Using neuroimaging to predict behavior:
An overview with a focus on the moderating role of sociocultural context

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How do we predict how an individual will behave in a particular situation? Across several decades, social scientists have identified many self-report measures that account for individual variability in behavior, yet a large percentage of the variance remains unaccounted for by these introspective reports (Armitage & Conner, 2001; O'Keefe, 2018). Recent advances in analytic approaches and computational tools have provided new, complementary avenues to investigate this difficult question. Non-invasive neuroimaging approaches (e.g., functional magnetic resonance imaging [fMRI], functional near infrared spectroscopy [fNIRS], and electroencephalography [EEG]) measure brain activity while participants view stimuli and make decisions, providing a powerful tool to capture objective measurements of individual differences during task performance (Berkman & Falk, 2013; Tompson, Lieberman, & Falk, 2015). Analytic tools for quantifying patterns of activation within and between brain regions further advance the power of neuroimaging approaches to predict how individuals will behave (Bassett & Sporns, 2017; Kriegeskorte, 2011), as well as how they will interact with one another, and how groups of individuals will make decisions. In short, the foundation of social neuroscience posits that measuring brain activity provides access to psychological processes and neural circuitry that may serve as the underlying mechanisms that explain individual differences in behavior.

In this review, we first discuss evidence that demonstrates the association between brain activation and individual decisions and behaviors. Studies within the domains of health and consumer behaviors have identified a consistent set of brain regions associated with individual decisions and behaviors. These brain regions have been implicated in processing information about the reward value of choice and behavioral options (valuation) as well as processing social information about the mental states of others (mentalizing). Second, we discuss evidence that these same brain regions are also linked to aggregate behavior for groups of individuals. Third, we discuss evidence that these brain regions are associated with how individuals will behave in social interactions. Finally, we discuss evidence that the association between brain activation and behavior is moderated by social factors including social network position, culture, and socioeconomic status. Throughout, we highlight recent advances that leverage multivariate and network analysis approaches that emphasize different components of brain activity patterns to understand the neural mechanisms underlying social behavior.


THE BRAIN-AS-PREDICTOR APPROACH

The human brain is a massively interconnected network consisting of 86 billion neurons with trillions of connections between neurons (Azevedo et al., 2009). Human cognition requires coordinated communication across macroscopic brain systems composed of both gray matter (cell bodies) and white matter (axons; Bassett & Sporns, 2017). The gray matter is typically divided into brain regions composed of large groups of adjacent neurons that have similar properties, and these regions demonstrate specialized information processing and knowledge representation. The white matter provides the structural connections between distant brain regions and is often described as the wiring in the brain (Vettel, Cooper, Garcia, Yeh, &

Verstynen, 2017). Together, brain networks support cognition and human behavior by communicating information among brain regions for integrated processing and rely on the structural connections to enable efficient and rapid responses across distant brain regions (Passingham, Stephan, & Kötter, 2002). Consequently, coordinated communication across the brain is fundamentally constrained by specialized processing in individual brain regions and patterns of interconnections reflected in functional connectivity of synchronized activity between regions.

The brain-as-predictor approach measures brain activation while individuals evaluate information about various behavioral options, and then uses that activation to predict subsequent behavioral outcomes, often over the course of weeks, months, or even years (see Cascio, Scholz, & Falk, 2015; Falk & Scholz, 2018; Knutson & Genevsky, 2018 for a review). The majority of these studies use functional magnetic resonance imaging (fMRI) to measure brain activation, although other imaging modalities such as electroencephalography (EEG), functional near infrared spectroscopy (fNIRS), magnetoencephalography (MEG), or positive emission tomography (PET) could also be used. To date, the brain-as-predictor approach has been applied to predict both individual behaviors and aggregate group behaviors in diverse domains, including health (Cooper, Bassett, & Falk, 2017; Falk, O'Donnell, Tompson, et al., 2015), consumer (Genevsky, Yoon, & Knutson, 2017; Levy, Lazzaro, Rutledge, & Glimcher, 2011), and political behaviors (Rule et al., 2009). Importantly, in many of these studies, brain activation provides additional information about the likelihood of engaging in a particular behavioral outcome, beyond what is explained by self-reported intentions, preferences, and other questionnaire items (Falk, O'Donnell, Tompson, et al., 2015; Genevsky et al., 2017; Venkatraman et al., 2015).

In addition to improving our ability to predict behavior, the brain-as-predictor approach can also yield important insights into the psychological processes underlying these behaviors. Studies using fMRI to predict behaviors frequently implicate three sets of brain regions that are broadly involved in processing self-relevance, social relevance, and overall value of incoming information (see Figure 1). In particular, vmPFC and PCC have been implicated in processing the relevance of information to the self (Denny, Kober, Wager, & Ochsner, 2012; Martinelli, Sperduti, & Piolino, 2013), such as whether a word or product describes the self or is part of the individual's identity (Kelley et al., 2002; Kim & Johnson, 2012). The dmPFC and TPJ have been implicated in social processing, including considering the mental states of others (i.e., mentalizing; Denny et al., 2012; Saxe & Kanwisher, 2013). The vmPFC and VS have been implicated in integrating information from different sources to compute a signal of the subjective value of the information (Bartra, McGuire, & Kable, 2013). It should be noted that these processes often overlap and that several of the brain regions listed are implicated across these functions as well. Indeed, researchers have argued that these brain regions work together to process information about the fit of the behavioral options to an individual's values, beliefs, and goals as well as to broader social norms, which are then integrated into a single value signal indicating the subjective value of the behavioral options being considered (e.g., whether to quit smoking, choose product A or B, donate to a charity, or share a news article; Knutson & Genevsky, 2018; Scholz et al., 2017; Tompson, Lieberman, & Falk, 2015).

FIGURE 1 BRAIN ACTIVATION
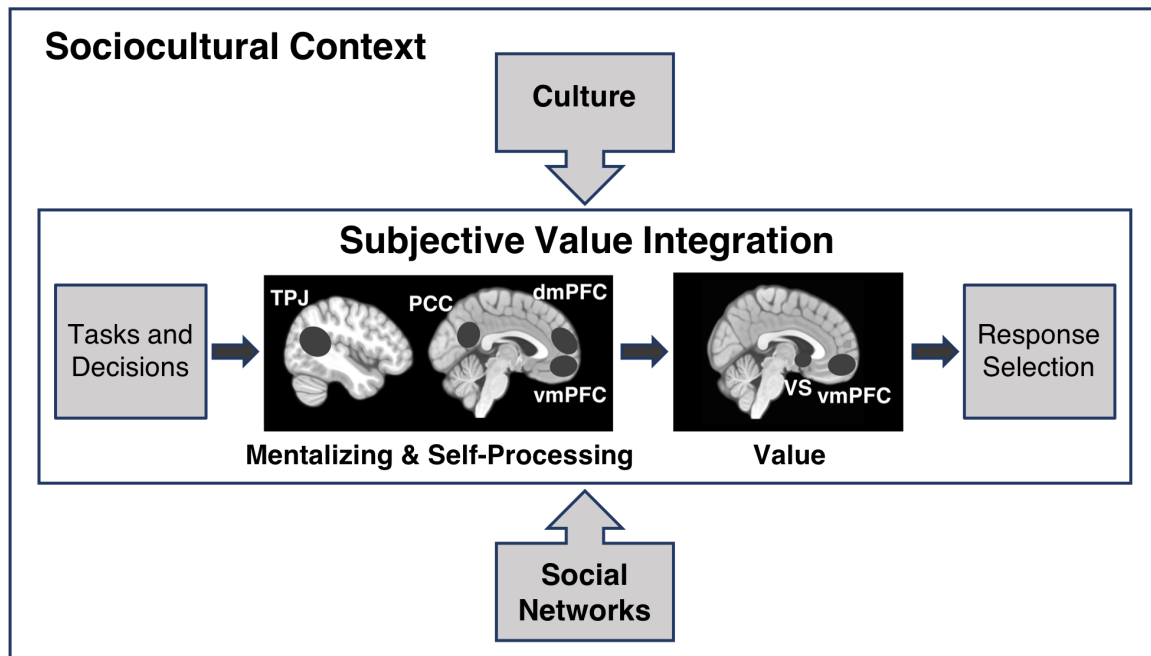
Note: Brain activation implicated in processing information about the self, others' mental states, and reward value can be used to predict how people will behave and make decisions. The relationship between brain activation and behavior is in turn moderated by sociocultural factors, including culture and social networks. Temporoparietal junction (TPJ), dorsal medial prefrontal cortex (dmPFC), and posterior cingulate cortex (PCC) are frequently implicated in thinking about the mental states of others (mentalizing). vmPFC and PCC are also implicated in thinking about the self. Ventral medial prefrontal cortex (vmPFC) and ventral striatum (VS) are frequently implicated in processing reward value. Specialized processing in these regions as well as communication of information between brain regions is thought to directly support behavior and decision-making, at least in part through integration of self and mentalizing processing into a subjective value signal.

PREDICTING INDIVIDUAL BEHAVIORS

The majority of research using brain activation to predict behaviors has focused on using an individual's brain activation to predict how that individual will behave in the weeks or months following the experimental session. Although a diverse set of research has used brain activation to predict behavior, we highlight two domains that have successfully used brain activation to predict behavior outside the scanner: health behavior and consumer behavior.

Within the health domain, the brain-as-predictor approach measures brain activation while an individual evaluates persuasive health messages, and then tracks their behavior over the next week or month. A study by Falk and colleagues (2010) measured individuals' brain activation while they viewed health messages promoting the benefits of wearing sunscreen. They then tracked individuals' sunscreen usage the week after the study and compared it to their sunscreen usage the week prior to the study. Participants who recruited vmPFC more during message evaluation were more likely to use sunscreen afterwards, even after controlling for sunscreen usage the week prior to the study (Falk, Berkman, Mann, Harrison, & Lieberman, 2010; Vezich, Katzman, Ames, Falk, & Lieberman, 2017). Similarly, research in other health domains has found that individuals who exhibit greater mPFC activation during message exposure are more

likely to engage in health behaviors endorsed by those messages, including increasing physical activity (Falk et al., 2015) and reducing smoking (Chua et al., 2011; Cooper, Tompson, O'Donnell, & Falk, 2015; Falk, Berkman, Whalen, & Lieberman, 2011; Wang et al., 2013). Why does vmPFC activation predict behavior change? Research suggests that vmPFC processes the relevance and value of the messages to the individual. In particular, the subregion of vmPFC involved in predicting behavior change overlaps with subregions of vmPFC known to be involved in both thinking about the self and processing the value of objects to the self (Cooper et al., 2015). Moreover, self-affirmation prior to being exposed to health messages promoting increased physical activity led to greater vmPFC activation (relative to presenting the messages without the self-affirmation) and greater subsequent behavior change (Falk et al., 2015), providing experimental evidence that self-processing plays a key role linking vmPFC activation and behavior change.

FIGURE 2. PHYSICAL ACTIVITY BEFORE AND AFTER HEALTH MESSAGES
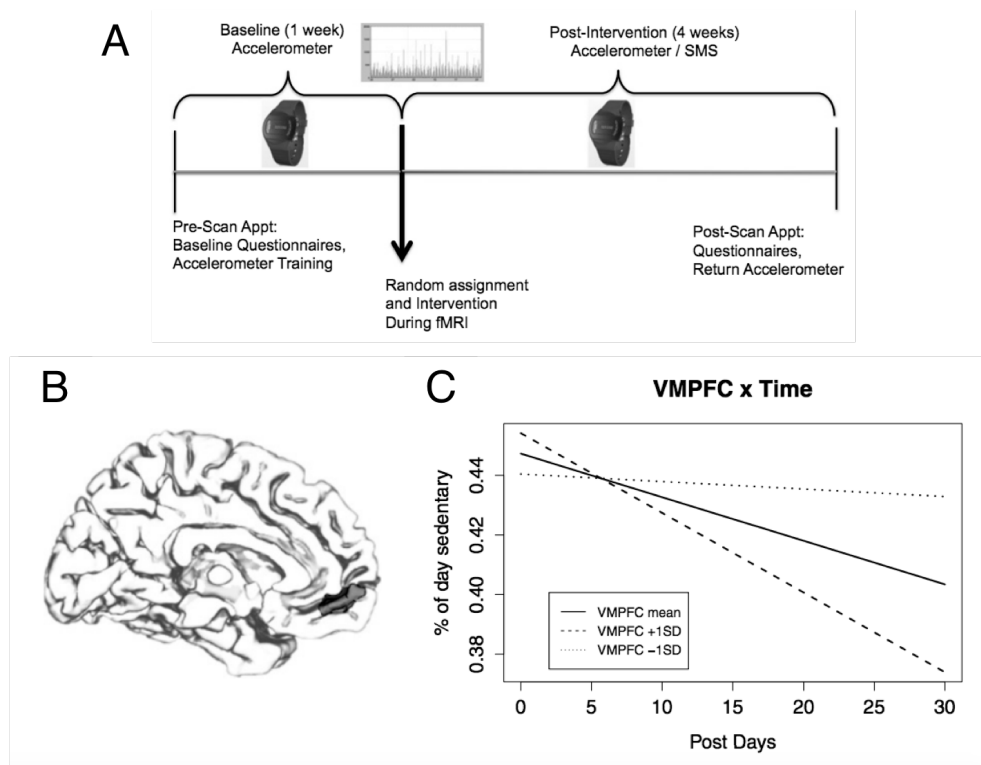
Note: Falk and colleagues measured physical activity before and after participants were presented with health messages promoting exercise while their brain activity was measured in an MRI scanner (2A). Participants exhibited greater activation in vmPFC when they were first given an opportunity to affirm positive attributes about the self (2B) and individuals who recruited vmPFC more during message exposure were more likely to have fewer sedentary days in the month after the study (2C; adapted with permission from Falk, O'Donnell, Cascio, et al., 2015).

In addition to predicting health behaviors, brain activation can predict consumer behaviors. Complementary experimental designs on consumer behaviors examined brain activation while participants evaluated explicit appeals designed to persuade the participant to purchase a particular product (e.g., Genevsky et al., 2017). Consumer products that elicited greater vmPFC and VS activation were more likely to be chosen by individuals (Knutson, Rick, Wimmer,

Prelec, & Loewenstein, 2007; Levy et al., 2011). Interestingly, brain activation can predict consumer choices even when participants are not explicitly evaluating the choice options. Levy and colleagues (2011) had participants passively view consumer products in an MRI scanner without making any explicit judgments about the products, and then had participants choose which products they wanted to own after the scan. The researchers could accurately predict which product a participant would choose based on activation in vmPFC and VS during the passive viewing task (Levy et al., 2011).

Across both domains, brain activity in vmPFC and VS reliably predicts individual differences in health change and consumer behaviors. These regions have been implicated in self-related and reward processing (Adolphs, 2009; Bartra et al., 2013; Denny et al., 2012; Lieberman, 2007; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014), suggesting that people are more likely to engage in behaviors or make choices that are high in self-relevance and subjective value. Importantly, in many cases brain activation predicts behaviors with an accuracy above and beyond those obtained from self-report measures of preferences or intentions (Falk et al., 2011; Genevsky et al., 2017). Objective measures of subjective value indexed by vmPFC and VS might therefore be providing novel insight into the value or relevance of the outcomes to the individual's salient values, beliefs, and goals.

INTERPRETING ASSOCIATIONS BETWEEN BRAIN ACTIVATION AND BEHAVIOR

How can understanding the relationship between brain activation and behavior improve our understanding of the psychological processes underlying health and consumer behaviors? In this review, we highlight three core neuroimaging analysis approaches that examine how the brain processes and represents the content of persuasive messages and how this processing predicts behavior. The first and most common univariate analysis compares brain activity between two conditions, where the only difference between them is the cognitive process of interest. This type of analysis underlies the research reviewed in the last section, identifying that brain activity in vmPFC and VS reliably predicts individual differences in health change and consumer behaviors. The second approach complements the univariate analysis by looking at multivariate patterns within a region. The core intuition is that the knowledge represented in a region may be distributed across the smaller units of brain tissue within a region (known as voxels in fMRI data). Whereas the conventional univariate analysis simply averages the functional activity across all subcomponents of an imaged brain region, a multivariate analysis assumes that understanding how a region gives rise to psychological processes of interest is coded by the distributed pattern in a region. Finally, our review highlights a third neuroimaging analysis approach that uses connectivity methods to estimates task-relevant network activity. Connectivity research posits that synchronized activity between regions demarcates the integration of information across regions, and thus, the functional network dynamics capture the spatiotemporal processes necessary for the brain to enable behavior.

Multivariate pattern analysis (MVPA) or representational similarity analysis (RSA) are two analysis methods to quantify how patterns of activation across voxels within a brain region (or across the whole brain) relate to behavior. They use the relative similarity of neural activity between pairs of trials to make inferences about the content encoded in that region (Kriegeskorte, 2011; Nili et al., 2014; Norman, Polyn, Detre, & Haxby, 2006). For example, Pegors and

colleagues (2017) used RSA to investigate how vmPFC represents information about persuasive messages. The multivariate patterns of activation within vmPFC successfully differentiated information about whether persuasive messages contained information about health, social, or risk consequences of smoking cigarettes (Pegors, Tompson, O'Donnell, & Falk, 2017). Furthermore, individual differences in the representation of message content in vmPFC predicted whether individuals would reduce their smoking behavior after the study (Pegors et al., 2017). Recently, researchers have also begun to employ connectivity-based approaches to predict behavior across a diverse set of domains (Brooks et al., 2018; Garcia et al., 2017; Muraskin et al., 2017; Passaro et al., 2017). Within the behavioral change literature, researchers have studied brain connectivity patterns while participants viewed persuasive health messages, and results demonstrated that greater connectivity within a network of brain regions associated with the processing of subjective value was linked to greater likelihood of engaging in the health behaviors being promoted in the messages (Cooper et al., 2018, 2017). These results suggest that integration of information about the subjective value of the messages to the individual is an important pathway through which persuasive messages lead to successful behavior change. Collectively, all three of these neuroimaging analysis approaches suggest that the individuals are more likely to be persuaded by persuasive appeals, choose consumer products, and engage in health behaviors when they evaluate those options as more relevant and valuable to the self (Falk, O'Donnell, Cascio, et al., 2015; Genevsky et al., 2017). The recent development of multivariate and connectivity approaches has improved our ability to predict behavior as well as understand how the brain is representing and processing task-relevant information. These burgeoning areas of research will likely play an important role in shaping the field in the coming years.

PREDICTING AGGREGATE, OUT-OF-SAMPLE GROUP OUTCOMES

Brain activation in regions that predict behavior change at the individual level can also be used to predict aggregate behavior across groups of individuals whose brains are not scanned (Berns & Moore, 2012; Falk et al., 2015; Falk, Berkman, & Lieberman, 2012; Genevsky & Knutson, 2015). In a persuasive messaging task, brain activation in a small group of participants predicted the population-level success of a set of health messages (Falk, O'Donnell, Tompson, et al., 2015; Falk et al., 2012); however, the relevance of the message content moderated the relationship between brain activation and aggregate group response (Falk, O'Donnell, Tompson, et al., 2015). For instance, the relationship between activation in vmPFC, dmPFC, PCC, and TPJ in a small group of participants who viewed anti-smoking messages and the percentage of individuals who clicked on an email link containing one of the ads (as part of a large-scale email campaign in the state of New York) was significantly stronger for ads that were smoking-relevant than for ads that were compositionally similar but behaviorally irrelevant (Falk, O'Donnell, Tompson, et al., 2015).

Figure 3 Brain Activation
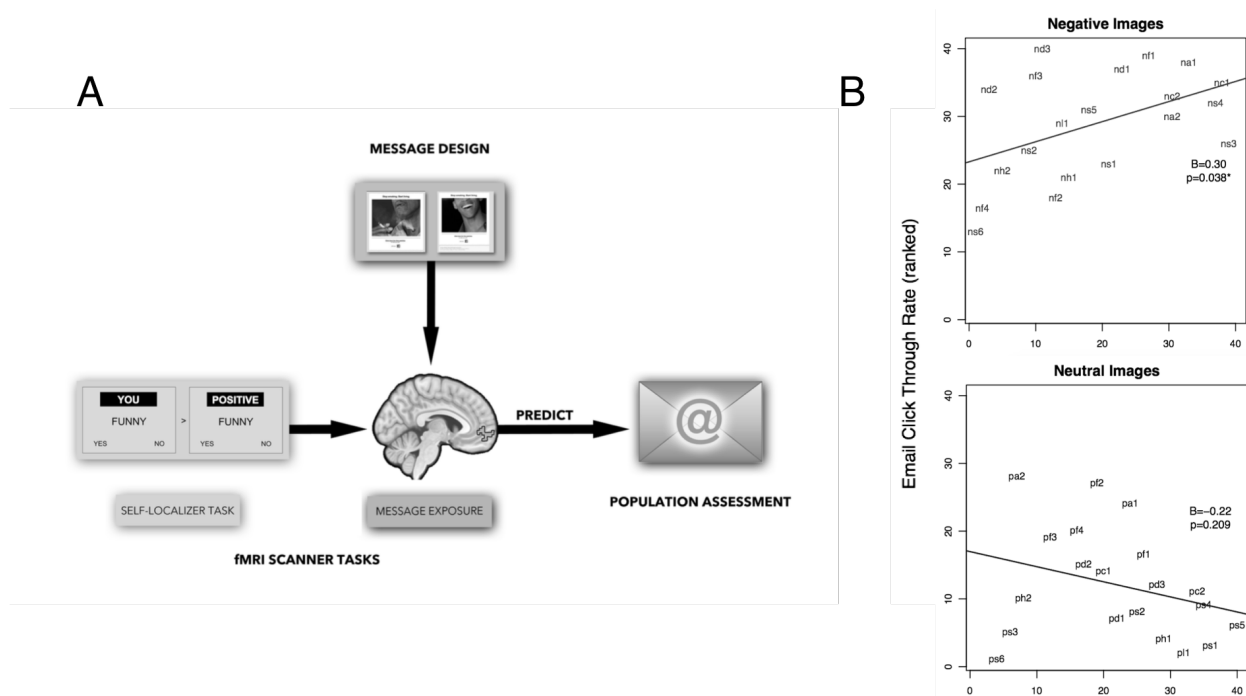
Note: Brain activation in subregion of vmPFC identified in self-localizer task predicted which messages would elicit greater responses in a large-scale email campaign (3A). Behavior-relevant messages that recruited vmPFC more were more likely to be clicked on, whereas behavior-irrelevant messages that recruited vmPFC were not any more likely to be clicked on (3B; adapted from Falk et al. (2015), by permission of Oxford University Press).

Additional research has shown that brain activation can also predict aggregate consumer behavior (Berns & Moore, 2012; Genevsky & Knutson, 2015; Genevsky et al., 2017; Kühn, Strelow, & Gallinat, 2016; Venkatraman et al., 2015). One study demonstrated that VS activation while a small sample of individuals listened to songs of relatively unknown artists predicted how popular those songs will be over the next 3 years, such that songs that elicited greater activation in VS sold more albums over the next 3 years (Berns & Moore, 2012). Activation in vmPFC and VS also predicted crowdfunding outcomes (Genevsky & Knutson, 2015; Genevsky et al., 2017). Images and descriptions for crowdfunding projects that elicited greater vmPFC and VS activation while a small group of participants evaluated the projects were more likely to receive enough investments to ultimately be funded (Genevsky & Knutson, 2015; Genevsky et al., 2017). Additionally, ads for chocolate products that elicited greater activation in vmPFC and VS led to greater increases in chocolate sales in a supermarket where they were sold (Kühn et al., 2016).

While the above research focused on average activation in single brain regions, multivariate patterns can in some case better predict behavior than average activation within a single brain region or group of brain regions (Genevsky et al., 2017). Whereas models incorporating average brain activation in vmPFC and VS (as well as amygdala, insula, and inferior frontal gyrus) successfully predicted funding outcomes for projects on a crowdfunding website with 59-61%

accuracy (significantly better than chance), whole-brain multivariate patterns were able to successfully predict funding outcomes with 65-67% accuracy (Genevsky et al., 2017). Across domains, the studies described above show consistently that brain activation improves our ability to predict aggregate group behaviors. Brain activation predicts group-level popularity of music songs (Berns & Moore, 2012) as well as the group-level success of persuasive health messages (Falk, O'Donnell, Tompson, et al., 2015; Falk et al., 2012), consumer product ads (Kühn et al., 2016; Venkatraman et al., 2015), and crowdfunding ads (Genevsky & Knutson, 2015; Genevsky et al., 2017) even after controlling for self-report measures of behavioral intentions or preferences of the test sample in response to the messages. In many cases, brain activation provides additional information about aggregate group behavior beyond self-report measures (Berns & Moore, 2012; Falk, O'Donnell, Tompson, et al., 2015; Genevsky & Knutson, 2015; Genevsky et al., 2017; Scholz et al., 2017; Venkatraman et al., 2015).

PREDICTING SOCIAL INTERACTIONS AND PEER INFLUENCE

In addition to being influenced by mass media campaigns (as described above), peoples' behavior is also routinely influenced by social norms and interpersonal influence (Cialdini, Kallgren, & Reno, 1991); to this end, a growing body of literature has explored brain processes associated with changing attitudes and behavior in response to peer influence (Cascio, O'Donnell, Bayer, Tinney, & Falk, 2015; Klucharev, Hytönen, Rijpkema, Smidts, & Fernández, 2009; Wasylyshyn et al., 2018), and on the other side of the coin, what motivates people to share information with others (Baek, Scholz, O'Donnell, & Falk, 2017; Falk, Morelli, Welborn, Dambacher, & Lieberman, 2013; Scholz et al., 2017).

Brain activity within the value system, as well as regions that help people understand the mental states of others (e.g., TPJ, dmPFC) have been implicated in conformity to peer judgments (Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Cascio, O'Donnell, et al., 2015; Klucharev et al., 2009; Mason, Dyer, & Norton, 2009; Nook & Zaki, 2015; Zaki, Schirmer, & Mitchell, 2011). A recent study found that individuals who had greater brain activity in VS and TPJ showed stronger susceptibility to conform to their peers' preferences (Cascio, O'Donnell, et al., 2015). In this case, both value regions and mentalizing regions are associated with adapting in response to information about others' preferences, suggesting that people may be integrating these two types of information (the value of objects to the self and the value to others). More broadly, people who are more sensitive to social cues in general are also more susceptible to conforming to peer influences. Individuals who exhibited the greatest activation in mentalizing regions during the common social experience of exclusion were then more susceptible to peer influence in a risky driving task in a driving simulator a few weeks later (Falk et al., 2014); these results suggest that if one's brain is more sensitive to potential social threats, it may be adaptive to fit in by conforming to peer influences. Individuals who showed greater connectivity between mentalizing regions and the rest of the brain were also more susceptible to peer influence (Wasylyshyn et al., 2018). These results support the idea that filtering information through mentalizing systems is an important pathway through which conformity in social groups operates.

In addition to capturing how people respond to others, brain activation in mentalizing and value regions is associated with how people exert influence on others. One way of measuring this behavior is by looking at the brain regions and psychological processes that underlie individuals'

choices to share novel information with others. Here, greater activation in vmPFC, VS, and TPJ predicted what ideas for television shows individuals were more likely to share (Falk et al., 2013). In other work, greater activation in vmPFC, VS, PCC, dmPFC, and TPJ was associated with decisions to select and share news articles (Baek et al., 2017).

Brain activation can also provide additional information about aggregate group social interactions. Scholz and colleagues (2017) tested whether brain regions involved in self-processing (e.g., vmPFC and PCC), mentalizing (e.g., dmPFC and TPJ), and subjective value (e.g., vmPFC and VS) would be associated with how viral a New York Times article was, indexed by how often people shared the article. Activation in all three sets of brain regions was positively correlated with greater article virality. More specifically, the effects of self-processing and mentalizing on article virality were mediated through subjective value, suggesting that brain regions involved in self and social processing index the relevance of the information to the self and close others, and that the relevance across domains is combined into a value index which then determines whether people share the article (Scholz et al., 2017).

Collectively, these results indicate that brain activation is a reliable predictor of broader susceptibility to social influences on behavior, demonstrating an influence on behavior that extends beyond explicitly persuasive messages. Activation in brain regions linked to processing the value of the social behaviors to the self as well as considering the social value of the behavior to others is particularly relevant to these broader forms of social influence. As we will see below, however, the relationship between brain activation and social behavior is also often contingent on social context. Social network position, cultural background, and socioeconomic status all influence what values, beliefs, and goals are salient for an individual (Markus & Kitayama, 1991; Stephens, Markus, & Phillips, 2014; Visser & Mirabile, 2004), which in turn influences how they process behavioral options such as whether to quit smoking (Pegors et al., 2017), respond to peer influence (O'Donnell, Bayer, Cascio, & Falk, 2017), or donate to a charity (Park, Blevins, Knutson, & Tsai, 2017).

SOCIOCULTURAL CONTEXT

The majority of studies examining the link between brain activation and behavior focus on a direct relationship between brain activation and behavior, but to improve our ability to understand social behavior, it is also important to understand the heterogeneity in the relationship between brain and behavior (Tompson et al., 2015). There are many ways that sociocultural context could influence behavior as well as the relationship between brain activation and behavior.; however, the two primary routes include (1) normative influence, where individuals engage in a behavior because of what other people care about, and (2) individual values and beliefs, where individuals engage in a behavior because of their personal interests and concerns. A number of psychological theories argue that both individual attitudes and social norms influence behavioral intentions (Cialdini et al., 1991; Fishbein & Ajzen, 1975). Extending this logic, one's position in their social network, cultural background, and socioeconomic status will also likely influence what norms and beliefs surround an individual. As such, sociocultural context may reinforce and promote different types of normative beliefs about how people should act and what they should care about; these norms may in turn influence the types of goals, values, and beliefs that people hold (Markus & Kitayama, 1991; Riemer et al., 2014). Moreover, sociocultural context should also influence how sensitive individuals are to these norms (Riemer,

Shavitt, Koo, & Markus, 2014; Stephens et al., 2014), which may be reflected in the brain regions recruited when making a choice or evaluating various behavioral options.

One social factor that likely influences how people evaluate behavioral options is social network composition. One study hypothesized the extent to which individuals have close friends who smoke should influence how people evaluate anti-smoking messages (Pegors et al., 2017). In particular, individuals with more smokers in their network might be exposed to more examples of negative impacts of smoking and conversations about the desire to stop smoking, which might influence how much the messages resonate with them (Pegors et al., 2017). Results confirmed that individuals with more smokers than non-smokers in their social networks who also had stronger multivariate patterns representing message content in vmPFC were more likely to reduce smoking when exposed to anti-smoking messages (Pegors et al., 2017). This work shows that persuasive content can affect behavior differently based on social context and thus how it is interpreted and received.

In addition to social network composition, an individual's position in their network also influences how they respond to information about others' opinions. Some individuals in a network are more ideally positioned to encounter, adopt, and share new information (Burt, Kilduff, & Tasselli, 2013). This experience sharing information between groups of individuals might relate to an individual's ability or motivation to take the perspective of others, which would in turn influence how they evaluate information about others' opinions. One study found that people who are in a more central position with greater potential opportunities to broker information between people in their social network exhibited greater activation in mentalizing brain regions when incorporating peers' preferences into a rating of a smart phone app (O'Donnell et al., 2017). Taken together, these studies suggest that social network properties influence how individuals process behavioral options.

Similarly, Schmaelzle and colleagues (2017) examined functional connectivity during one common social experience, social exclusion, and found that individuals showed stronger connectivity between brain regions involved in mentalizing during exclusion compared to inclusion. Interestingly, they also found that this relationship was moderated by social network density, such that individuals with less dense friendship networks showed a stronger link between mentalizing network connectivity and rejection sensitivity (Schmälzle et al., 2017). It is possible that social network composition influences what strategies individuals use when interacting with others, which may in turn influence how they respond to social exclusion. Frequently interacting with people who are not connected with others in your social group may sensitize individuals to potentially excluding others and make them more likely to consider others' perspectives during social interactions.

Figure 4 Brain Networks and Social Networks
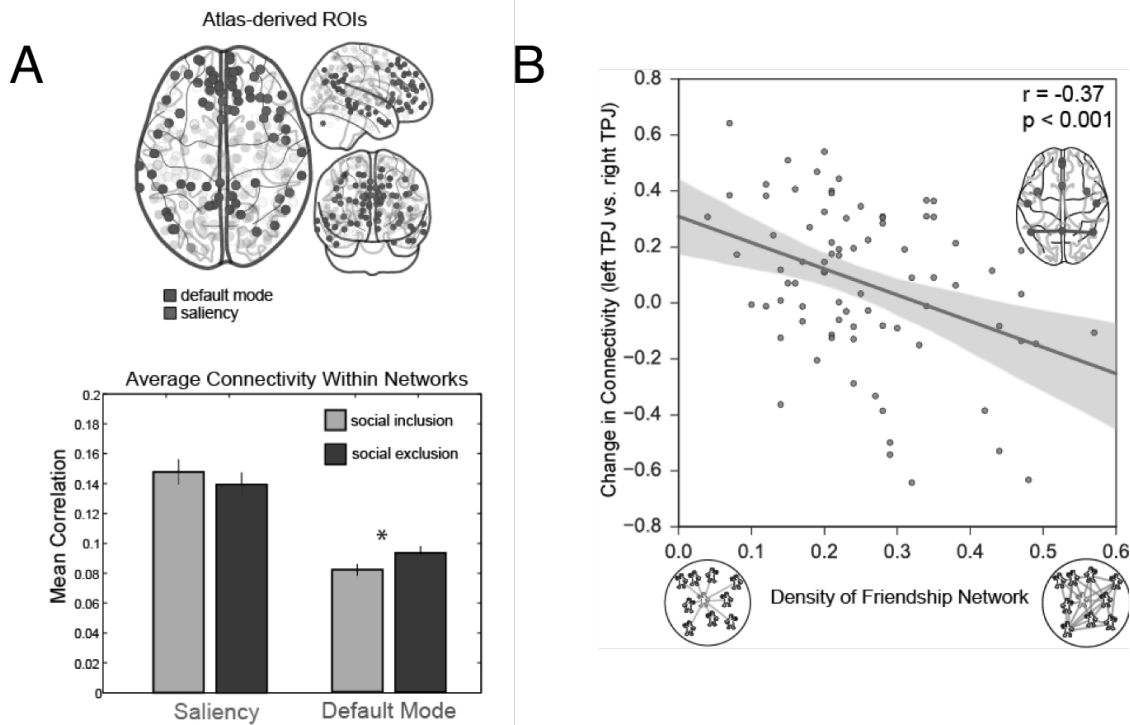
Note: Brain networks and social networks. Recent work shows that network connectivity within parts of the default mode subnetwork is greater following social exclusion (4A), and this effect is moderated by the density of an individual's social network (4B; adapted with permission from Schmaelzle et al., 2017).

Culture also influences brain activation, including the link between brain activation and behavior. Across various different social, cognitive, and affective tasks, people from Western cultures were more likely to show greater activation in self-processing or value regions including vmPFC, whereas people from Asian cultures were more likely to show greater activation in mentalizing regions, including dmPFC and TPJ (Han & Ma, 2014). Results demonstrated that when making trait judgments either about the self or a friend, Chinese participants were more likely to recruit TPJ to make these judgments whereas Danish participants were more likely to recruit vmPFC, and these cultural differences were mediated by differences in interdependence (Ma et al., 2012).

Cultural differences in normative beliefs also influence how people behave when asked to donate to charities. People from East Asian cultures value balanced emotions over high arousal, highly positive emotions (Tsai, 2007), and as a result, are more likely to donate to recipients whose emotional expression matches their cultural norms (Park et al., 2017). That is, East Asians trust and donate more money to charities represented by people with calm, balanced facial expressions, whereas European Americans trust and donate more money to charities represented by people with excited facial expressions (Park et al., 2017). The researchers further found that increased trust for people expressing culturally sanctioned emotions led to a stronger value signal but reduced mentalizing, and ultimately greater likelihood of donating. Specifically, cultural differences in donations were linked to differences in brain activation in VS, PCC, and TPJ (Park et al., 2017). TPJ activation was negatively correlated with the fit between an individual's cultural beliefs about what emotions are valued, and individuals were more likely to donate to

charities that elicited greater VS activation but weaker PCC and TPJ activation (Park et al., 2017).

Lastly, socioeconomic factors such as parents' educational status strongly influence how individuals perceive choice options (Stephens, Markus, & Townsend, 2007) and their motivation to influence versus adjust to their environment (Savani, Markus, & Conner, 2008). As described above, activation in social pain and mentalizing regions when individuals are excluded from a group was associated with how susceptible individuals were to peer influence in a driving simulation weeks later (Falk et al., 2014); however, this effect was moderated by socioeconomic status (SES): adolescents from lower SES backgrounds showed a stronger relationship between social pain regions and susceptibility to peer influence, whereas individuals from high SES backgrounds were more susceptible to peer influence when they exhibited weaker activation in social pain and mentalizing regions (Cascio, O'Donnell, Simons-Morton, Bingham, & Falk, 2017). This work suggests that how individuals respond to and manage negative affective reactions to exclusion differs as a function of SES, and activation in social pain regions might actually promote susceptibility to peer influence.

Taken together, these three lines of research on moderating roles of social networks, culture, and SES show that the relationship between brain activation and behavior is context-dependent. In order to accurately predict behavior, it is therefore important to consider biological factors such as brain activation as well as sociocultural factors such social networks, culture, or SES. However, none of these studies have considered how multiple sociocultural factors might interact. Future research could examine whether social network composition might buffer against the effects of SES on neural responses to social exclusion, or investigate if differences in cultural values modulate the relationship between social network position and behavior.

FUTURE DIRECTIONS

Across the research highlighted in this review, results demonstrate that incorporating measures of brain activation improves our ability to predict human behavior at both the individual and group level. Furthermore, the specific brain regions and network connectivity patterns provide insight into the psychological processes underlying social behaviors such as persuasion, peer influence, and information sharing. Critically, these associations were identified between brain activation and real-world behaviors, indicating the utility of laboratory research to capture behavioral variability within our daily lives; however, there is still progress and advances to be made in the experimental paradigms employed to better capture the richness and complexity of real-world behaviors and social interactions.

The majority of the research reviewed here utilized fMRI where participants lie on their backs in a scanner with minimal head and body movement, responding to isolated stimuli presented on a single computer monitor. While this environment is designed for studying specific cognitive processes, without excessive noise overriding the physiological signal of interest or confounds of concurrent tasks, the laboratory may not fully capture how tasks are performed in the real-world, where our bodies and eyes move freely while we perform multiple, concurrent tasks (Vettel et al., 2012). Even in laboratory settings, complex, naturalistic stimuli elicit different patterns of activation and inter-regional connectivity compared to more controlled, experimentally manipulated stimuli (Hasson, Malach, & Heeger, 2010). This complements additional studies that have also identified performance differences when tasks are embedded in naturalistic

contexts (Gramann et al., 2011; Kingstone, Smilek, Ristic, Kelland Friesen, & Eastwood, 2003; Oie & McDowell, 2011; Shackman, Maxwell, McMenamin, Greischar, & Davidson, 2011). Recent advances in portable neuroimaging technologies, such as several commercial EEG systems (Hairston et al., 2014; Ries, Touryan, Vettel, McDowell, & Hairston, 2014) make it possible to measure brain activation while individuals are navigating complex environments (McDowell et al., 2013; Melnik et al., 2017; Oliveira, Schlink, Hairston, König, & Ferris, 2016a, 2016b). Thus, we contend that the brain-as-predictor approach provides a productive framework to study real-world behaviors when combined with ongoing innovations in mobile neuroimaging and artifact rejection techniques (Lawhern, Hairston, McDowell, Westerfield, & Robbins, 2012; Oliveira, Schlink, Hairston, König, & Ferris, 2017). For example, in many studies on social exclusion and peer influence, participants never actually meet their interaction partners. Mobile neuroimaging makes it possible to measure brain activation while individuals are navigating complex social dynamics, which can provide further insight into how individuals behave in naturalistic social interactions. For instance, the degree to which students in a classroom have brain patterns that are in sync with one another predicts classroom engagement and social dynamics, suggesting that shared attention in group settings is a potentially important feature of successful teaching (Dikker et al., 2017). Ongoing work in our laboratories examines how dyadic communication is influenced by the real-world risk of driving along the interstate while a passenger communicates stories to the driver (Vettel et al., 2018). Likewise, tools from computational social science (e.g., social network analysis; computational linguistic methods; geolocation tracking) are rapidly making it more possible to integrate large amounts of information about an individual's specific social environment into models of brain-behavior relationships.

In addition to considering how new tools (such as mobile neuroimaging) might enable researchers to better model brain-behavior relationships, it is also important to consider how this knowledge might be applied to influence or inform how individuals behave. In other cases, this work might be helpful in understanding how to increase more personal resilience to deception or manipulation. The studies described above reveal a few key insights. First, neuroimaging research can help identify which messages or techniques are most likely to be effective in influencing behavior (e.g., Falk, O'Donnell, Tompson, et al., 2015). Second, neuroimaging research can help identify which individuals are more or less susceptible to influence (e.g., Wasylyshyn et al., 2018). However, the third, and most important, insight is that these studies indicate that brain connectivity is shaped by, and malleable to, environmental factors. Contextual factors such as social networks (e.g., Pegors et al., 2017) and short-term shift in mindset (e.g., Falk, O'Donnell, Cascio, et al., 2015) can influence the brain-behavior relationship, including how people respond to persuasive appeals. Thus, while neuroimaging research can potentially identify which individuals will be more likely to change their behaviors, it is also possible to use neuroimaging to identify how and when persuasive appeals are more or less effective.

CONCLUSION

In this chapter, we have discussed evidence that brain activation, including multivariate patterns of activation within and connectivity between brain regions, is associated with individual and aggregate health behaviors (Cooper et al., 2015; Falk, O'Donnell, Cascio, et al., 2015; Falk et al., 2011), individual and aggregate consumer behaviors (Genevsky & Knutson, 2015; Genevsky et

al., 2017; Levy et al., 2011), responses to social exclusion (Schmälzle et al., 2017), responses to peer influence (Cascio, O'Donnell, et al., 2015; Falk et al., 2013; Wasylyshyn et al., 2018), and information sharing (Baek et al., 2017; Scholz et al., 2017). In many cases, brain activation provides information that predicts behavior with an accuracy that is above and beyond that obtained from self-report measures of attitudes, preferences, or intentions (Falk, O'Donnell, Tompson, et al., 2015; Genevsky et al., 2017; Venkatraman et al., 2015)

Across these diverse domains, brain regions involved in social and reward processing are frequently associated with behavior, suggesting that brain activation might be providing insight into how people process information about the reward value of various options or outcomes as well as how they consider the perspective and mental states of others. In particular, vmPFC and VS are most often associated with behavior in domains where behaviors are primarily self-focused (e.g., health behavior change, consumer choices). By contrast, dmPFC and TPJ are more often implicated in domains where others' thoughts and opinions are relevant (e.g., information sharing, social influence, and exclusion).

Moreover, the association between brain activation and individual and group behavior is context-dependent. Social factors including social network position, culture, and socioeconomic status influence individuals' beliefs, values, and goals (Markus & Kitayama, 1991; Stephens et al., 2014; Visser & Mirabile, 2004), which in turn influence how they make decisions (Perry-Smith & Shalley, 2003; Riemer et al., 2014; Stephens et al., 2007), interact with close and distant others (Xie, Cairns, & Cairns, 1999; Wagner, Humphrey, Meyer, & Hollenbeck, 2012), and process persuasive messages (Uskul & Oyserman, 2010; van Noort, Antheunis, & van Reijmersdal, 2012). These effects of social context are then reflected in the relationship between brain activation and behavior. The extent to which social and reward-related brain regions are linked to individual behavior is influenced by social network position (O'Donnell et al., 2017; Pegors et al., 2017), culture (Park et al., 2017; Tompson et al., 2015), and socioeconomic status (Cascio et al., 2017; Muscatell et al., 2012).

Recent advances in multivariate approaches for analyzing brain data can also improve our ability to predict behavior and provide additional insight into the psychological processes mediating this effect. MVPA and RSA provide insight into how individual brain regions encode information about behavioral options (Kriegeskorte, 2011), whereas network approaches provide insight into how brain regions work together to evaluate information about the behavioral options (Bassett & Sporns, 2017).

In sum, neuroimaging research can advance understanding of how group-level dynamics emerge, including how public service announcements influence ad campaign success (Falk et al., 2015; Venkatraman et al., 2015), how information spreads throughout a group (Baek et al., 2017; Scholz et al., 2017), and how information about group members' opinions influence individual behaviors (Berns, Capra, Moore, & Noussair, 2010; Cascio, O'Donnell, et al., 2015; Tomlin, Nedic, Prentice, Holmes, & Cohen, 2013). These methods provide novel insights into how individuals behave in a social world and will serve as useful tools for researchers aiming to understand and predict human behavior.

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Biographies

Steven Tompson is currently the Robert J. Eichelberger Distinguished Postdoctoral Fellow under the Human Sciences Campaign in the U.S. Army Research Laboratory. He received his PhD in Social Psychology from the University of Michigan in 2016 and worked as a postdoctoral researcher at the University of Pennsylvania from 2016-2018. While in graduate school, he received an NSF fellowship to study decision-making in the US and Japan. He uses neuroimaging and experimental methods to understand how people think about the self and their relationships, make choices, and engage in healthy behaviors. Along these lines, he has conducted research on how cultural background and social network properties influence decision-making in consumer and health contexts, as well as how people learn and acquire knowledge about their social context (e.g., cultural norms and social networks). A key theme in his research is understanding how biological factors (including brain activation and genes) interact with social context to influence behavior.

Emily Falk is an expert in the neurobiology of social influence and behavior change. She serves as an Associate Professor of Communication, Psychology, and Marketing at the University of Pennsylvania, where she also directs Penn's Communication Neuroscience Lab and serves as a Distinguished Fellow of the Annenberg Public Policy Center. Her research examines what makes messages persuasive, why and how ideas spread and what makes people effective communicators. Her recent work also examines how people's social networks change the way they use their brains. Prof. Falk's work has been honored by career awards from the International

Communication Association and The Society for Personality and Social Psychology as well as funding from the National Institutes of Health, including the NIH Director's New Innovator Award, the Department of Defense, including the DARPA Young Faculty Award, the National Science Foundation and by private foundations. She was named a Rising Star by the Association for Psychological Science, and has served as a PopTech Science and Innovation Fellow. Prior to her doctoral work, Prof. Falk was a Fulbright Fellow in health policy. She received her bachelor's degree in Neuroscience from Brown University, and her Ph.D. in Psychology from the University of California, Los Angeles (UCLA).

Danielle Bassett is currently a MacArthur Fellow, as well as the Eduardo D. Glandt Faculty Fellow, and Associate Professor of Bioengineering at the University of Pennsylvania. Dr. Bassett has 14 years of experience in developing and applying tools from network science to understand large-scale brain network organization estimated from structural and functional neuroimaging data from a wide range of modalities including MRI, fMRI, ECOG, DTI, DSI, and MEG in humans. Dr. Bassett has published extensively on topics related to network science, the work includes 174 accepted or published articles that have together garnered >12,600 citations (h-index = 46). Dr. Bassett received a B.S. in physics from the Pennsylvania State University and a Ph.D. in physics from the University of Cambridge, UK. Following a postdoctoral position at UC Santa Barbara, she was a Junior Research Fellow at the Sage Center for the Study of the Mind. In 2012, she was named American Psychological Association's `Rising Star' and given an Alumni Achievement Award from the Schreyer Honors College at Pennsylvania State University for extraordinary achievement under the age of 35. In 2014, she was named an Alfred P Sloan Research Fellow and received the MacArthur Fellow Genius Grant. In 2015, she received the IEEE EMBS Early Academic Achievement Award, and was named an ONR Young Investigator. In 2016, she received an NSF CAREER award and was named one of Popular Science's Brilliant 10. In 2017 she was awarded the Lagrange Prize in Complexity Science. She is the founding director of the Penn Network Visualization Program, a combined undergraduate art internship and K-12 outreach program bridging network science and the visual arts. Her work has been supported by the National Science Foundation, the National Institutes of Health, the Army Research Office, the Army Research Laboratory, the Office of Naval Research, the Defense Advanced Research Projects Agency, the ISI Foundation, the Alfred P Sloan Foundation, and the John D and Catherine T MacArthur Foundation.

Jean Vettel earned her PhD in Cognitive Neuroscience from Brown University, funded by an NSF Graduate Fellowship (2004-2007) and a DoD SMART Fellowship (2007-2009), following a lab position at Washington University in St. Louis and BA from Carnegie Mellon. Since Sept 2009, she has been a civilian neuroscientist at the U.S. Army Research Laboratory (ARL) and was promoted to Senior Science Lead in the Future Soldier Technologies Division under ARL's Human Sciences campaign. In support of ARL's Open Campus, Jean was appointed as adjunct faculty at University of California, Santa Barbara in 2014 and a visiting scholar at University of Pennsylvania in 2015. She was competitively selected for two of NAE's Frontiers of Engineering symposia for outstanding engineers under 45, received numerous Army Commendations and Certificate of Achievements for her impact to the Army, and invited to brief senior leadership in the Army, DoD, OSD, and White House. Her collaborative research investigates how physiological signals from the brain and body can be used in adaptive technology to enhance human-agent teaming by accounting for individual differences and the influence of social

context. Jean has over 100 publications and reports as well as several dozen media interviews and invited panels to communicate the value of neuroscience and human sciences research for the Army across a wide range of audiences.