Mavratzakis et al., 2013). From these and a number of other studies it can be concluded that whenever such discrepancies occur respective self-reported likes or dislikes have to be treated with great caution.

Some of these studies utilized a long known approach to tap into non-conscious raw affective processing in the human brain, a phenomenon known as startle reflex modulation (SRM). SRM is a valid approach to selectively measure the valence of affective information processing. It is easy to apply also in a field setting and can perfectly be combined with methods measuring the associated level of arousal, like skin conductance and heart rate (Dawson et al., 1999; Walla et al., 2011). Measuring the underlying forces of behavior other than mere stated intention is also crucial regarding health-related issues with respect to consumption. Applying neuroscientific methods like SRM and maybe electroencephalography (EEG) (Bosshard and Walla, 2013) can be useful in this regard as well (e.g., Walla et al., 2010 used these methods to study the emotion impact of food intake).

WHAT SPECIFIC RESEARCH SHOULD WE FOCUS ON?

Although obviously different in many respects, a closer look at climate change, environment-friendly energy as well as health reveals that their individually associated behaviors are all remarkably dependent on attitudes. Attitudes form important bases for behavior and thus knowing them allows us to predict behavior. For instance, an attitude like “global warming is natural, not man-made” is likely associated with future behavior that does not really do anything against it. Also, health issues do of course strongly depend on the right attitudes. Attitudes are consciously (explicitly) and non-consciously (implicitly) learned and as such are prone to change be it driven by more or less random individual experiences or by planned and strategic political or marketing campaigns. They are shaped by intellectual elaboration, but they also have a strong affective component, which reflects aspects of basic like or dislike. Crucially, and that is what makes attitudes empirically testable, they can be modified as a consequence of learning processes such as conditioning (e.g., Hofmann et al., 2010). In particular, evaluative conditioning is often used where for instance “nature” is repeatedly paired with positive unconditioned stimuli to finally create a positive nature-attitude in children preparing them for a nature protecting adulthood. Through evaluative conditioning, *unknown* and even *disliked* can be turned into *liked*. Obviously, evaluative conditioning and its effects on attitudes seems to be a very promising and meaningful field to investigate. Together with neuroscientific methods and techniques the investigation of attitudes, their formation and their changes are here clearly emphasized as being most successful when it comes to predicting human behavior (see Bosshard and Walla, 2013).

THE MAIN TAKE HOME MESSAGE

Crucially, and this forms the main take home message of this opinion article, the use of surveys only taps into the explicit (conscious) aspect of a consumer’s attitude, whereas implicit aspects are not at all reflected in self-reported data (see Rugg et al., 1998; Walla et al., 1999).

This is potentially misleading, because implicit attitudes have been shown to be better predictors of particularly spontaneous behavior (Gawronski and Bodenhausen, 2012). Explicit attitudes are deliberate evaluations formulated through reasoning and consequently even if the individual subjectively perceives their outlook toward it to be positive, negative associations can be activated, and vice versa (Devine, 1989). Implicit attitudes are independent of higher cognitive resources and occur irrespective of their alignment with the individual’s introspective assessment. They are non-conscious and thus only accessible via objective measures such as SRM and EEG.

TALK BETWEEN SCIENCE COMMUNITY AND SOCIETY

It is necessary to continuously engage in an educated dialog with the average consumer. This means that one precondition for being able to realize such a dialog is to translate the research findings into a language that is actually being understood by the society. Doing so allows creating added value for the society through science. In a nutshell, this opinion article outlines how consumer neuroscience may be used to create societal value. The more we know about non-conscious processes that drive human behavior the more each individual consumer knows and thus can better understand and finally control his own behavior. Neuroscientific methods in general and SRM and EEG in particular, might serve as valid instruments for addressing consumption-related issues of the topical triad that are important to build a larger picture in terms of society and well-being. This opinion article may provide vital insights for advancing academic knowledge but also provide the basis for guidelines for experts and policy makers.

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AUTHOR CONTRIBUTIONS

All three authors (Peter Walla, Monika Koller, and Julia L. Meier) meet all of the below listed criteria:

- Substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data for the work; AND
- Drafting the work or revising it critically for important intellectual content; AND
- Final approval of the version to be published; AND
- Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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