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Abstract

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The subject of the current work is a highly polymorphic region on the gene coding for D4 type dopamine receptors (DRD4) consisting of a variable number of tandem repeats (VNTR) of a 48 base pair sequence. Convergent evidence from psychology, population genetics and animal behavior research support the important role the DRD4 VNTR polymorphism plays in promoting exploratory behavior.

Awe is an emotion felt in the presence of vast stimuli that are not accounted for by existing mental schema (Keltner & Haidt, 2003). In the current work I made the claim that awe signals the opportunity for exploration. Given the demonstrated relationship between the DRD4 VNTR polymorphism and exploratory behavior, the main aim of the current work is to test the relationship between this polymorphism and emotional reactivity to awe-eliciting situations. Specifically, I hypothesized that people with DRD4 VNTR variants that have been associated with exploratory behavior (carriers) would experience more awe than people who do not have those variants (non-carriers) across a range of situations.

Study 1 used a college sample to test this hypothesis, both in a controlled laboratory environment and in people's daily lives using diary methodology. Specifically, in a laboratory setting, carriers reported more awe than non-carriers in response to a film clip that had been validated as a reliable elicitor or awe, but no differences were found between groups in response to film clips that elicited compassion and amusement. Furthermore, analyses of daily diary data showed a trend such that carriers reported more awe across a 14-day diary period than non-carriers. Study 2, an ecologically valid test of my hypothesis, found that in a sample of adolescents from underserved communities who went white-water rafting, carriers reported more awe than non-carriers. Importantly, DRD4 VNTR did not have a consistent effect on any of the other emotions measured across these three contexts. I discussed the implications these findings have for our understanding of the emotion of awe and programs that aim to increase well-being through the experience of awe.

Dedication

To my parents, for instilling in me a love of learning.
To Isabelle, for the love, support, and shared adventures.

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The relationship between the D4 Dopamine Receptor gene (DRD4) and the emotion of awe

Known to play a fundamental role in learning and motivation (Wise, 2004) the neurotransmitter dopamine underpins reward-related processing in both humans and animals (Barron, Søvik, & Cornish, 2010; Deyoung, 2013; Humphries, Khamassi, & Gurney, 2012; Kayser, Mitchell, Weinstein, & Frank, 2015). A polymorphism in the D4 dopamine receptor gene (DRD4) consisting of a variable number of tandem repeats (VNTR) has been shown through previous research to be related to reward seeking behaviors and exploration (Alcaro, Huber, & Panksepp, 2007; Bardo, Donohew, & Harrington, 1996; Bodi et al., 2009; Helms, Gubner, Wilhelm, Mitchell, & Grandy, 2008; Hills, 2004a; Panksepp & Moskal, 2008; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Powell, Paulus, Hartman, Godel, & Geyer, 2003). In the current work I conceptualize awe as an emotional response to opportunities for exploration and hypothesize that certain variants of the DRD4 VNTR polymorphism are associated with an increased experience of awe. By demonstrating that the experience of awe is related to dopaminergic functioning this work contributes to a greater understanding of the nature of awe and the role awe plays in the way people learn about the world.

Dopamine and seeking behavior

Dopamine is an organic chemical that functions as a neurotransmitter in most animals (Barron et al., 2010). Broadly speaking, dopamine critically underpins organisms' reward systems. For example, dopamine neurons are activated by receiving a reward (Ljungberg et al., 1991; Ljungberg et al., 1992; Schultz et al., 1993; Mirenowicz & Schultz 1994) and dopamine is crucial to reward-based learning (Miller et al. 1981; Schultz, 1986; Schultz and Romo 1990; Mirenowicz & Schultz 1994; Flagel et al., 2011).

Another key aspect of reward-related behavior that is mediated by dopamine is what Panksepp and colleagues refer to as "seeking" behavior (Alcaro et al., 2007; Ikemoto & Panksepp, 1999; Panksepp & Moskal, 2008). Seeking is defined as an appetitive state in which organisms search their environment for life-sustaining stimuli (Alcaro et al., 2007), the most common example being food. For example, in *C. elegans*, a species of worm with a very simple nervous system, dopamine-mediated seeking behavior takes the form of making more frequent high-angle turns which increase the possibility of finding food in the immediate area (Hills, 2004b). The link between dopamine and seeking behavior is apparent in mice as well. For example, mice who were bred to lack the ability to create dopamine showd less exploratory behavior and ate less food than normal mice (Szczypka et al., 1999). Furthermore, mice that lack functioning dopamine transporters and thus, have chronically elevated dopamine levels, were found to exhibit more seeking behavior of highly-palatable chocolate-flavored food compared to mice with intact dopamine transporters when standard rodent food was freely available (Cagniard, Balsam, Brunner, & Zhuang, 2006).

Finally, seeking behavior has also been linked to dopamine in humans. For example, a body of evidence demonstrates that individual differences in activation of dopaminergic pathways in the brain predict drug seeking behaviors (for a review, Bardo, Donohew, & Harrington, 1996). Furthermore, experimental work has shown that drugs that act on the dopaminergic system can also affect how people seek rewards. For example, in a pharmacological experiment, people who were administered L-dopa, a drug that enhances dopaminergic function, picked the most rewarding option in an instrumental learning task more often than people who had been administered haloperidol, a drug that reduces dopaminergic function (Pessiglione et al., 2006). This pattern is further supported by a study of people with Parkinson's disease, a syndrome produced by the death of cells that underpin dopaminergic

pathways in the brain. People with Parkinson's disease who had never been treated with drugs before were found to demonstrate lower levels of both trait-level reward-seeking and reward learning measured by a computerized probabilistic classification task. However, when the participants began drug therapy with dopamine agonists they showed a significant increase in both trait-level reward seeking and learning (Bodi et al., 2009). In sum, in animals with nervous systems that range from very simple (*C. elegans*) to very complex (humans) dopamine plays a crucial role in promoting seeking behavior.

Dopaminergic pathways in the human brain

Empirical research demonstrates that dopamine critically underpins reward-related behavior generally, and seeking behavior specifically, in both humans and animals. However, given that humans have complex nervous systems, to begin understand the role that the DRD4 gene plays in seeking behavior, it is necessary to identify the specific circuits on which it exerts influence.

Broadly speaking, there are four main dopaminergic circuits in the brain (Agerström & Björklund, 2009). First, the mesocortical pathway, which originates in the ventral tegmental area (VTA) in the midbrain and projects to the frontal cortex, has been found to mediate the cognitive control of behavior (Le Moal & Simon, 1991). Dysfunction of the mesocortical circuit has been implicated in attention deficit hyperactivity disorder (ADHD; Heilman, Voeller, & Nadeau, 1991; Viggiano, Vallone, & Sadile, 2004) and the negative symptoms of schizophrenia (Davis, Kahn, Ko, & Davidson, 1991). Second, the mesolimbic pathway, which also originates in the VTA and projects to the nucleus accumbens (NAc), has been shown to underpin reward processing and reinforcement (Le Moal & Simon, 1991). Third, the nigrostriatal pathway, originates in the substantia nigra and projects to the caudate nucleaus and the putamen and is involved in learning and motor function. Cell death in this pathway has been implicated in Parkinson's disease (Dauer & Przedborski, 2003). Finally, the tuberoinfundibular pathway transmits from the hypothalamus to the pituitary gland and plays a role the release of hormones (Vallone, Picetti, & Borrelli, 2000).

The functionality of dopamine, its different circuits, and how they underpin reward-related processes is a massive topic: a Google Scholar search with the keywords "dopamine" and "reward" returned over 15,000 results published since 2015 alone. While many types of dopamine receptors are widely distributed in the brain, the subject of the current work, D4 type receptors, are highly localized in comparison. This localization sheds light on the dopaminergic pathway that DRD4 impacts which in turn, offers a better understanding of how and why DRD4 might be related to awe.

Five subtypes of dopamine receptors have been identified in humans. Unlike the D1 and D2 subtypes which are found in many structures throughout the brain, the D4 subtype is highly localized and expressed primarily in the prefrontal cortex, with concentrations also in the hippocampus, amygdala, and the hypothalamus (Oak, Oldenhof, & Van Tol, 2000). This localization in the prefrontal cortex suggests that that the influence of the D4 receptors will be exerted primarily through the mesocortical dopaminergic pathway, a circuit which has been associated with cognitive control (Le Moal & Simon, 1991). The limited neuroimaging work on the functional differences between different DRD4 genotypes supports this conclusion. For example, in samples of people with substance dependence, variation in the DRD4 gene has been found to predict activation in both the superior frontal gyrus (McClernon, Hutchison, Rose, & Kozink, 2007), inferior frontal gyrus (Filbey, Claus, Morgan, Forester, & Hutchison, 2012), and orbitofrontal cortex (Filbey et al., 2008) when exposed to substance use cues. Having

established that D4 type receptors are expressed primarily in the mesocortical dopaminergic circuit, which suggests that D4 receptors impact reward-processing by exerting influence on cognitive control, I proceed by reviewing the functional relevance of the DRD4 VNTR polymorphism.

The function of the DRD4 VNTR polymorphism

The current research focuses on a specific polymorphism in the exon III region of the gene that codes for D4 type dopamine receptors called the DRD4 VNTR, which consists of a 48-base pair sequence that is repeated between two and eleven times (Van Tol et al., 1991). Two repeat (2R), four repeat (4R) and seven repeat (7R) variations occur most frequently (Chang, Kidd, Livak, Pakstis, & Kidd, 1996), representing 90% of the observed allelic diversity (Ding et al., 2002). The 4R variant, which is the most common of all, is considered to be the "oldest" variant (Lichter et al., 1993). It is estimated that the 7R variant mutated from the 4R variant as a result of a rare mutational event that occurred around 40,000 years ago during the Upper Paleolithic era (Ding et al., 2002). This period of time was characterized by the rapid advancement of technology and migration out of Africa, which has been speculated to be related to the appearance of the 7R variant (Ding et al., 2002; Wang et al., 2004). That the 7R variant, the second most common DRD4 VNTR variant, is found more frequently than would be expected by chance alone suggests that it was positively selected for during this critical time for our species (Chen, Burton, Greenberger, & Dmitrieva, 1999; Ding et al., 2002; Wang et al., 2004). The 2R variant, the third most common variant, is found in high frequencies in Asian populations but rarely in populations in Africa and the Americas (Chang et al., 1996) and is thought to have been the result of a single mutation event that occurred after human populations diverged in Asia (Ding et al., 2002; Reist et al., 2007; Wang et al., 2004).

The number of times the 48 base pair sequence is repeated affects the length of the protein in the D4 dopamine receptor's third cytoplasmic loop. This structural difference changes the biochemical function of the D4 dopamine receptor. Specifically, 7R and 2R variants have a diminished ability to reduce cyclic adenosine phosphate (cAMP) compared to 4R variants (Asghari et al., 1995). cAMP is second messenger that is released within neurons when dopamine binds to their receptors that results in the cell generating electrical impulses. Unlike D1-type dopamine receptors, which increase cAMP when bound by dopamine, D4 receptors inhibit cAMP production when bound by dopamine (Beaulieu & Gainetdinov, 2011). Given that the 2R and 7R variants have diminished ability to reduce cAMP, the net result is an increase in activation compared to 4R variants. Thus, 2R and 7R variants are characterized by a partial loss of DRD4-mediated inhibition to the prefrontal cortex (Beaulieu & Gainetdinov, 2011; Matthews & Butler, 2011; Rondou, Haegeman, & Van Craenenbroeck, 2010), which is consistent with localization of D4 receptors in the mesocortical dopaminergic pathway (Oak et al., 2000).

While the majority of the extant DRD4 literature identifies cAMP reduction as the probable mechanism of the polymorphism's effect on behavior, more recently a second functional difference between DRD4 VNTR variants has been identified. For example, research has shown that DRD4 VNTR variants differ in their ability to form heteromers, a group formed of two or more different receptors that have functional characteristics that are distinct from their constituent parts in isolation (Ferré et al., 2009). Specifically, researchers have demonstrated that, compared to 2R and 4R variants, the 7R variant has a diminished ability to form functional heteromers with D2-type dopamine receptors (Borroto-Escuela et al., 2011; González et al., 2012). There are two variants of D2 receptors, short (D_{2S}) and long (D_{2L}), and the proportion in which they are expressed is affected by the a single-nucleotide polymorphism (SNP) on the

DRD2 gene rs228326. The variant that results in more numerous long receptors has been linked to deficits in working memory and attentional control (Zhang et al., 2007). Research has shown that the 7R variant of the DRD4 VNTR polymorphism does not form functional heteromers with D_{2S} receptors (González et al., 2012) and is less effective at forming heteromers with D_{2L} receptors (Borroto-Escuela et al., 2011). In effect, this constitutes a gene by gene interaction such that the pathway by which the DRD4 VNTR polymorphism affects biochemical function in the brain depends on the DRD2 gene. Indeed, researchers have found evidence of this interactive effect on alcohol dependence in humans (Mota et al., 2012). Specifically, dysfunctional D2-D4 heteromers have been found to have lower presynaptic dopaminergic control of glutamate signaling, which has been hypothesized to explain in part the relationship between the DRD4 VNTR polymorphism and ADHD (González et al., 2012) and alcohol dependence (Mota et al., 2012).

While DRD4 VNTR variants have been found to have functional differences in dopamine signaling and heteromer formation, neither of these differences has been definitively proven to be driving observed differences in complex human behavior. While determining the biochemical mechanism of the effect of the DRD4 VNTR polymorphism on human behavior is beyond the scope of the current work, the pattern of results I present may speak to one of the two pathways described above. In the method section I detail my grouping strategy and its rationale, while Appendix A contains a full treatment of the effects of alternative grouping strategies on the analyses presented.

A Note on Nomenclature

Early research on the DRD4 VNTR polymorphism made the assumption that the number of repeats was directly responsible for the observed differences in phenotype, and thus compared "short" variants, between 2 and 5 repeats, to "long" variants, consisting of more than 6 repeats (e.g. Klugar, Siegfried, & Ebstein, 2002). Another grouping strategy commonly used in the literature is to compare people with the 7R variant to those who do not have it (e.g. Schinka, Letsch, & Crawford, 2002). One limitation of these grouping strategies is that the 2R variant, which has been shown to have biochemical properties similar to the 7R variant with regards to cAMP reduction (Reist et al., 2007), would not be included in the same group as the 7R variants (Reist et al., 2007).

Given that the grouping approach and nomenclature varies widely in the extant literature, in the interest of readability in the literature review below I use the term *non-carrier* to denote the group of people that always includes those with 4R variants, which have the intact capability to reduce cAMP and form functional heteromers. The term *carrier* denotes groups of people that include the 7R variant, which has diminished capabilities to reduce cAMP and form functional heteromers. When the exact grouping strategies used in a particular study is relevant to interpreting its findings I go into further detail. Full justification of which variants are included in each group for the purposes of the current work is given in the method section.

DRD4 VNTR and exploration

Empirical research has shown that in both animals and humans, seeking behaviors are mediated by the dopaminergic system (Alcaro et al., 2007; Bardo et al., 1996; Bodi et al., 2009; Helms et al., 2008; Hills, 2004; Panksepp & Moskal, 2008; Pessiglione et al., 2006; Powell et al., 2003). While seeking behavior in nematodes consists almost entirely of searching for food; in organisms with more complex nervous systems seeking behavior is more diverse and falls into two broad categories. Generally, organisms can seek specific stimuli that meet a current need; such as, water when they are thirsty and food when they are hungry, or they may engage in more

diversive seeking, which is characterized by seeking new stimuli, or information for its own sake (Berlyne, 1954). For clarity, in the current work I use the term *exploration* to describe the diversive type of seeking in which organisms explore — most often physically, but sometimes conceptually (Litman & Spielberger, 2003) — new territory not with a specific goal, but for the sole purpose of seeking novel stimuli.

Early research exploring the relationship between the DRD4 VNTR polymorphism and exploration focused on the trait of the Novelty Seeking (NS), described as the "exhilaration or excitement in response to novel stimuli" (Cloninger, 1987, p. 575). The initial set of findings—counted as among the first to demonstrate a relationship between genes and human personality (Oak et al., 2000) — found a positive association between DRD4 and NS. Specifically, NS measured by the Tridimensional Personality Questionnaire (TPQ; Cloninger, Przybeck, & Svrakic, 1991; Cloninger et al., 1993) was found to be higher in carriers than non-carriers in both Israeli and German samples (Ebstein et al., 1996; Strobel, Wehr, Michel, & Brocke, 1999). Both of these studies found that extraversion measured by the NEO Personality Inventory (NEO-PI-R; Costa & MacCrae, 1992), was significantly related to the DRD4 VNTR polymorphism, but that the effect of the gene on NS held when controlling for extraversion. The relationship between the DRD4 VNTR polymorphism and NS replicated in U.S. and Japanese samples as well (Benjamin et al., 1996; Tomitaka et al., 1999). However, it should be noted that several studies failed to find evidence supporting a relationship between DRD4 and NS (Jonssonet al., 1997, 1998; Vandenbergh et al., 1997) and that two meta-analyses conducted in 2002 also did not find a significant effect (Klugar et al., 2002; Schinka et al., 2002). However, the conclusions of these meta-analyses may be biased by the fact that the authors classify people with 2R variants as non-carriers despite evidence from the biochemistry literature that 2R variants are more similar to 7R (Asghari et al., 1995) and should be included in the carrier group (Armbruster et al., 2009; Kang, Namkoong, & Kim, 2008; Reist et al., 2007).

While the DRD4 VNTR research assessing NS using self-report measures is equivocal, studies using population genetics clearly supports the relationship between the DRD4 polymorphism and exploration. For example, in a study of 2,320 people from 39 populations from around the world, migration of populations during the past 10 to 30,000 years (estimated from archaeological and historical linguistics records) was positively related to the prevalence of the 7R variant in the population (Chen et al., 1999). Specifically, the higher the proportion of 7R variants found in a given population, the further that population was found to have migrated. More recently, this pattern was confirmed for both 2R and 7R variants (Matthews & Butler, 2011). The authors interpret these findings as evidence that carrier variants may be linked to behaviors that are adaptive in novel environments, such as exploration (Chen et al., 1999), increasing the likelihood that the carrier genes would be passed to subsequent generations.

Research using a lifespan perspective further supports the role that the DRD4 VNTR polymorphism plays in exploration. In a study of European adults over the age of 90, researchers found that compared to non-carriers, carriers were twice as likely to exercise at least two hours a day (Grady et al., 2013). The older group also contained a significantly higher carrier to non-carrier ratio than a younger control group. Interpreting this set of findings, the authors posit that increased exercise is the mechanism by which carriers live longer. These findings converge with genetic anthropological research done with the Ariaal people of Kenya, which demonstrates that carriers are healthier when they live a nomadic lifestyle conducive to exploring new environments (Eisenberg, Campbell, Gray, & Sorenson, 2008).

The role of that DRD4 gene plays in exploration is further supported by animal models. In vervet monkeys (*Cercopithecus aethiops*), for example, individuals with the primate analog of carrier variants were found to be more likely to approach a large novel object that was placed in their home enclosure (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007). A similar effect is found in an avian model as well. In great tits (*Parus major*), variation in the DRD4 gene was found to predict the likelihood that birds would explore a new enclosure, and would approach (e.g. land on, peck at) a novel object placed in their home enclosure (Fidler et al., 2007). Finally, mirroring the study conducted with an older adult European sample, mice without D4 dopamine receptors were found to explore enriched environments that allowed for physical exercise and social contact less often than mice with intact D4 receptors (Grady et al., 2013). Also consistent with the human literature, the DRD4 knockout mice in this study lived shorter lives, which is thought to be a function of their decreased physical activity. Across three different animal models the DRD4 gene has shown to play an important role in exploratory behavior.

In sum, empirical work in psychology, behavioral genetics, and with animal models converge in support of the crucial role that the DRD4 gene plays in exploratory behavior. With these findings in mind, I make the case that the emotion of awe is elicited by situations that signal the possibility of exploration, which sets the stage for the main thesis of the current work, that the DRD4 VNTR polymorphism is related to awe.

Awe signals the opportunity for exploration

Awe has been conceptualized as a member of a family of affective states called epistemic emotions, which involve reactions to congruity (or more commonly, lack thereof) between one's own knowledge and information found in the external world (Keltner & Haidt, 2003; Keltner & Shiota, 2003; Silvia, 2010). Examples of epistemic emotions include interest, which is elicited when the complexity of a stimulus and one's ability to understand it are both appraised as high (Silvia, 2005a; Silvia, 2005b); and confusion, which is elicited when the appraised complexity of a stimulus far exceeds one's ability to understand it (Silvia, 2010). These emotions reflect specific states of understanding about the world, and motivate appropriate learning behaviors such as stimuli engagement in the case of interest and stimuli disengagement in the case of confusion.

Awe is thought to be produced by two central appraisals: perceptual vastness and need for accommodation (Keltner & Haidt, 2003). Vastness signifies a departure from one's typical human-sized frame of reference and can be instantiated by physical, temporal, and social dimensions. For example, vastness may be perceived in the gigantic size of a Redwood tree in Muir Woods National Monument (the tallest known Redwood is 112 m. tall), in trying to conceptualize how long such trees live (the oldest known Redwood is over 2,200 years old), or in the political power of President Roosevelt, who made Muir Woods a National Monument (Noss, 1999). Accommodation is necessary when new information is not accounted for by existing mental schema and thus requires updating existing schemas or creating new ones altogether (Piaget, 1976). In sum, awe is elicited by a vast mismatch between one's existing knowledge and information in the immediate environment.

Empirical research lends credence to this conceptualization of awe that impacts how people learn and explore the world around them. For example, awe has been shown to make people more likely to reject weak persuasive arguments (Griskevicius, Shiota, & Neufeld, 2010), to ascribe agency to randomly generated number patterns (Valdesolo & Graham, 2014), and to shift attention away from the self (Shiota, Keltner, & Mossman, 2007). These findings reveal

that awe promotes outward-focused attention that prioritizes more sophisticated processing of information.

Furthermore, the dual appraisals of vastness and need for accommodation in response to awe-eliciting stimuli result in the perception of a large gap in knowledge. Perceived gaps in knowledge have been theorized to be a primary motivator of curiosity (Loewenstein, 1994). Given that awe is elicited by gaps in knowledge that are vast in nature, I posit that curiosity and exploration, that is, actively seeking information, is a primary action tendency of awe. Empirical work supports the relationship between awe and exploration. For example, the link between awe and curiosity has been shown at multiple levels of analyses (Anderson et al., 2016). At the personality level, trait level awe-proneness measured by the Dispositional Positive Emotion Scale (DPES; Shiota, Keltner, & John, 2006) was found to be uniquely and positively related to the Curiosity and Exploration Inventory (CEI-II: Kashdan et al., 2009) even when controlling for related constructs such as openness to experience and the general tendency to experience positive activation. Similarly, using peer-report methodology, participants' awe-proneness scores uniquely predicted how curious participants were rated by their friends. Finally, lagged analyses of daily diary data indicated that experiences of awe on a given day predicted curiosity the next day, but that curiosity did not predict future awe. This supports my directional claim that awe leads to downstream curiosity. In a similar vein, other research has shown that awe leads people to be more open with regards to their social environment in the form of increased prosocial behavior (Piff, Dietze, Feinberg, Stancato, & Keltner, 2015) and humility (Stellar et al., 2016). In sum, awe is elicited by a vast mismatch between one's existing knowledge and information in the environment that motivates people to explore their physical and social environments.

A Social-Psychological Approach to Candidate Genes Studies

In the review above I summarized a diverse literature supporting the link between the DRD4 VNTR polymorphism and exploratory behavior. Given my characterization of awe as an emotional response to opportunities for exploration, the primary aim of the current work is to demonstrate that the DRD4 VNTR polymorphism is related to awe. To test this relationship I take a social-psychological approach, which offers advantages over other methodological approaches that have been used previously in candidate gene studies.

Most of the research on the relationship between DRD4 and human behavior has used either personality or neuroimaging approaches. These methodologies have both advantages and disadvantages. The personality approach has the advantage of being relatively inexpensive as participants can complete many measures, over multiple sessions across time, which can be correlated with the genes of interest. This approach was useful in the early research on candidate genes to help explore the range of different personality constructs that are related to by genes. Much of the literature on the DRD4 VNTR polymorphism uses a personality approach: there are over 30 studies of the relationship between the DRD4 VNTR polymorphism and personality measures of NS (Munafò, Yalcin, Willis-owen, & Flint, 2007). However, one disadvantage of this approach is that it has yielded very small effects sizes and difficulty in replication in both the DRD4 literature (Munafò et al., 2007; Schinka et al., 2002) and other candidate gene literatures more generally (Duncan & Keller, 2011; Manuck & McCaffery, 2014).

Two studies have used a neuroimaging approach to understand the how the DRD4 VNTR polymorphism relates to activation in the brain. For example, in samples of people with chemical dependency, carriers have higher activation in the mesocortical dopaminergic circuit than non-carriers when exposed to substance use cues (Filbey et al., 2008, 2012; McClernon et al., 2007). While these studies yield useful information about the neural circuits that the DRD4

VNTR polymorphism affects, difficulties of neuroimaging approaches include high expense, low sample sizes, and use of impoverished stimuli.

An alternative to personality and neuroimaging approaches is a social-psychological approach, which tests the relationship of the DRD4 VNTR polymorphism and participants' responses to carefully selected situations. This approach is valuable because it affords the opportunity to test participants' reactions to rich and ecologically valid social situations.

The social-psychological approach has been successfully used in research on other candidate genes, such as the gene that codes for oxytocin receptors, OXTR. People with OXTR variants that have been linked with increased sensitivity to social support (Kim et al., 2010) were shown to have lower cortisol levels if they interacted with a supportive friend before they participated in a stressful speech task in a laboratory setting (Chen et al., 2011). In contrast, people with OXTR variants associated with lower empathy (Rodrigues, Saslow, Garcia, John, & Keltner, 2009) did not exhibit lower cortisol levels even after receiving social support. This research converges with other work that has used stimuli-rich social tasks such as judging people's emotions (Rodrigues et al., 2009) or affiliative behavior during a face-to-face social interaction (Kogan et al., 2012) to highlight the important role that the OXTR polymorphism plays in social connection. Other research on CD38, a gene that linked to blood plasma levels of oxytocin in humans, further supports the role of oxytocin in social connection. Specifically, people with a polymorphism associated with higher circulating levels of oxytocin were found to experience more positive emotions, display more gratitude behaviors, and be more responsive when engaging in a laboratory-based social interaction with a romantic partner than people with CD38 genotype associated with lower levels of oxytocin (Algoe & Way, 2014).

Research on the serotonin transporter gene (5-HTTLPR) also supports the value of the social-psychological approach as the literature on its relationship with negative mental health outcomes, which is composed largely of studies using a personality-level approach, has been equivocal, just like the literature on DRD4 and NS. Despite early work linking certain 5-HTTLPR polymorphisms with trait-level anxiety (Lesch et al., 1996) and depression (Caspi et al., 2003), subsequent meta-analysis did not find evidence of an effect of 5-HTTLPR on negative mental health outcomes (Munafò, Durrant, Lewis, & Flint, 2009). Nevertheless, when people were exposed to rich social stimuli in a laboratory setting, a relationship was found such that people with 5-HTTLPR variants associated with negative mental health outcomes were more emotionally and physiologically reactive to both the suffering of others and being in an embarrassing situation themselves (Gyurak et al., 2012). In this case, a social-psychological approach found robust results when previous research using personality approaches had been equivocal. More broadly, the social psychological approach is a methodology that has been proven to be valuable to candidate gene literature as its use of strong situations appears to result in larger effect sizes than personality approaches. Furthermore, the ability to test the relationship between genes and behavior in rich, ecologically valid social contexts affords the opportunity to make inferences about social behavior in a way that neuroimaging studies cannot.

The Current Investigation

Given that the carrier variants of the DRD4 VNTR polymorphism have been shown to be linked to increased exploration relative to non-carrier variants, the primary aim of the current work is to test the hypothesis that carriers are more reactive to situations that signal the possibility for exploration, namely awe-eliciting situations. To examine the relationship between the DRD4 VNTR polymorphism and awe, I implemented a social-psychological approach that used varied and immersive situations as contexts. In Study 1, a multiphase study, I first

examined the emotional reactivity of carriers and non-carriers across different emotional contexts in a controlled laboratory environment using film clips. In the same sample, I used a daily diary methodology which supplemented the laboratory approach by examining how the DRD4 VNTR polymorphism related to experiences of awe and other emotions in the context of people's everyday lives. Given that Study 1 used the contexts of tightly controlled laboratory conditions and people's daily lives, Study 2 builds on Study 1 by examining the effect of the DRD4 VNTR polymorphism on awe and other emotions in the context of an immersive nature experience, a white-water rafting trip. Experiences in nature have been found to reliably elicit awe (Piff et al., 2015; Shiota et al., 2007) and thus provide an ecologically valid context in which to examine the effect of the DRD4 VNTR polymorphism on awe and other emotions. In three contexts across two studies I tested the following hypotheses:

Primary hypothesis: Carriers will report more awe than non-carriers. Given that the DRD4 VNTR polymorphism has been linked to exploration, and that awe is an emotional response to opportunities for exploration, in each of these three contexts I tested my main hypothesis that DRD4 carriers would report more awe than non-carriers. Specifically, I predicted that DRD4 carriers would report higher levels of awe in response to an awe-eliciting film clip (Study 1), more awe in their daily lives (Study 1), and more awe during a white-water rafting trip (Study 2).

Competing hypothesis: Carriers will report more emotions in general than non-carriers. An alternative hypothesis that would still account for carriers reporting more awe than non-carriers is that carriers are simply more emotionally reactive. Importantly, testing this competing hypothesis will illuminate if the relationship between the DRD4 VNTR polymorphism and awe is truly unique, or if the effect extends to the other positive emotions.

Specifically, in the laboratory session in Study 1 I tested if carriers reported more compassion in response to a compassion-eliciting film clip and more amusement in response to an amusement-eliciting film clip. Furthermore, in the diary I tested if carriers experienced more compassion, amusement, pride, gratitude, and happiness on a day-to-day basis than non-carriers. In Study 2, I examined this alternative hypothesis by testing if carriers reported more of other positive emotions during the white-water rafting trip, including amusement, gratitude, pride, and happiness.

Study 1: Awe in the Laboratory and Daily Life

Study 1 was a multi-phase study that examined the effects of DRD4 genotype on emotional reactivity both in a controlled laboratory setting and in the context of people's daily lives. The laboratory phase of the study consisted of participants viewing a series of film clips which had been validated to elicit certain distinct emotions and then reporting on their emotions. In addition to an awe-eliciting film clip, participants also viewed compassion and amusement-eliciting film clips. Compassion and amusement were selected as comparison emotions because they share key features with awe. For example, both compassion and amusement, like awe, are approach-related emotions: compassion motivates care taking behavior and amusement facilitates social play (Shiota, Campos, Keltner, & Hertenstein, 2004). Furthermore, compassion is similar to awe in that it directs attention outwards and away from the self (Goetz, Keltner, & Simon-Thomas, 2010; Shiota et al., 2007). Finally, amusement is similar to awe in that it often includes elements of accommodation (Ruch, 2008). Study 1 also included a daily diary component, which complemented the controlled laboratory component by affording an opportunity to examine how the levels of awe and other emotions that carriers and non-carriers experience in the context of their day-to-day lives are different.

Consistent with my primary hypothesis, I expected that during the laboratory session DRD4 carriers would report feeling more awe during the awe film clip, and that in the daily diary carriers would report more awe than non-carriers. Furthermore, I tested the competing hypothesis that carriers are more reactive to all emotional contexts by examining if carriers reported more emotion in response to the compassion and amusement-eliciting film clips during the laboratory session and also if they reported more of other emotions besides awe in the daily diary.

Method

Participants. One hundred and three first year undergraduates were recruited at the beginning of spring semester to participate in exchange for payment (M_{age} = 18.40, *range* 18 - 22 years, 68% female). The self-reported racial identity of the sample (participants could select multiple categories) was: 63% Asian, 21% White, 5% Black, 14% Latino, 3% Middle Eastern , and 1% Native American. We sampled from the student body at large, with only 8% of participants reporting Psychology or Cognitive Science as their intended majors. A total of 1,366 entries were completed during the 14-day diary phase of the study. Protocol compliance was excellent: participants filled out an average of 12.89 diaries on time and 72 participants completed all 14 diaries on time.

Procedure. Participants were recruited at the beginning of the semester via flyers posted throughout campus. After enrolling in the study, participants reported demographic information online. On average six weeks after enrollment, participants participated in a laboratory session in which they watched a series of film clips validated to elicit specific target emotions, reporting their emotions after each one. Film clips were presented in a fixed order: neutral, awe, neutral, compassion, and amusement. After the conclusion of the clips, participants provided a saliva sample that was used for genotyping purposes and were then briefed on the daily diary protocol they would begin that evening. Each night for 14 consecutive days participants were asked to complete an online survey in which they reported on the emotions and experiences they had during the day.

Materials and Measures.

Self-report emotions after film clips. After watching each film clip, participants reported how much of each of 10 different positive emotions they felt during the film clip on a scale from 1 (*none at all*) to 10 (*as much as I ever felt*). Responses to three items—*awe*, *wonder*, and *amazement*— were combined to form a composite measuring awe for each film clip (αs > .82). Other positive emotion items (happy, compassion/sympathy, pride, moved, relaxed/comfortable, warmth/tenderness, appreciation, and amused) were collapsed into a composite (αs > .81) with the exception that the items pertaining to the emotion targeted by the film clips (i.e. compassion or amusement) were pulled out and analyzed separately.

Film clip stimuli. The awe-inducing film clip demonstrated the size of the Earth compared to increasingly large celestial bodies, ending with VY Canis Majoris, a large star with a radius over 2,000 times larger than our own sun. Reported awe during this film clip (M = 6.72, SD = 2.16) was significantly higher than the positive emotion composite (M = 3.60, SD = 1.70), t = 18.30, $p < .001$). The compassion-inducing film clip depicted a commercial for a research hospital depicting sick children and has been used in previous compassion research (Stellar, Cohen, Oveis, & Keltner, 2015). Reported compassion during this film clip (M = 6.62, SD = 2.35) was higher than both awe (M = 3.97, SD = 2.54) and the positive emotion composite (M = 4.12, SD = 1.56), ts > 12.50, ps < .001. The amusement film clip depicted a humorous scene from the television show *I Love Lucy*. Reported amusement during this film clip (M = 7.00, SD

= 2.39) was higher than both awe (*M* = 2.14, *SD* = 1.61) and the positive emotion composite (*M* = 3.54, *SD* = 1.34), *t*s > 19.59, *p*s < .001. The neutral film clips, used in previous research (Stellar et al., 2015), depicted an instructional video on landscaping, and elicited low levels of positive emotions (*M*s < 3.60).

Daily diary emotions. For each diary entry, participants reported the extent to which they experienced different emotions that day on a scale from 1 (*not at all*) to 10 (*as much as I've ever felt*). Three items were combined to form a measure of daily experience of awe: *awe*, *wonder*, and *amazement* (average within-day α = .89). General positive emotion (*happiness*) and four discrete positive emotions (*pride*, *compassion*, *appreciation*, and *amusement*) were assessed with one item each. Additionally, participants wrote about an experience of awe they had that day, and indicated the context of these experiences. The methods and statistical analyses related to these narrative data are detailed in Appendix B.

DNA collection. During the laboratory session, saliva for the purpose of genotyping was collected via Oragene-DNA (OG-500) devices that used a stabilizing reagent so that samples could be kept viable at room temperature.

DNA extraction. Sample were centrifuged to pellet cells and the saliva was removed. Cell pellets were re-suspended in cell lysis buffer containing proteinase K and incubated at 55 C. For all samples, DNA was purified on PureLink genomic DNA silica based membrane columns. DNA was eluted from the columns using Tris HCl-EDTA, quantitated, and the purity and yield determined for each sample by measuring the absorbance of the purified DNA at A260 and A280 by spectrophotometry. Samples were aliquoted and stored at -20C until further analysis. DNA was successfully extracted from 100% of saliva samples.

DRD4 VNTR genotyping. The genomic regions of interest were PCR amplified using VNTR-specific fluorescent-labeled primers. The amplified fragments were then analyzed by capillary electrophoresis to detect the number of repeats present for the VNTR under investigation.

DRD4 VNTR grouping. In the past, human research on the DRD4 VNTR polymorphism has taken one of two analytic approaches. The most common is to compare people with at least one copy of the 7R allele to people without the 7R allele (Munafò et al., 2007). The other approach has been to separate groups based on allele length such that people with "short" alleles (2, 3, or 4-repeats) are compared to people with "long" alleles (5, 6, or 7-repeats). One important limitation of these approaches is that the length of the allele is not linearly related to biochemical function. A more current approach based on what is known about biochemical function and population genetics is to group the 2R variants with the 7R rather than the 4R (Armbruster et al., 2009; Kang et al., 2008; Reist et al., 2007). Given that my samples contain large proportions of Asian participants who, based on population genetics research are more likely to carry 2R variants (Chang et al., 1996), my own analytic strategy mirrors this approach.

Also related to grouping, rare alleles variants (e.g. 3R, 5R, 6R, 8R) occur so infrequently that their function remains poorly understood (Ding et al., 2002). It is unclear which grouping, carrier or non-carrier, would be appropriate for these rare variants. To avoid possible confounds we take what we believe is the most conservative approach and exclude people with rare alleles, leaving people with 2R, 4R, and 7R variants, which account for 90% of the allelic diversity in the DRD4 VNTR polymorphism (Ding et al., 2002), an approach with precedent in the literature (Mota et al., 2012). In light of these considerations, in the current work the carrier group is classified as participants with either 2R or 7R alleles and the non-carrier group is composed of people who are 4R homozygotes, that is, have two 4R alleles.

Results and discussion

Preliminary analyses. The frequencies of DRD4 VNTR genotypes are displayed in Table 1. Consistent with my grouping strategy participants with rare variants were excluded, in this case nine total participants with either 3, 5, 6, or 8 repeat variants. This resulted in 45 participants classified as carriers and 49 as non-carriers. DRD4 VNTR genotype was not independent from identifying as Asian, $X^2(9, N = 104) = 39.98$, $p < .001$, and thus in subsequent analyses I control for Asian race.

Laboratory session results. To test the primary and competing hypotheses that DRD4 carriers would be more reactive to the awe film clip but not the compassion or amusement film clips for each film clip I conducted a separate MANOVA with carrier status (0 = non-carrier, 1 = carrier) and race (0 = not Asian, 1 = Asian) as independent variables and the self-reported emotions as dependent variables. Consistent with my primary hypothesis, carriers reported significantly more awe during the awe-eliciting film clip than non-carriers, $t(103) = 3.00$, $p = .003$, but not higher levels of the positive emotion composite, $t(103) = 1.48$, $p = .14$. Furthermore, analysis of the compassion and amusement film clips did not support the competing hypothesis that DRD4 carriers are more reactive to all emotional contexts. Specifically, there were no significant differences between carriers and non-carriers in reported compassion, awe, or the positive emotion composite during the compassion-inducing film clip, $ts(103) < .93$, $ps = .35$. Furthermore, there were no significant differences between carriers and non-carriers in reported amusement, awe, or the positive emotion composite during the amusement-eliciting film clip, $ts(103) < 1.21$, $ps = .22$. Finally, there were no differences between groups in awe or the positive emotion composite in response to either of the neutral film clips, $ts(103) < .74$, $ps = .41$. In sum, results from the laboratory session suggest that the effect of the DRD4 VNTR polymorphism is unique to the experience of awe during an awe-eliciting film clip, and that DRD4 carriers are not simply more emotionally reactive in general[1].

Daily diary results. To test my primary and competing hypotheses that DRD4 carriers would report higher awe in the diary but not more of other positive emotions I entered the dummy coded DRD4 VNTR carrier status and race variables as independent variables into a MANOVA predicting the averages of the six positive emotions assessed across the 14 day diary: awe, amusement, compassion, gratitude, pride, and happiness. Results displayed in Table 2 indicate DRD4 VNTR carriers reported more awe than non-carriers over the diary period, a difference that was nearly significant, $p = .053$ [2]. Additionally, there were two other emotions for which there was a trend for DRD4 carriers reporting higher levels in the diary than non-carriers: amusement and happiness. Additional analyses of the narratives that participants wrote in the diaries are found in Appendix B.

Using a series of validated film clips in a controlled setting, the laboratory session of Study 1 supports my primary hypothesis that carriers would report more awe than non-carriers in response to an awe-eliciting film clip. In contrast, the competing hypothesis that carriers would be more reactive than non-carriers across all emotional contexts was not supported as there were no differences between carriers and non-carriers in emotional responding to the compassion and amusement film clips.

Results from the daily diary phase of the study are less clear. I found a trend supporting my primary hypothesis that carriers would report more awe in the diary than non-carriers; however, there were also weaker trends for carriers reporting more amusement and more happiness than non-carriers which would seem to support the competing hypothesis. However, given evidence that awe has been shown to lead to a more open social orientation (Piff et al.,

2015; Stellar et al., 2016) and increased well-being (Rudd, Vohs, & Aaker, 2012) it is possible that carriers did in fact experience more awe than non-carriers in their daily lives, and that these experiences of awe in turn led to increased connection with others and well-being, which might explain the higher levels of amusement and happiness. The diary methodology, which entails one report at the end of each day, does not have the temporal resolution to test this. One possibility for future research is to use experience sampling, which entails participants reporting their emotions multiple times each day, to test if it is the case that carriers experience more awe than non-carriers, and if awe leads to increases in downstream emotions that are other-oriented and related to well-being.

On the whole, in the contexts of a controlled laboratory setting and people's daily lives Study 1 suggests that the DRD4 VNTR polymorphism is uniquely related to the emotion of awe. Study 2 aims to build on these findings by testing my hypotheses in the context of an intense outdoors experience.

Study 2: Awe during White-water Rafting

The power of nature to elicit awe is a common literary theme brought to fruition in the writings of authors such as John Muir, Rachel Carson, and Ralph Waldo Emerson. Their contention that nature is a primary source of awe finds support in recent empirical work, which complements existing research on the benefits of nature experience (Berman, Jonides, & Kaplan, 2008; Duvall & Kaplan, 2014; Faber-Taylor & Kuo, 2006; for a review, Bratman, Hamilton, & Daily, 2012). For example, in one open-ended narrative study, when asked to write about a recent experience of awe, the most common elicitor people reported was a nature experience (Shiota et al., 2007). In more recent work, looking up into a stand of tall Eucalyptus trees led participants to feel awe and behave more prosocially compared to appropriate controls (Piff et al., 2015).

Given that nature is a reliable and powerful elicitor of awe, Study 2 built on the findings from Study 1 by testing the relationship between the DRD4 VNTR polymorphism and awe experienced during a white-water rafting trip, an ecologically valid context. Furthermore, Study 2 used a sample of adolescent high-school students from underserved communities who do not typically have the resources to take outdoors trips, which afforded the opportunity to test if the pattern observed in Study 1 generalized to non-university samples. Consistent with my primary hypothesis, I predicted that carriers would report having experienced more awe than non-carriers during the white-water rafting trip. I also tested the alternative hypothesis that carriers are more generally emotionally reactive by examining if carriers reported more amusement, gratitude, pride, and happiness during the rafting trip than non-carriers.

In this study I was further able to test the primary and competing hypotheses using data on whether participants had been white-water rafting previously. According to my primary hypothesis, I predicted that carriers would report high levels of awe regardless of whether they had been rafting before. An account consistent with the competing hypothesis would be that carriers are more reactive to novelty, and thus would report more awe that non-carriers if the white-water rafting trip was their first, but similar levels as non-carriers awe if they had been rafting previously. Specifically, I predicted an interaction such that that carriers who had been rafting before would not report less awe than carriers who had not been rafting before, but that non-carriers would show a habituation effect such that they report less awe if they have been rafting before.

Method

Participants. The sample was recruited from seven groups of high school-aged adolescents who participated in the Sierra Club's Inspiring Connections Outdoors (ICO) program in the San Francisco Bay Area. The Bay Area ICO program partners with organizations from underserved communities that do not have access to nature experiences, and enables them to go on white-water rafting trips on the South Fork American River. Participants were 92 high adolescents in high school (62% female). Fifty-six (Sample A) participated during the 2014 summer rafting season and 36 (Sample B) participated during the 2015 rafting season. The self-reported racial identity of the sample (participants could select multiple categories) was: 45% Asian, 22% Latino, 15% White, 11% Black, and 8% Native American[3]. Participants also reported whether they had been white-water rafting before.

Procedure. Two of the seven groups (29%) went on a two-day, one night rafting trip and the remainder went rafting for one day. Parental consent forms, adolescent assent forms, and baseline measures unrelated to the current work were collected at the rafting launch site in the morning before the trip began. Saliva samples were also collected before the trip began via passive drool. For Sample B only, Go Pro cameras were mounted to the front of each raft, aimed back at its occupants and recorded the entirety of the rafting trip. This footage would later be subjected to behavioral coding, the methods and results of which are detailed in Appendix C.

Rafting diaries, in which participants reported on the emotions they experienced during the trip, were distributed to participants at the end of the first day of rafting: the timing of this measure was the same regardless of whether participants were on one or two day rafting trips. At the end of the study participants were sent a $25 gift card for their participation.

Measures.

Rafting diary emotion measures. Participants rated the extent to which they felt four distinct emotions. Each emotion was assessed with single items consisting of synonym clusters (Impett et al., 2012; Srivastava, Tamir, McGonigal, John, & Gross, 2009): awe (*awe/amazement/wow!*), amusement (*amused, having fun, laughing*), gratitude (*grateful/appreciative/thankful*), and pride (*proud/sense of accomplishment/successful*). For Sample A, a five point scale was used ranging from 0 (not at all) to 4 (extremely). As the experience was very positive for most participants, the means for these emotions were within one point of the scale maximum. In an attempt to remedy this, in Sample B the scale was increased to eleven points. Descriptive statistics for each sample's measures are displayed in Table 3 and z-scored values are used in primary analyses due to difference in scaling. Another measurement difference between samples was that in Sample A general positive affect was measured with a single item (*happy/pleased/joyful*) and in Sample B positive affect was measured more precisely by differentiating between high (*excited/energetic/enthusiastic*) and low activation positive affect (*content/relaxed/peaceful*).

DNA collection. Saliva was collected for the purpose of genotyping using two different approaches depending on the sample. For Sample A, saliva was collected in 2ml cryovials via passive drool and immediately placed in a cooler of dry ice until samples could be transferred to a -20 C freezer. In Sample B, saliva was collected via passive droop with Oragene-DNA (OG-500) devices that used a stabilizing reagent so that samples could be kept viable at room temperature. DNA extraction and genotyping using PCR amplification were conducted in the same manner as described in Study 1.

Results

Preliminary analyses. One participant did not consent to be genotyped. The frequency of the different DRD4 VNTR genotypes of the remaining 92 participants in Study 2 are

displayed in Table 4. The non-carrier group consisting of 4R homozygotes represented 40.2% of the sample. Carriers, defined as people with at least one 2R or 7R allele accounted for 48.9% of the sample. In accordance with my grouping plan nine participants with rare variants were excluded from analyses. As in Study 1, Asian race was not independent of DRD4 VNTR genotype $X^2(7, N = 92) = 17.42$, $p = .015$. Thus, in these and subsequent analyses I include Asian race as a covariate to rule out the possibility that cultural differences may be driving observed effects.

Emotion reports. Emotions reported in the rafting diary from Samples A and B were z-scored and combined to test our main hypothesis that carriers would report more awe than non-carriers. Given that awe reported in the rafting diary was positively correlated with the four other positive emotions, rs > .43 , ps < .001, we tested our hypothesis using a MANCOVA, which accounted for the correlations between the dependent variables and avoids the increase in Type I error associated with testing each dependent variable separately. Carrier and non-carrier groups were dummy coded (1 and 0, respectively) and entered as a predictor with race as a covariate (Asian = 1, not Asian = 0) into a MANCOVA with the five positive emotions entered as dependent variables. As illustrated in Figure 1, results indicated that DRD4 carriers reported more awe in the rafting diary than non-carriers, $F(2,67) = 9.84$, $p = .003$, $\eta_p^2 = .13$. DRD4 carriers also reported more pride, $F(2,67) = 11.14$, $p = .001$, $\eta_p^2 = .15$, but not more amusement or gratitude, or general positive affect, Fs(2,67) < .62, ps > .38, $\eta_p^2 \leq .012$.

Examining each sample separately, carrier status did not predict general positive affect in Sample A and neither high nor low activation positive affect in Sample B. Furthermore, increasing the scale of the emotion items in the rafting diary in Sample B appears to have resulted in stronger effects with a smaller sample. Looking only at Sample B and controlling for Asian race, carriers reported more awe than non-carriers, $F(2,25) = 3.67$, $p = .011$, $\eta_p^2 = .23$, but not more of other positive emotions, including pride, Fs(2,25) < 1.70, ps > .20, $\eta_p^2 \leq .065$.

Moderation by previous rafting experience. To further test my primary and competing hypotheses, I examined if previous rafting experience interacted with carrier status to predict reports of awe in the rafting diary. Sixty-six percent of participants had never been white-water rafting before. Using the PROCESS.sps macro (Hayes, 2013) I tested if DRD4 carrier status interacted with rafting experience, which was coded dichotomously, 0 (no white-water rafting experience) and 1 (white-water rafting experience). Results indicated a significant interaction, $b = .83$, $t(78) = 2.07$, $p = .042$ [5]. As illustrated in Figure 2, there were no differences in the level of awe reported by carriers who had never been rafting before and carriers who had been rafting before. In contrast, the non-carrier group habituated to rafting: specifically, non-carriers who had been rafting before reported significantly less awe than non-carriers who had not been rafting, $b = -.71$, $t(36) = -2.36$, $p = .021$. Previous rafting experience did not interact with carrier status to predict pride, $b = .26$, $t(78) = .62$, $p = .54$.

Study 2 showed that carriers reported more awe than non-carriers in the rafting diary, providing additional support for my primary hypothesis. Further support for my primary hypothesis was provided by an interaction indicating that carriers did not show evidence of habituation if they had been rafting previously, but non-carriers did. Furthermore, carriers did not report more amusement, gratitude, or positive affect than non-carriers, which does not support the competing hypothesis that carriers are more reactive to all emotional contexts.

Carriers did in fact report higher levels of pride in the rafting diary than non-carriers. However, this effect was not found in Sample B, and in Study 1 there was no effect of carrier status on pride reported in the daily diary. The lack of systematic effects of carrier status on

pride across studies and samples suggests the possibility that the result is simply spurious. However, another possibility is that the increased awe that carriers experienced led to downstream effects such as curiosity and connection with others, behaviors known to be associated with awe (Anderson et al., 2016; Piff et al., 2015; Stellar et al., 2016), which subsequently contributed to feelings of having successfully coped with a challenge, and thus pride. As it is not feasible for participants to make reports while white-water rafting, future research using experience sampling methodology in an outdoors context where participants can make multiple reports across a day, such as hiking, is needed to test if the experience of awe in the outdoors in fact leads to downstream pride and related behaviors.

General Discussion

Empirical work from psychology, population genetics, and the animal literature support that variation in the DRD4 VNTR gene is associated with exploratory behavior (Barron et al., 2010; Chen et al., 1999; Deyoung, 2013; Humphries et al., 2012; Kayser et al., 2015; Matthews & Butler, 2011). The role that the DRD4 VNTR polymorphism plays in exploration is further suggested by the fact that the appearance of carrier variants coincided with humanity's rapid migration out of Africa and across the globe 40,000 years ago during the Upper Paleolithic era (Ding et al., 2002). Given that emotions help people respond to opportunies and threats in the environment by promoting adaptive behavior (Griskevicius et al., 2010; Keltner & Gross, 1999; Tracy, 2014), in light of the link between the DRD4 VNTR polymorphism and exploration one would expect this gene would be related to emotions that facilitate exploratory behaviors, such as the emotion of awe.

Based on theory that awe is elicited by vast and novel stimuli (Keltner & Haidt, 2003) I make the case that awe signals the opportunity for exploration. This assertion has been supported in recent empirical work demonstrating that awe leads to a more open social orientation characterized by increased prosocial and humble behavior (Piff et al., 2015; Stellar et al., 2016) which should facilitate the exploration of one's social environment and resources. Furthermore, converging evidence using personality, daily diary, and peer-report methods has demonstrated the link between awe and curiosity (Anderson et al., 2016). This characterization of awe as an emotion elicited by signals of vast opportunities for exploration provides the foundation for the current work investigating the relationship between the DRD4 VNTR polymorphism and reactivity to awe-eliciting situations.

The primary hypothesis of the current work was that people with DRD4 carrier variants, which have been linked previously with exploration, would react more strongly to awe-eliciting situations than non-carriers. This hypothesis was supported in three sets of analyses across two studies in two different populations. In a university sample, Study 1 demonstrated that in a controlled laboratory environment carriers reported more awe in response to an awe-eliciting film clip than non-carriers. Furthermore, in the same sample there was a trend such that carriers reported more awe than non-carriers in a 14 day diary protocol. Study 2 tested the primary hypothesis in a sample of high-school aged adolescents who participated in a white-water rafting trip. Consistent with my hypothesis, carriers reported more awe during the white-water rafting trip than non-carriers.

In all sets of analyses I also tested a competing hypothesis that would also explain why carriers reported more awe than non-carriers, namely, that carriers are simply more reactive across all emotion-eliciting contexts. This took the form of testing if there were differences between carriers and non-carriers in emotions besides awe. By and large this hypothesis was not supported. In Study 1 during the laboratory session there were no differences between carriers

and non-carriers in emotions reported after viewing compassion and amusement-eliciting film clips. In the daily diary phase there were no differences between carriers and non-carriers in how much compassion, gratitude, and pride they reported. However, there was a trend such that carriers reported more amusement and happiness than non-carriers. Similarly, Study 2 on the whole did not support the competing hypothesis. There were no differences between carriers and non-carriers in how much amusement, gratitude, and general positive affect they reported experiencing during a white-water rafting trip. There was however, an effect in one of the samples such that carriers reported more pride and non-carriers. Overall, there were no emotions that showed an effect of the DRD4 VNTR polymorphism across multiple analyses besides awe. Taken together, these results do not support the competing hypothesis, and suggest that the relationship between the DRD4 VNTR polymorphism and awe is unique among positive emotions.

Implications

These findings inform our understanding of the emotion of awe and its function. Given that the dopaminergic system plays an established role in learning and exploration (Barron et al., 2010; Deyoung, 2013; Humphries et al., 2012; Kayser et al., 2015; Wise, 2004), the results linking the DRD4 VNTR polymorphism to awe support the characterization of awe as an epistemic emotion that affects how we seek out and process information in our environment. An analogous situation can be found in the gratitude literature. That the experience of gratitude has been linked to genes that are related to oxytocin (Algoe & Way, 2014), a neuropeptide crucial to social bonding, speaks to the important social bonding function that gratitude serves. Similarly, that awe has been linked to a part of the dopaminergic system critical to exploration demonstrates the important role that awe plays in how we seek out information from our physical and social environment.

Given that awe has been shown to lead to increased well-being (Rudd et al., 2012) the current work also has important implications for how interventions might use awe to help people with certain mental and emotional challenges. While the current work demonstrates a link between the DRD4 VNTR polymorphism and awe, this gene has also been linked to maladaptive outcomes such as attention deficit, substance use, and post-traumatic stress disorders (Dragan & Oniszczenko, 2009; Hutchinson, McGeary, Smolen, Bryan, & Swift, 2002; Li, Sham, Owen, & He, 2006; McGeary, 2009). Given that carriers appear to be more susceptible to these challenges it is possible that they also may especially stand to benefit from experiences of awe. Specifically, programs that use nature experience as an intervention (Poulsen, Stigsdotter, & Refshage, 2015) may be particularly effective for carriers. In an era where medical treatment is being individualized based on people's genetics (Rosenberg & Restifo, 2015), research like the current work is a small step towards making it possible to optimize psychological interventions based on people's genetics.

The current work also has implications for candidate gene studies. Generally speaking, research attempting to link candidate genes to traits or disorders assessed using a personality approach have struggled to replicate initial findings and when they do, often find that the size of the effect is smaller than in initial studies (Dick et al., 2015; Duncan & Keller, 2011; Tabor, Risch, & Myers, 2002). In comparison, the current work demonstrated relatively large effect sizes. I believe a key difference is that this work used a social psychological approach that assessed the effects of the gene in question on people's emotional responding to carefully selected, stimuli-rich situations as opposed to people's self-judged general tendencies. Consistent with this argument, it is notable that the weakest effect in the current work was found

with the daily diary, in which people reported their aggregate experience over the day. Overall, the current work supports the value of the social-psychological approach to candidate gene approaches.

One limitation of the current work is that it was conducted only with North American samples. While the samples overall were racially and socioeconomically diverse, it may be the case that culture may moderate the effect of the DRD4 VNTR polymorphism on exploratory behavior, and thus awe. This possibility is supported by research demonstrating that DRD4 carriers more readily adopt culturally prescribed behaviors. Specifically, in Asian Americans carriers show a more interdependent orientation than non-carriers while in European Americans, carriers are more independent than non-carriers (Kitayama et al., 2014). Consistent with these results, it may be that exploration is consistent with an independent orientation which is the reason carriers showed increased awe reactivity in the current study, whereas in a more interdependent culture this might not be the case. However, the fact that the samples in the current work included a large proportion of people racially identifying as Asian and that in all cases the effect of the DRD4 VNTR polymorphism on awe remained after controlling for Asian race seems to speak against this alternative, culturally-based interpretation. Nevertheless, more research is needed to investigate the role that the DRD4 VNTR gene has on people's emotional lives in different cultures around the world.

Conclusion

Empirical work has characterized awe as an emotion that promotes an open orientation to our social environment (Piff et al., 2015; Stellar et al., 2016) and curious exploration of our physical environment (Anderson et al., 2016). In the current research I have added to this characterization by showing that the DRD4 VNTR gene, which has been found to predict exploratory behavior in both people and animals, is related to people's emotional reactivity to awe-eliciting situations. Given the evidence tying the emergence of DRD4 VNTR carrier variants to the human diaspora (Chen et al., 1999; Ding et al., 2002; Matthews & Butler, 2011), it is compelling to contemplate that it was the awe that our ancestors felt as they gazed out on the vast unknown Earth which spurred them toward exploration.

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Footnotes

[1] Using the Bonferroni correction, a very conservative approach to controlling Type I error when conducting multiple comparisons, to set the significant level for five tests (awe clip, compassion clip, amusement clip, and two neutral clips) to $\alpha = .01$ the patters of results remains the same.

[2] Given that data were clustered such that diary responses were nested within participants, multi-level modelling (MLM) would be an appropriate analytic approach to this data. However, using an MLM approach with carrier status and race modelled as fixed effects and intercept and participant modelled as random effects produces the same pattern of results as the MANOVA, which I present in the main text for simplicity's sake.

[3] In the first summer's sample age and race were assessed as part of a follow up survey which 79% of the sample responded to. In this sample, the mean age was 16.65 (SD = 1.65). In the second summer's sample race was assessed at the beginning of the study, and age was not measured.

[4] Controlling for Asian race, the effect becomes weaker, $b = .82$, $t(82) = 1.50$, $p = .066$.

Table 1

Frequency of DRD4 VNTR Genotypes in Study 1 and their grouping status

Genotype	Frequency	Grouping
4-4	49	Non-carrier
2-4	23	Carrier
4-7	14	Carrier
3-4	6	Excluded
2-2	5	Carrier
2-7	2	Carrier
7-7	1	Carrier
4-5	1	Excluded
4-6	2	Excluded

Note. The genotype column indicates the number of repeats at each of the two DRD4 VNTR alleles separated by a hyphen. Total n = 103.

Table 2

Distinct emotions reported in the Study 1 daily diary as a function of DRD4 carriers status

	t	*p*
Awe	1.99	.053
Amusement	1.69	.10
Compassion	1.41	.16
Gratitude	1.32	.51
Pride	.74	.46
Happiness	1.78	.072

Note. Positive t values indicate higher levels reported by carriers

Table 3

Descriptive statistics for emotions reported during white-water rafting

	Sample A (*n* = 56)		Sample B (n = 36)	
	M	*SD*	*M*	*SD*
Amusement	3.61	.68	8.77	1.94
Awe	3.30	1.03	8.47	1.77
Gratitude	3.30	.96	8.31	1.99
Pride	3.04	.89	8.67	2.00
General positive affect	3.55	.69	-	-
High activation positive affect	-	-	8.57	1.97
Low activation positive affect	-	-	7.47	2.49

Table 4

Frequency of DRD4 VNTR Genotypes in Study 2 and their grouping status

Genotype	Frequency	Grouping
4-4	37	Non-carrier
2-2	5	Carrier
2-4	20	Carrier
2-7	2	Carrier
4-7	18	Carrier
3-4	1	Excluded
4-5	3	Excluded
4-6	5	Excluded

Note. The genotype column indicates the number of repeats at each of the two DRD4 VNTR alleles separated by a hyphen. Total n = 91.

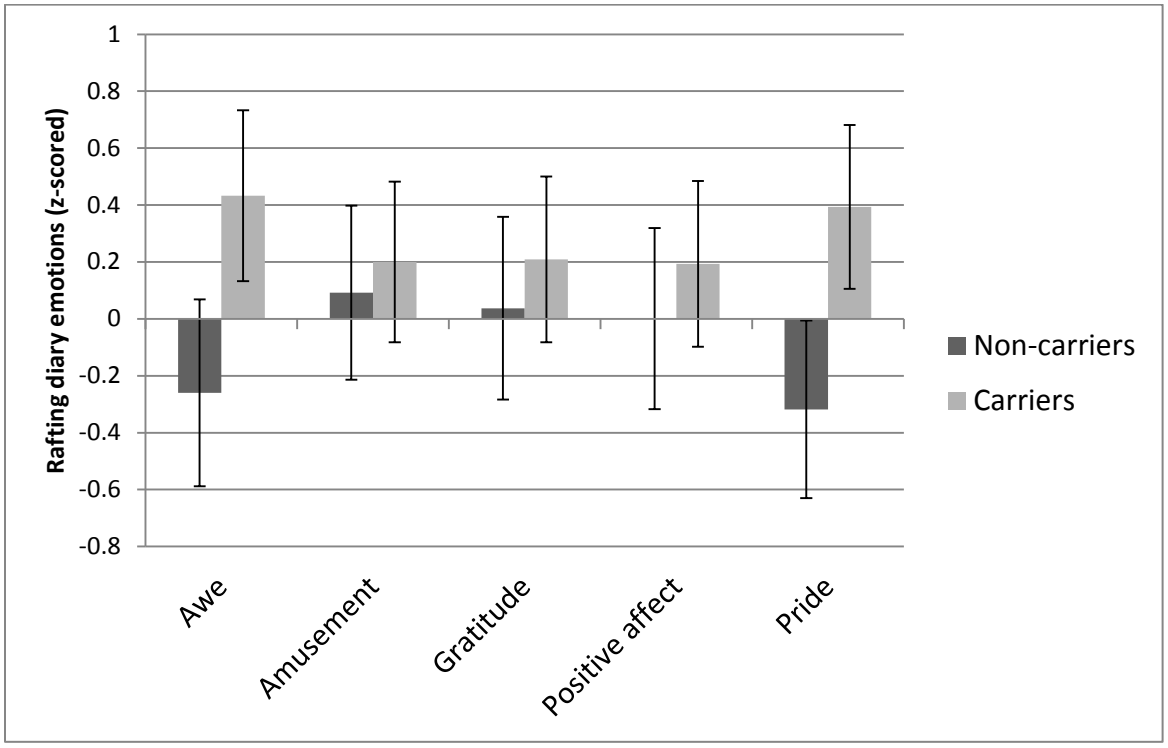

Figure 1. Emotions reported in rafting diaries as a function of DRD4 VNTR carrier status. Bars represent 95% confidence intervals.

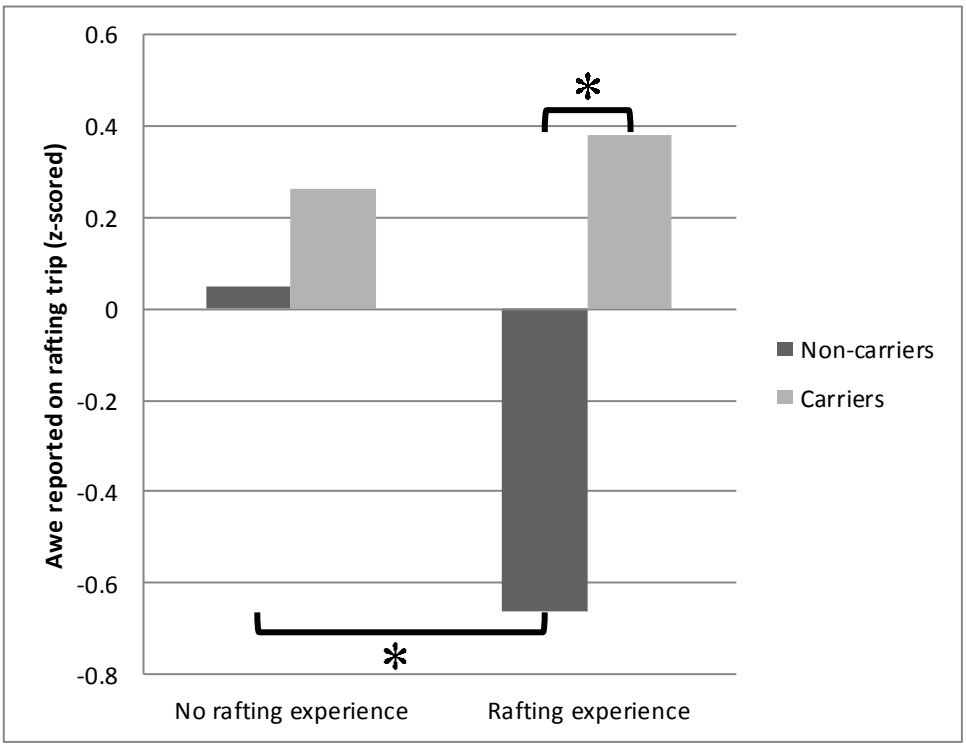

Figure 2. Reported awe as a function of DRD4 VNTR carrier status and previous rafting experience. Asterisks indicate significantly different simple slopes.

Appendix A

Alternative grouping by DRD4 variant

The analyses presented in the main text use the prevailing grouping convention, specifically categorizing people with 2R and 7R variants as carriers (Reist et al., 2007) and comparing them to 4R homozygotes, the non-carriers. These three variants make up over 90% of the allelic diversity (Ding et al., 2002) and thus, little is known about the remaining eight rare variants. As such, in the main text I take what I believe to be the most conservative approach and exclude people with these rare variants from analyses, leaving only people with 2R, 4R, and 7R variants. In this appendix I conduct exploratory analyses that test the effect of alternative grouping strategies of these three variants on awe reactivity, which may speak to the underlying biological mechanism producing these effects. I test three alternative models: an additive model based on the assumption that having two carrier alleles would have a greater effect on awe than one, a model based cAMP reduction, and a model based on what is known about different variants and their abilities to form functional heteromers.

Additive model. The grouping strategy used in the main text uses a model in which carrier variants are dominant. That is, people with two carrier alleles are grouped with people who have one carrier and one non-carrier alleles and compared to people with two non-carrier alleles. An alternative to this is an additive model, which in the context of the current work would predict that people with two carrier alleles would exhibit greater awe reactivity than people with only one carrier allele, who in turn would exhibit greater awe reactivity than people with no carrier alleles. In other words, the mean of the heterozygotes would be in between that of the homozygote carriers and non-carriers. I explored the effects of this additive model in the data from both Studies 1 and 2.

Study 1. The additive grouping strategy resulted in 49 homozygote non-carriers, 37 heterozygotes, and eight carrier homozygotes. Entering the categorical additive model carrier status variable as the predictor in an ANOVA and awe in response to the awe-eliciting film clip as the outcome resulted in a significant omnibus model, F (2,93) = 3.88, p = .024. However, this effect seems to be driven by a significant difference between the homozygote non-carrier group (M = 6.05, SE = .31) and heterozygote group (M = 7.25, SE = .35), t = 2.55, p = .024. There was no significant difference between the heterozygotes and homozygote carriers (M = 7.46, SE = .76), t = .25, p = .80. Furthermore, the additive model did not predict compassion or amusement reported in response to the compassion and amusement eliciting film clips respectively , ps > .30. Although the cell size of the homozygote carrier group is not large enough to draw definitive conclusions, these results do not support an additive model.

I also tested if the additive model predicted emotions reported in the daily diary. I entered the categorical additive carrier variable as a predictor into a MANOVA with the five positive emotions as outcomes: awe, amusement, compassion, gratitude, happiness, and pride. The additive model did not significantly predict any of the outcome emotions, ps > .17. In sum, neither the laboratory session nor daily diary support the additive model as a better fit that the model used in the main text.

Study 2. In Study 1, grouping based on an additive model resulted in 37 non-carrier homozygotes, 38 heterozygotes, and 7 carrier homozygotes. I conducted a one-way ANOVA with a three-level categorical independent variable reflecting this grouping strategy predicting z-scored awe reported in the rafting diary. Results indicated that homozygote non-carriers reported significantly less awe (M = -.18, SD = .15) than heterozygotes (M = .31, SD = .14), t(75) = 2.45, p = .019. There were no statistically significant differences in reported awe between

homozygote carriers (M = .32, SD = .33) and either of the other groups due to small cell size. However, the mean awe reported by homozygote carriers and heterozygotes was practically identical, which would appear to not lend support to an additive model approach.

In conclusion, I did not find evidence for the additive model in the current data. However, the cell size for homozygote carriers was too small to draw firm conclusions so the feasibility of an additive model in the context of awe reactivity remains an open question.

cAMP reduction model. As noted in the introduction, 2R and 7R variants are similar in that compared to the 4R variant they exhibit diminished ability to reduce cAMP, an important secondary messenger in the brain. However, the diminished functionality is greater in 7R variants than 2R variants, 70% versus 40%, respectively (Asghari et al., 1995). If the effect of the DRD4 VNTR polymorphism on awe reactivity were a strictly a direct function of capacity to reduce cAMP, those with 7R variants would exhibit higher awe reactivity than those with 2R variants. Thus, I tested if there were differences in awe reactivity between people with 2R and 7R variants.

Study 1. There were not enough 2R and 7R homozygotes to statistically compare them, so instead I compared 2R heterozygotes, that is, people with one 2R and one 4R variant (n = 23) and 7R heterozygotes, those with one 7R and one 4R variant (n = 14). There were no differences between 2R and 7R heterozygotes in reported awe, compassion, or amusement to the film clips validated to elicited those emotions, ps > .90.

I tested the cAMP reduction-based grouping strategy on the diary data as well. Using the same MANOVA approach as described above, the cAMP reduction-based grouping predictor was not significantly associated with awe, $F(1, 83) = 1.88$, $p = .16$. Thus, an alternative grouping strategy based on ability to reduce cAMP was not supported in Study1.

Study 2. Similar to Study 1, the sample in Study 2 did not contain enough 2R and 7R homozygotes — five and zero, respectively—to test for differences between the two groups. Instead, I tested for differences between 2R heterozygotes, that is, people with one 2R and one 4R variant (n = 20) and 7R heterozygotes, those with one 7R and one 4R variant (n = 18). There were no significant differences between the z-scored level of awe reported in the rafting diary by 2R heterozygotes (M = .48, SD = .21) and that of 7R heterozygotes (M = .43, SD = .28), t = -.07, p = .94.

Overall, a model based on cAMP reduction was not supported by the data: there were no significant differences between 2R and 7R heterozygotes in awe across all three contexts examined.

Heteromer formation model. While the bulk of the DRD4 VNTR literature identifies differences in cAMP reduction as a possible mechanism explaining how the gene affects human behavior, recently an alternative biological mechanism has been discussed. The common DRD4 VNTR variants have been found have differing abilities to form functional heteromers with other receptors: specifically, the 7R variant has a diminished ability to form heteromers compared to the 2R and 4R variants (Borroto-Escuela et al., 2011; González et al., 2012). Thus a grouping strategy based on heteromer functionality would group people with 2R and 4R variants together and compare them to people with the 7R variant. I tested this model based on heteromer formation in the current data.

Study 1. In Study 1 grouping based on ability to form functional heteromers resulted in 77 people classified as non-carriers group (coded as 0) and 17 classified as carriers (coded as 1). This dichotomous variable was entered as a predictor in linear regression predicting awe, compassion, and amusement in response to the film clips that had be validated to elicit those

emotions. None of these models were significant, *p*s > .47. Similarly, in the diary data using the same MANOVA approach as outlined above, the predictor was not significantly related to any of the emotions reported in the diary, *p*s > .58. Study 1 does not support an alternate grouping strategy based on heteromer formation.

Study 2. I grouped people with 2R and 4R variants (n = 55) together and compared them to people with at least one 7R allele (n = 15). There was a trend such that the people with at least one 7R allele (M = .51, SD = .13), exhibited higher z-scored awe in the rafting diary than the comparison group of people with 2R and 4R variants (M = .004, SD = .26), t = -1.72, p = .091. While this model approached significance, the model presented in the main text show a much stronger effect and thus better fit the data.

In sum, I tested three different approaches to grouping participants: an additive model, a model based on cAMP reduction, and a model based on ability to form heteromers. None of these models were supported by the data in Study 1 and 2. It is noted that some of these grouping strategies resulted in underpowered analysis and that these results should not be considered definitive. Nevertheless the grouping used in the main text, which is consistent with recent approaches in the DRD4 literature (Armbruster et al., 2009; Kang et al., 2008; Reist et al., 2007), appears to be the best fit for the data.

Cluster analyses

Up to this point in this appendix I have tried alternate grouping of participants based on biochemical properties of different DRD4 VNTR variants. In this section I attempted a bottom-up approach by using cluster analysis on awe reports to test if they generate grouping consistent with the approach used in the main text.

As awe was measured in Study 1 with one item only, I conducted cluster analyses only in Study 2 data, which measured awe with three items and thus make such analyses more viable. In the laboratory session data, I conducted a hierarchical cluster analysis with the three emotion items related to awe—*awe*, *wonder*, and *amazement*— that were reported after the awe-eliciting film clip. Visual inspection of the resulting dendrogram suggested between two to four clusters. I then conducted k-means clustering specifying two, three, and four clusters. Specifying two clusters resulted in a distance of 7.34 between cluster centers and did not appear to discriminate between participants specified as carriers and non-carriers. In this case entering carrier status and cluster membership into a chi square analysis did not yield significant results $X^2(1, N= 91) = 1.60$, p = .21. Specifying three clusters resulted in a distance of 9.89 between clusters that contained a majority of carriers and non-carriers respectively. A third intermediate cluster was specified that contained a similar number of carriers and non-carriers. A chi-square test with carrier status and cluster membership was significant, $X^2(2, N= 91) = 6.80$, p = .033. Specifying four clusters was not a better solution than three clusters as the distance between clusters was smaller.

I used a similar approach to the three awe-related items assessed in the daily diary: *awe*, *wonder*, and *amazement*. Visual inspection of the dendrogram suggested two or three solutions. I then conducted k-means cluster analysis, with two and three solutions. While the three cluster solution produced a greater distance than the two cluster solution, neither was significantly related to carrier status, $X^2 < 2.66$, *p*s > .15.

Overall, there was limited support for a bottom-up clustering approach generating groups that were significantly related to the carrier grouping variable used in in the main text. However, any conclusions should be tempered by the fact that that the sample sizes in the current work are

much smaller than is typical in work using cluster analyses: a review of research using cluster analysis found that the mean sample size for such work is almost $n = 700$ (Dolnicar, 2003).

Appendix B

Supplemental diary analyses

In study 2 in addition to the self-reported emotions, the results of which are reported in the main text, in each diary entry participants were asked to write a narrative about an experience of awe they had that day and make a series of ratings about the context of the experience. These analyses afford the opportunity to explore if carriers differ from non-carriers in terms of the thematic content and context of their awe experiences.

Method. At the end of each diary, participants wrote a short narrative about an experience of awe from that day. Participants were asked a series of questions about situational characteristics of the experience they wrote about such as the location. Germane to the current work, participants made dichotomous rating indicating whether or not the experience they wrote about occurred outside, in nature, and if it occurred in an unfamiliar place. Of the 1,366 valid diary entries, 258 (19%) were coded by participants as occurring in an unfamiliar place, 447 (33%) were coded as occurring outside, and 210 (15%) were coded as occurring in nature.

Each day participants were prompted to write about an experience of awe, however, given that awe is characterized by novelty on a vast scale we deemed it unlikely that everybody would experience awe every single day during the course of the diary. Indeed, many narratives did not reflect experiences that would likely have elicited awe (e.g. standing in a long line for coffee) and some participants wrote simply that they did not experience awe that day. Thus, narratives were coded for intensity of awe experience by coding if they explicitly involved appraisal themes both of vastness and need for accommodation (Keltner & Haidt, 2003). Coders assigned a 1 to narratives that involved both of these themes and a 0 if they did not. Two coders were assigned to each narrative: coders initially agreed on 65% of the narrative. In cases where they disagreed, a new coder broke the tie.

Results and discussion. 419 out of 1,194 narratives (26%) were coded as intense experiences of awe. Carriers and non-carriers did not differ in the number of narratives that were coded as intense, $B = .03$, $t = .73$, $p = .47$. In analyses of the participant ratings of the narratives, I conducted two sets of analyses. The first examined the relationship between carrier status and the situational ratings in the entire diary. The second set of analyses tested this effect in the subset of diary entries that had been confirmed by coders.

DRD4 carrier status was not associated with participant codes of unfamiliarity in neither the full diary sample and nor in the subset of intense awe, Bs $< .05$, ts < 1.23, ps $> .22$. Similarly, DRD4 carrier status was not significantly associated with whether participants indicated they were in nature in neither the full diary sample nor the subset of awe narratives, Bs $< .07$, ts < 1.34, ps $> .19$. In the intense awe subset, but not the full sample I found that DRD4 carriers were significantly more likely to report being outside during their awe experience, $B = .16$, $t = 2.48$, $p = .016$. None of these situational codes interacted with carrier status to predict awe ratings in the diary, Bs $< .35$, ts < 1.32, ps $< .19$.

It is intriguing that carriers were found to be outside more than non-carriers during experiences of intense awe. This finding converges with other research showing that carriers are more likely to be physically active (Grady et al., 2013). However, these results should be interpreted with caution given that only 26% of the narratives were coded as intense. More well-powered work is needed to test the robustness of this effect.

Appendix C

Behavior coding of emotions

In addition to the self-report data presented in the main text, in Study 2, Sample B emotions were also measured via behavior coding of video-taped footage. Video data were collected via Go Pro cameras that were suction cup mounted on the front of the rafts, pointing back at the participants in the raft. In addition to awe, three other emotions we coded for that preliminary viewing of the footage suggested occurred frequently in the video data: amusement, pride, and fear. Consistent with my primary hypothesis, the purpose of the behavior coding was to test if carriers expressed more awe than non-carriers. Furthermore, I tested the alternative hypothesis that carriers were more emotionally expressive in general, that is, if they expressed more amusement, pride, and fear during the rafting trip.

Method. Video footage was only collected from the second summer's data collection, Sample B. Twelve rafts were videotaped, which generated over 70 hours of footage. To reduce this data, ten clips from each raft's footage were cut that depicted the raft going through a rapid. Rapids footage was selected as the context for the behavior coding as it was the most emotionally expressive event from the footage. The ten clips were selected based on the ten largest rapids in a given camera's footage. The five seconds before the raft entered the rapid to until the five seconds after the raft had exited the raft were cut into film clips for coding.

To code a participant in a given film clip, coders watched the entire clip focusing on a single participant and used dichotomous codes (0 = absence, 1 = presence) to indicate whether the participant expressed each of the four emotions of interest. Each clip was coded by two coders, and in cases where coders disagreed, a third coder broke the tie. The following summarizes the instructions used by coders to identify emotion expressions with action units corresponding to the Facial Action Coding System (FACS; Ekman & Friesen, 1978), although coders were not FACS certified.

Awe. In the upper face, look raised eyebrows (AUs 1+2), and widened eyes (AU 5). In the lower face, the mouth is open (AUs 25+26), but not stretched as in fear (AU 20), and teeth are not displayed prominently.

Amusement. In the upper face the cheek is raised, which may result in crinkling at the outside corner of the eyes (AU 6) and the lower eyelid may be tightened (AU 7). The lips are stretched and raised (AU 12), and the lips may be parted in a smile (AU 25) and the jaw may be dropped if participant is laughing (AU 27).

Pride. Pride is expressed mostly in the body by participants raising one or both arms in the air over the head with expansive posture and often head up or raised. It may be accompanied by smiling or laughing.

Fear. In the upper face, eyes can be widened (AU 5) and brows knit and raised (AUs 1+2+4). In the lower face, lips are stretched (AU 20) and lips can be parted (AU 25) exposing teeth, and jaw is possibly dropped (AU 27), but with no upward raising of cheeks as in smiling (AU 12).

Results. A total of 360 coding instances were possible for each emotion. Twenty three percent of the footage was not able to be coded due to camera failure, or individual participants being obscured or not present in the raft. The initial two coders agreed 82% of the time. In the footage coders identified five clips with expressions of awe, 245 clips with expressions of amusement, 28 clips with expressions of pride, and 48 clips with expressions of fear. The correlation between coded awe and self-report awe was $r = .22$, $p = .21$. Coded amusement and pride similarly did not show significant correlations with their self-reported items, rs < .12, ps >

.50. Coded fear, however, correlated with the fear item in the diary (*nervous/anxious/worried*) $r = .36$, $p = .036$.

The five expressions of awe were generated by three individuals. With such a low occurrence inferential statistics are not possible. However, I note that all three individuals that expressed awe were carriers. There were no difference between carriers and non-carriers in how many amusement, pride, and fear faces were observed, Fs < .26, ps > .61.

In conclusion, the behavior coding of emotion did not yield significant differences between carriers and non-carriers. Of special note, a very low occurrence of awe expressions was observed in the rapids footage. While rapids footage was selected due to high emotional expressivity — indeed, participants were more likely to be expressing amusement than not — it is possible that going through rapids is not conducive to the open, receptive attention that is associated with awe (Shiota et al., 2007). To increase the chance of capturing expressions of awe, future coding attempts should focus on segments in which the rafts are on relatively still water when participants' attention is less constrained and they are more likely to appreciate the beauty of nature.