PALGRAVE RESEARCH HANDBOOK OF VOLUNTEERING AND NONPROFIT ASSOCIATIONS

Chapter 33: Physiological correlates of volunteering: health, neurology, hormones, and genetics

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Abstract
We review the evidence on physiological correlates of volunteering, a neglected but promising field of research. Volunteers are in better health, both self-reported and assessed, and perform better on cognitive tasks. Research thus far has not examined neurological, neurochemical, hormonal and genetic correlates of volunteering. Studies on charitable giving suggest that these physiological characteristics are related to volunteering, including specific genes (such as OXTR genes, AVPR genes, DRD4, 5HTTLPR). We recommend that future research is extended to non-western populations, focuses specifically on volunteering, and differentiates between forms of volunteering.

A. INTRODUCTION

This chapter reviews the evidence on physiological correlates of volunteering. In what way could the physiology of volunteers be different from non-volunteers? We discuss six groups of physiological correlates: in the areas of health, cognition, neurology, hormones, and genetic factors. The chapter is written from a growing awareness that most of the research on volunteering in the social sciences has ignored physiological aspects of human sociality (Baerman 2008; Von Scheve 2011), while a comprehensive explanation of volunteering clearly requires an integration of physiological aspects (Smith, 2014; more generally see Freese, Li and Wade 2003). An important part of research on volunteering is conducted by sociologists, as the reviews by David Horton Smith (1994) and John Wilson 2000; 2012) show. In the spirit of Durkheim (1897), who sought to establish sociology as a science of human behavior separate from biology, sociologists "have allowed the fact that we are social beings to obscure the biological foundations upon which our behavior ultimately rests" (Massey 2002; also see Van den Berghe 1990). Perhaps the neglect of physiological correlates of social behavior is a result of fear that evidence may be found that indeed there are such physiological correlates. Such knowledge could be dangerous. The holocaust reminds us that knowledge on physiological correlates of human behavior can be very dangerous when it gets into the wrong hands (Benton 1991). While sociologists have only recently become more open to biosocial explanations of social behavior (Freese 2008), economists have been more open to behavior genetics since the 1970s (Bowles and Gintis 2001). Also in demography (D'Onofrio and Lahey 2010) and criminology the acceptance of biological factors is growing (Ishikawa and Raine 2002; Boisvert and Vaske 2011; DeLisi, Beaver, Wright, and Vaughn 2008). In the past five years an impressive body of evidence on physiological correlates of political attitudes and behavior has been amassed (Fowler and Dawes 2008, 2013; Hatemi, Alford, Hibbing, Martin and Eaves 2009; Smith et al. 2012).

We have set ourselves the ambitious task to review the literature and weed out the false positives by seeking out replicated research results. We seek to contribute to a correction of the ignorance of physiological correlates of volunteering by reviewing the evidence on genes, hormones, neurological phenomena and health as correlates of volunteering. We distinguish between physiological causes of volunteering and the physiological consequences of volunteering. While the health consequences of volunteering have been studied quite extensively in social epidemiology and gerontology, little to no attention has been paid to physiological causes of volunteering.

B. DEFINITIONS

The general definitions in the *Handbook* Appendix are accepted in this chapter. To date, few studies have directly assessed physiological correlates of volunteering. There is more research on physiological correlates of related social behaviors, such as voting, giving to charitable organizations, and money transfers to specific other individuals. To some extent the results of these studies can be generalized to volunteering because they share a common core: they are all forms of prosocial behavior, which have collective benefits but are costly for individuals. The willingness to sacrifice own resources for the benefit of others lays at the foundation of voting (Fowler 2006) as well as other forms of prosocial behavior like charitable giving and blood donation (Bekkers 2004; Lee, Piliavin and Call 1999; Ferguson, Farrell and Lawrence 2008) and helping strangers (Ottoni-Wilhelm and Bekkers 2010). Civic duty (Loewen and Dawes 2012), social capital (Putnam 2000), and the moral principle of care (Ottoni-Wilhelm and Bekkers 2010), but not the 'prosocial personality' (Bekkers 2004), are among the variables that could explain why volunteering is positively correlated with other forms of prosocial behavior. However, volunteering also differs from other forms of prosocial behavior in its dependence on time, energy, and physical strength as resources. These unique features are in part physiological – hence this chapter.

C. HISTORICAL BACKGROUND

The current review draws primarily upon what has been called 'biosocial research' (Udry 1995) in a variety of disciplines that are normally not considered to belong to the social sciences, such as behavior genetics, neurology, and gerontology. An implicit assumption in much of the literature is that biological traits and phenomena are fairly stable over time at the population level. From a long run historical perspective it is clear that this is not the case: huge population health gains have been realized in the past centuries, and relationships obtained in high income countries do not necessarily generalize to low or middle-income countries (Calvo et al. 2012).

D. KEY ISSUES

1. Six Sets of Physiological Correlates

While few studies have examined physiological correlates of volunteering directly, many correlates of volunteering have physiological aspects. Also many studies on other forms of prosocial behavior have documented biological correlates. Therefore the chapter takes a broader view, discussing five types of biological correlates of volunteering and related behaviors and traits:

(a) Health correlates, including physiological measures;
(b) Cognitive performance, including intelligence tests;
(c) Neurological correlates: brain size and activity measured using fMRI techniques;
(d) Neurochemicals, including dopamine and serotonin;
(e) Hormones, including oxytocin, testosterone, and cortisol;
(f) Genetic factors, including specific genes (such as OXTR genes, AVPR genes, DRD4, 5HTTLPR).

2. Data and Methods

Biosocial research typically relied on small samples, until biomarkers were collected among respondents in several large US national panel surveys, such as AddHealth, Midlife in the United States (MIDUS), the Wisconsin Longitudinal Study (WLS), the National Social Life, Health, and Aging Project (NSHAP), and the Health and Retirement Survey (HRS). Recently, health data have also been collected and made available for researchers in the British Household Panel Survey (BHPS) and the Whitehall II Study. Each of these panel surveys also include measures of volunteering. To date, very few scholars have used these data to investigate physiological correlates of the dynamics in volunteering. We expect more work to be published in the near future.

While the empirical evidence on physiological correlates of volunteering is fairly limited, the body of evidence on physiological correlates of human prosociality in the biosocial sciences has exploded in the past decade due to the development of cheaper and faster techniques to collect biomarkers from DNA and hormone levels with noninvasive procedures such as collecting saliva (D'Onofrio and Lahey 2010). In earlier research, hormone levels could only be identified with blood samples. Genetic association studies require collection of DNA material such as hair, nails, or saliva.

The collection of neurological data still requires expensive and impractical equipment located mostly in (university) hospitals and that only specialized personnel can handle. The methods include PET (positron emission tomography), fMRI (functional magnetic resonance imaging), EEG (electroencephalography), TMS (Temprorary Magnetic Stimulation). The noisy fMRI machines require research participants to lay still in a narrow space that does not allow for natural social interaction. This lowers the ecological validity of the research. The location of the equipment in hospitals implies that research participants need to be recruited and paid specifically for the study. Participants can only be run one by one, increasing the costs and time required to collect fMRI data.

In the near future, collecting data on physiological correlates of volunteering will be much cheaper and less inconvenient. The spread of smartphones will allow for the collection of several physiological measures such as heartbeat, physical location, movement, and emotional states (Lakens 2013).

3. Health Correlates

Volunteering may help delay the decline, maintain, or even improve health. Chapter 55 discusses some of these impacts on volunteers. At the same time, health facilitates volunteering. Teasing out the direction of causality is difficult and requires longitudinal panel data at the individual level. Even if longitudinal data are available it is of paramount importance to check whether health conditions at base line influence the selection of individuals into and out of volunteering. Ignoring health based selection is almost certainly leading to an overestimation of the health benefits of volunteering (Li and Ferraro 2005). The use of fixed effects models is one possible strategy to deal with such selection bias (Halaby 2004). Such models analyze the variance over time within individuals, ignoring differences between individuals.

Subjective wellbeing. Research on the relationship between volunteering and well-being (Ryff 1989) has a long history (e.g. see Carp 1968). Like prosocial spending (Aknin et al. 2013), volunteering is associated with higher well-being in many cultures worldwide (Plagnol and Huppert 2010; Calvo et al 2012). A meta-analysis involving 29 studies from the 20th century found that on average, volunteers scored higher on measures of well-being than non-volunteers, even when adjusting for health or socioeconomic status (Wheeler, Gorey, and Greenblatt 1998). In addition, volunteers who engaged in directly helping others had higher well-being than those who engaged in more indirect tasks. We recommend an updated meta-analysis that includes more recent studies. Longitudinal studies confirm that volunteering at one time point predicts higher life satisfaction, happiness, self-esteem, and psychological well-being, at a later time point (for reviews see Konrath, 2014; Konrath and Brown 2012). These results are typically consistent when potential confounds are considered. Confounds are important to consider since people with higher well-being are more likely to volunteer (Thoits and Hewitt 2001). Experimental and quasi-experimental interventions to increase volunteering behavior produce more positive affect and higher self-esteem, compared to control groups (Hong and Morrow-Howell 2010; Midlarsky and Kahana 1994; Switzer, Simmons, Dew, Regalski, and Wang 1995).

Mental health. Volunteers have lower anxiety and depression than non-volunteers (Benson, Clary, and Scales 2007; Handy and Cnaan 2007; Hunter and Linn 1980). Moreover, people who volunteer at one time point have fewer depressive symptoms at a later time point, even when controlling for potential third variables (Kahana et al. 2013; Lum and Lightfoot 2005; Schwingel, Niti, Tang, and Ng 2009; Thoits and Hewitt 2001). This finding has been confirmed cross-culturally (e.g. in Singapore; Schwingel et al. 2009). Experimental interventions to increase volunteering behavior produce fewer depressive symptoms, compared to control interventions (Hong and Morrow-Howell 2010; Switzer et al 1995). However, the type of volunteering may be a factor in mental health outcomes. For example, one study found that volunteer firefighters had more symptoms of posttraumatic stress compared to control participants (Wagner and O'Neill 2012). Thus, the potential for vicarious traumatization must be considered in high-risk volunteer positions (e.g. crisis counseling for victims of sexual assault and violence; Baird and Jenkins 2003).

Subjective health. Self-reported measures of health are strong predictors of longevity (Idler and Benyamini 1997), and volunteers score higher on self-reported measures of health (Benson, Clary, and Scales 2007; Harris and Thoresen 2005; McDougle, Handy, Konrath, and Walk 2013; Oman et al 1999; Shmotkin, Blumstein, and Modan 2003). Volunteering is associated with higher subjective health in many cultures worldwide (Kumar et al. 2012). Moreover, longitudinal studies confirm that volunteering predicts higher self-reported health at a later time point, even when controlling for plausible confounds (Lum and Lightfoot 2005; Luoh and Herzog 2002; Morrow-Howell et al. 2003; Piliavin and Siegl 2007; Thoits and Hewitt 2001; Van Willigen 2000). However, there may be limits on the number of years that such effects last, since one 30 year longitudinal study found null results (Moen et al. 1989). The people who are most likely to benefit from volunteering are older adults, compared to younger adults (Van

Willigen 2000), and those who are less socially integrated, compared to those who are more socially integrated (Piliavin and Siegl 2007).

Physical functioning. Physical functioning indicators include objective tests (e.g. strength, agility, walking speed) and health indicators (e.g. functional limitations, physician-diagnosed health conditions, nursing home residence rates, doctor visits for physical illness, overnight hospital visits). Studies find that volunteers are more likely to show better physical functioning to begin with (Choi and Tang, 2014). Thus, in order to avoid selection effects, it is important to control for baseline indicators of physical functioning when trying to isolate effects of volunteering. Longitudinal studies find that volunteering predicts having fewer functional limitations at a later time point even when controlling for a number of plausible confounds (Choi and Tang, 2014; Lum and Lightfoot 2005; Luoh and Herzog 2002; Morrow-Howell et al. 2003). In addition, another longitudinal study found that volunteering predicted fewer doctor visits for physical illness, and fewer overnight hospital stays in nationally representative sample of older adults, even when adjusting for covariates (Kim and Konrath, 2014). However, other studies have found that volunteering is unrelated to the later number of physician-diagnosed health conditions or nursing home residence rates (Lum and Lightfoot 2005). Experimental interventions to increase volunteering behavior increase participants' physical strength and balance, halt declines in walking speed over time, and produce fewer falls and functional limitations, compared to control interventions (Fried et al 2013; Hong and Morrow-Howell 2010). Because there is limited cross-cultural research on physical functioning indicators it is unclear whether these results would generalize widely across cultures.

Health risk behaviors. Health risk behaviors include smoking, drinking, BMI, physical activity, and preventative healthcare utilization (e.g. getting flu vaccines). Among adolescents, pregnancy, school failure, and problem behaviors at school are also considered health risk behaviors. Compared to non-volunteers, volunteers report engaging in fewer health risk behaviors (e.g. smoking, drinking, sedentary lifestyles; Harris and Thoresen 2005; Musick, Herzog, and House 1999; Oman, Thoresen, and Mcmahon 1999; Shmotkin et al 2003). Among teens, volunteering is associated with fewer risky behaviors (e.g. alcohol, tobacco, and drug use; antisocial behavior; violence) and more beneficial ones (e.g. physical activity; school success; Benson, Clary, and Scales 2007; Murphey, Lamonda, Carney, Duncan 2004; Uggen and Janikula 1999). In a longitudinal study, volunteering predicted more preventative healthcare utilization (e.g. flu vaccine, cholesterol test) in a nationally representative sample of older adults, even when adjusting for covariates (Kim and Konrath, 2014). Experimental interventions to increase volunteering behavior produce increased physical activity among older adults (Fried et al. 2004; Tan et al 2009), and decreased rates of pregnancy, school failures, and problem behaviors at school among adolescents (Allen et al. 1997; Switzer et al. 1995). It is unclear whether the links between volunteering and health risk behaviors would generalize widely across cultures.

Basic physiological measures. Research has clearly shown that volunteering is associated with better physical health. Yet knowledge about physiological pathways of such outcomes (e.g. cardiovascular measures, hormones, biomarkers) remains sparse. Elevated resting pulses and blood pressure (i.e. hypertension) are both risk factors for cardiovascular disease and later mortality, even when controlling for other lifestyle-based risk factors (Chobanian, Bakris, Black, Cushman, Green, Izzo, et al 2003; Gillum, Makuc, and Feldman 1991). Only two known studies have examined the link between volunteering and such cardiovascular variables, finding that in nationally representative samples of older adults, volunteers have lower resting pulses and lower blood pressure compared to non-volunteers, controlling for plausible confounds (Burr, Tavares, and Mutchler 2011; Konrath 2013). C-reactive protein is a biomarker of systemic inflammation that is also associated with cardiovascular disease (VanLente 2000). Volunteers have lower c-reactive protein levels compared to non-volunteers (Konrath 2013). This effect was confirmed in an experimental study that found that adolescents who were randomly assigned to a 4 month volunteering program had marginally lower inflammatory biomarkers (c-reactive protein and interleukin 6) than wait-list control group participants (Schreier 2012; Schreier, Schonert-Reichl, and Chen 2013). They also had lower levels of cholesterol and a lower body mass index. However, there was no effect of the intervention on blood pressure. A strength of all of these studies is that they used real-time physiological assessments conducted by trained personnel. More studies are needed. In particular, it is unclear whether the physiological consequences of volunteering would generalize across cultures.

Longevity. Ultimately, the better health of volunteers may reduce their mortality risk. Indeed, a meta-analysis of 14 longitudinal studies conducted from 1986 to 2012 found that volunteering at one time point was associated with a 47% reduction in mortality risk (24% for adjusted models), a few years later (Okun, Yeung, and Brown 2013). This meta-analysis also found that the mortality risk benefits associated with volunteering are especially strong for people who are more religious. Other research finds that the reasons why people volunteer can also affect whether they experience lower mortality risk after volunteering (Konrath, Fuhrel-Forbis, Lou, and Brown 2011). Even when adjusting for covariates, people who volunteer for more other-oriented reasons (e.g. compassion) have a significant mortality risk reduction, but those who volunteer for more self-oriented reasons (e.g. to learn something new, or to feel good about themselves) have a marginally higher risk of mortality. Although there are some experimental studies that assess health consequences of volunteering, we know of none that assess mortality risk. Moreover, there are only limited cross-cultural studies examining longevity benefits of volunteering.

4. Cognitive Performance

Several US surveys show that membership and active participation in voluntary associations are positively related to verbal ability measured in a vocabulary test, but once the level of education is controlled verbal ability does not have much predictive value for the number of memberships in associations (Hauser 2000). Data from the Wisconsin Longitudinal Study (WLS) reveal this pattern over a long period of time. Performance on an intelligence test in 1957 was positively associated with social participation some 35 years later, but this relationship disappeared completely when the level of education in 1975 was controlled. While volunteers typically perform better on cognitive tests than non-volunteers, this difference does is often reduced when the level of education is controlled statistically (Bekkers and Ruiter 2008; Carabain and Bekkers 2011a, 2011b). Intentions to volunteer in a scenario experiment conducted among a random population sample in the Netherlands were not correlated with performance on a vocabulary test when the level of education was controlled (Bekkers 2010).

Studies of social participation programs for older adults have generally found higher cognitive performance among volunteers (Krueger et al. 2009; James, Wilson, Barnes and Bennett 2011). However, this finding does not prove that volunteering enhances cognitive performance, because the difference may well be a reflection of a higher level of education at entry into the program. Collapsing volunteer work with other forms of social participation, Aartsen et al. 2002) found no additive cognitive performance benefit of social participation.

Using data from the Fullerton Longitudinal Study, Reichard et al. 2011) found that intelligence measured by Wechsler Adult Intelligence Scale-Revised (WAIS-R) was positively correlated with non-work leadership positions, such as in a religious group, community service group, or sports organization, but this study did not include a measure of the level of education achieved.

5. Neurological correlates

From the 'social brain hypothesis' (Dunbar 1998) it is likely that volunteering as a social activity is facilitated by the large cognitive capacity of humans as a species. Brain volume determines the capacity to process information required to maintain social relationships (Dunbar 1992). One study among 58 US adults found that the relative size of the amygdala (adjusted for total intracranial volume) is positively correlated with the size and complexity of social networks (Bickart et al. 2011a, 2011b). Another study on 40 US adults found that the size of the prefrontal cortex is positively correlated with the size and complexity of social networks (Powell et al. 2012). The prefrontal cortex is of particular importance for human sociality and consciousness (Dunbar 1998) in part because of its involvement in understanding the intentions of others (Walter et al. 2004; Lewis et al. 2011). The prefrontal cortex consists of two areas: the dorsal prefrontal cortex, which is involved in higher order cognitive functions such as planning, and orbital prefrontal cortex, which is involved in mood, affective behavior and social cognition.

Thus far, no studies have specifically investigated brain activity in relation to volunteer work. Because of the heterogeneity of tasks that volunteers can perform this would not make much sense. However, many studies have investigated brain activity involved in functions and conditions correlated with volunteering such as social acceptance (Eisenberger, Lieberman and Williams 2003), and empathy (Singer et al. 2008). A growing number of studies are using fMRI to investigate cognitive functioning in older adults recruited in volunteer programs (e.g., Carlson et al. 2011). These studies typically find enhanced cognitive functioning among volunteers.

While fMRI studies are not yet common in research on volunteering, several studies have found differential neural activation in reward areas when making charitable donations (Harbaugh et al 2007; Moll et al 2006; James and Boyle 2012; James, forthcoming). Such studies could be conducted among volunteers, e.g. while they are thinking about their volunteer job versus a control activity, contrasting volunteers with different motives for volunteering.

6. Neurochemicals

Dopamine is a neurotransmitter involved in the experience of pleasure. Originating in the midbrain, dopamine produces neurons that consecutively go to the nucleus accumbens and the prefrontal cortex (Eisler and Levine 2002). Dopamine is not specific for social experiences. It is involved in all kinds of positive moods, including those as a result of substance abuse and other addictive behaviors. The warm glow of giving (Andreoni 1990) often cited by volunteers as a motive for volunteering may reflect that volunteering is a pleasurable experience. Obviously, the finding that volunteers self-report warm glow does not show why volunteering is a pleasurable experience. Also it does not prove that volunteering produces warm glow. The warm glow may be specific to donors. In a study on the relationship between blood donation and charitable giving, blood donors reported a stronger warm glow as they gave more to charity, but non-donors did not. This finding suggests that donating generates less of a warm glow to non-blood donors (Ferguson, Taylor, Keatley, Flynn and Lawrence 2012, Study 3).

7. Hormones

Oxytocin. Oxytocin is a neuropeptide that is released during childbirth, breastfeeding, and sexual behaviors (Carter 1992; 1998). It is also implicated in more general social interactions, trust, and in stress regulation (Heinrichs, Baumgartner, Kirschbaum, and Ehlert 2003). For example, one experimental study found that nasally administered oxytocin (compared to a placebo) caused male participants to donate significantly more money to a charitable cause (Barraza, McCullough, Ahmadi, and Zak 2011). Many other studies have conceptually replicated these results (Zak, Stanton, and Ahmadi 2007; Zak and Barraza 2013). However, we know of no work that explicitly links oxytocin with volunteering behavior, and such research would be promising, as long as future researchers are aware that oxytocin is only linked with prosociality in certain groups of people and under certain contexts (Bartz, Zaki, Bolger, and Ochsner 2011).

Vasopressin. Arginine vasopressin is another neuropeptide implicated in social behavior. Compared to oxytocin, much less is known about its role in prosociality in humans. However, in rats, vasopressin injections are associated with prosocial-like tendencies compared to placebo controls (Ramos et al 2013). In humans, there are no known studies directly examining prosocial tendencies or volunteering specifically, yet studies on related processes are emerging. For example, experimentally administered doses of vasopressin in males produce a better recall of emotional faces (Guastella et al. 2010), but inconsistent findings with respect to actually identifying the emotional expressions (impaired performance: Uzefovsky et al. 2012; no effects: Kenyon et al. 2013). Moreover, there may be sex specific results of vasopressin, with one study finding that after nasally administered vasopressin (compared to placebos) males see faces as more unfriendly, while females see them as friendlier (Thompson et al. 2006). This area is ripe for future research.

Cortisol. Cortisol is a stress hormone that is associated with cardiovascular mortality risk (Kumari et al. 2011; Vogelzangs et al. 2010). Although there have been studies conducted examining the effect of other prosocial behaviors on cortisol levels (e.g. Field et al 1998; Smith et al 2009), there is only one known study examining cortisol in relation to volunteering. This experimental study that found that a 4 month volunteering program had no effect on adolescents' cortisol levels compared to a wait-list control condition (Schreier 2012; Schreier, Schonert-Reichl, and Chen 2013). More research is needed to examine the relationship between cortisol and volunteering.

Testosterone. Testosterone is a male sex hormone, but it is also present to a lesser degree in women. There has been some research on testosterone and prosocial tendencies, but no study that we know of specifically examines testosterone and volunteering. Experimentally administered testosterone produces less facial mimicry of emotional facial expressions (Hermans, Putman, and Van Honk 2006), decreases the ability to recognize emotional facial expressions (i.e. cognitive empathy; Van Honk and Schutter 2007; Van Honk et al. 2011), and reduces trust in others, especially among highly trusting people (Bos, Terburg, and Van Honk 2010). Several studies examine the effect of testosterone on generosity in economics games (e.g. the Ultimatum Game), with contradictory results. Two find that testosterone administration causes less generosity (Boksem et al. 2013; Zak et al. 2009), two find that testosterone administration causes more generosity (Eisenegger 2010; Van Honk et al. 2012), and another finds null results (Zethraeus et al. 2009). One study finds that even as testosterone lowers initial generosity, it simultaneously increases reciprocal generosity – giving to others who first gave to the self (Boksem et al. 2013). Some contradictory results may be due to beliefs about how testosterone affects people (Eisenegger 2010), and these need to be considered in all testosterone administration studies.

8. Genes

Genes have long been implied as biosocial causes of behavior. Turkheimer (2000) summarized the results of thousands and thousands of studies in behavioral genetics in three laws, the first being that “everything is heritable”. While this law may not be true in its extreme formulation, almost every aspect of human social behavior that has been studied with behavioral genetic data has indeed been found to have some genetic origins, including the size of social networks (Fowler, Dawes and Christakis 2009), and even mobile phone use (Miller et al. 2012). Political party preference seems to be one of the few exceptions (Hatemi, Alford, Hibbing, Martin and Eaves 2009). Also general prosocial tendencies and volunteering are subject to genetic effects (Ebstein, Israel, Chew, Zhong and Knafo 2010). Before we discuss these findings we go into the methodology used to obtain estimates of genetic effects.

Biometric models. Behavioral genetic models, also called biometric models, decompose variance in human behavior by using samples of individuals with systematically different genetic similarity such as twins and siblings. Building on several assumptions the variance in phenotypic traits can then be decomposed into effects of additive genetic factors (a^2), shared environmental (c^2) and unique environmental components (e^2). These models show that many traits have substantial genetic heritability (Turkheimer’s first law) and that additive genetic factors typically explain more of the variance than shared environmental factors (the second law). On the other hand, however, there are few traits that have exclusively genetic origins. In fact, behavior genetics tells us how amazingly complex the interplay between nature and nurture is in determining human behavior. Most traits in humans are genetically complex, meaning that there is a complex of many genes associated with the trait. There are only a few traits that are determined by a single gene. An example is phenylketonuria (PKU), a disorder caused by a deficiency of the enzyme phenylalanine hydroxylase, giving rise to mental retardation and eczema. Thus far, the search for effects of specific genes on human behavior has been disappointing. Genome Wide Association Studies (GWAS) have failed to identify genes with substantial effects on specific human differences of interest to social scientists (Turkheimer 2012). Typically, all single nucleotide polymorphisms (SNPs) combined explain less variance than the is estimated in biometric models. The discrepancy between the sizeable genetic heritability estimates from biometric models and the much smaller variance explained by all SNPs combined is called the ‘missing heritability problem’ (for a discussion see Turkheimer 2011).

Many studies have investigated ‘altruism’ and related aggregate constructs of prosocial tendencies, often including volunteering as well as informal forms of prosocial behavior and prosocial values and attitudes with biometric models. While most studies have found genetic effects on prosocial tendencies (e.g., Rushton 2004; Rushton, Fulker, Neale, Nias and Eysenck 1986; Koenig, McGue, Krueger and Bouchard 2007; Gregory, Light-Häusermann, Rijsdijk, and Eley 2009), some have not (Krueger, Hicks and McGue 2001; Bouchard and Loehlin 2001) and more generally estimates of genetic effects have varied widely from 0% up to 50%. Three studies have specifically investigated volunteering using behavioral genetic models. Son and Wilson (2011) used the MIDUS twins and siblings samples to estimate genetic variation in the number of volunteer hours. The best fitting biometric models included no genetic effects for males and a relatively small genetic variance component (.30) for females. Gibson (2001) analyzed data from a small sample of New Zealand twins, finding that the higher educated twin of a monozygotic pair typically spent less time volunteering than the lower educated twin. This finding suggests that the positive relationship between education and volunteering in the general population is positive due to genetic effects. Recently, Bekkers (2014) also used the MIDUS twin sample to analyze religion and education as mediators of unique environmental effects on volunteering. The analysis was limited to monozygotic twin pairs to exclude genetic variance. All differences within monozygotic twin pairs must be due to unique environmental factors. The study concluded that education did not explain any variance in volunteering among monozygotic twins. This finding implies that the relationship between education and volunteering, one of the most commonly found relationships in the literature (Smith 1994; Musick and Wilson 2008), is mostly due to genetic effects. The conclusion for religion, another common correlate of volunteering, was very different: the strength of religiosity was positively related to the number of hours volunteered, implying that the relationship cannot be explained by genetic effects.

Which genes are likely to be involved in volunteering? Several specific genes have been studied in detail as candidates that could play a role in prosocial behavior: the dopamine D4 receptor (DRD4) genes, oxytocin receptor (OXTR) genes, arginine vasopressin receptor (AVPR) genes, and serotonin transporter (5-HTTLPR) genes. No study thus far has specifically examined these genes in conjunction with volunteering, however.

DRD4 genes. DRD4 genes enable the production of the D4 dopamine receptor protein, which is involved in the expression of emotions and for the stimulation of cognitive faculties (Schmidt, Fox, Perez-Edgar, Hu, and Hamer 2001). Song, Li and Arvey (2011) found a weakly negative relationship between DRD4 7R and paid work job satisfaction. Future research could test whether this relationship holds for unpaid work as well. Jiang, Chew and Ebstein (2013) provide a summary of papers investigating relationships between DRD4 variants and prosocial behaviors. Bachner-Melman et al. (2005) and Anacker et al. (2013) find negative relationships, i.e. higher altruism scores in the absence of the dopamine receptor D4 7-repeat allele (DRD4 7R). Zhong et al. (2010) find an association with fairness in the ultimatum game. Knafo, Israel and Ebstein (2011) did not find a relationship, but found a more complicated pattern: children with a DRD4 7R allele were more susceptible to positive parenting practices than children without this allele. One interpretation of this finding is that an environmental factor (positive parenting) is able to repair a lack of prosociality among children with a specific genetic risk factor (the DRD4 7R).

Several findings in studies of other social behaviors are consistent with the more general interpretation that individuals with the DRD4 7R are more susceptible to social influence. Using the AddHealth data, DeLisi et al. (2008) report an association between DRD4 polymorphisms and age of first criminal arrest among adolescents from low risk families, but not among high risk families. Settle, Dawes, Christakis and Fowler (2010) found that among participants in the NLSAH with the D4 7-repeat allele, the number of friendships in adolescence was significantly associated with liberal political ideology, while there was no such association among those without the gene variant. Sasaki et al. (2013) show that the influence of priming participants with religion positively affects the willingness to volunteer for environmental causes among those who carry the D4 2 or 7-repeat allele but not among those carrying other variants.

Reuter et al. (2011) examined another dopaminergic candidate polymorphism for altruistic behavior, the functional COMT Val158Met SNP, and found that the Val allele (representing strong catabolism of dopamine) is positively related to charitable giving towards poor children in a developing country.

OXTR genes. Oxytocin receptor (OXTR) genes are also implicated in prosocial traits and behaviors (for reviews, see Kumsta and Heinrichs 2013; Ebstein et al. 2012). For example, people with GG genotypes (in rs53576) are more sociable, empathic and trusting than A-allele carriers (Tost et al. 2010; Rodrigues et al. 2009; Krueger et al. 2012). They are also rated as more empathic by observers (Kogan et al 2011). Yet these effects are not found for all potential OXTR SNPs: only 4 out of 10 SNPs in one study (rs2254298, rs2268491, rs237887, rs4686302: Wu, Li, and Su 2012), and only 3 out of 15 SNPs in another (rs1042778, rs2268490, rs237887: Israel et al. 2009). A meta-analysis of OXTR effects revealed weak relationships across the board (Bakermans-Kranenburg and Van IJzendoorn 2014). Clearly, the specific SNP within the OXTR gene matters. Behaviorally, OXTR GG genotypes are related to better emotion recognition performance (rs53576, rs2254298, and rs2228485: Lucht et al. 2013; Rodrigues et al. 2009; Wu and Su 2013), but their effects on generosity within economics games (e.g. Dictator Game, Trust Game) are either limited (e.g. to 3 out of 15 possible OXTR SNPs: Israel et al. 2009) or non-existent (Apicella et al. 2010).

These inconsistent main effects might reflect underlying interactions with contextual variables. For example, although one study found no main effect of the OXTR SNP (rs53576) on prosocial behavior (including volunteering), there was an interaction between genotype and levels of environmental threat in predicting prosociality (Poulin, Holman, and Buffone 2012). Another study found that the OXTR gene (rs2254298) interacted with volunteering status to predict mortality risk (Konrath, 2014). Specifically, the widely documented decline in mortality risk for volunteers was only found for OXTR A-allele carriers, and not GG carriers. Research is needed to better understand factors that may influence the relationship between OXTR genes, prosociality, and health. In addition, more cross-cultural research is needed, considering one study finding that the OXTR genotype had opposite effects in the US and Korea (Kim et al. 2011).

AVPR genes. Arginine vasopressin receptor (AVPR) genes have also been implicated in prosocial traits and behaviors. Participants with longer versions of the AVPR1a RS3 gene scored higher on prosocial traits and allocated more money to others in the Dictator Game than those with short versions of this gene (Knafo et al. 2008).Similar to OXTR genes, AVPR genes may best predict prosocial behavior in concert with contextual factors (Poulin et al. 2012).

5-HTT genes. 5-HTT genes regulate the function of the neurotransmitter serotonin. One common polymorphism in the promoter region of the gene (5-HTTLPR) has been linked not only to aggressive behavior (the short variant; Duman and Canli 2010) but also to voting (the long variant; Fowler and Dawes 2008). The 5-HTTLPR was one of the first to be discovered as interacting with environmental conditions (life stress) in depression (Caspi et al. 2003). Carriers of the short variant suffer more adverse consequences of childhood maltreatment (Karg et al. 2011). Song, Li and Arvey (2011) found a weakly positive relationship between 5-HTTLPR and paid work job satisfaction. Whether this relationship holds for unpaid work as well remains to be seen in future research. Colzato et al. (2013) showed that intake of a tryptophan food supplement, containing an amino acid that is found in food such as fish, soybeans, eggs, and spinach, and a biochemical precursor of serotonin, increases trust in an economic game. Stoltenberg, Christ and Carlo 2013) found that the association between 5-HTTLPR triallelic genotype and helping behavior was mediated by anxiety in social situations. Students carrying the S' allele reported lower rates of helping others, partly as a result of higher levels of social avoidance.

9. Discussion

We should be careful not to reify physiological differences (Dar-Nimrod and Heine 2011). An image of brain activity or a correlation between genetic polymorphisms and volunteering does not imply causality. The rules for causal inference also apply to physiological data: correlates may reflect a causal influence of physiological properties, but they may also be observed as a result from social behavior influences on physiological functioning or selection on some third variable. Only studies that use random assignment of participants to treatment and control groups allow for easy causal inference on the effect of a specific cause (Shadish, Cook and Campbell 2002; Firebaugh 2008). However, brain activity or hormone levels are usually not manipulated. Primate studies in which group size was varied show that network size determines the grey matter volume and prefrontal cortex activity (Sallet et al. 2011). Thus the correct interpretation of a study showing a correlation between prefrontal cortex and network size is *not* that brains cause networks, as suggested in the causal model of one study (Figure 1 of Powell et al. 2012). The same study does acknowledge that the causal direction of the relationship between prefrontal cortex and network size may run in both ways. An adequate representation of the association between the volume of grey matter in the brain with the number of social contacts in online social networks is that 'social network size is reflected in human brain structure' (Kanai, Bahrami, Roylance and Rees 2013). Lesion studies on patients with damage to specific parts of the brain (e.g., Shamay-Tsoory, Aharon-Peretz and Perry 2009) show that specific cognitive and social functions are impaired. From such studies, however, we cannot conclude how individual differences in brain volume and activity among healthy individuals determine cognitive and social functioning.

Another shortcoming is that participants in fMRI studies are almost exclusively originating from western countries (Chiao and Cheon 2010). The use of samples from WEIRD (Western, Educated, Industrialized, Rich and Democratic) countries reduces the potential for generalization of research findings to all of humanity (Henrich, Heine and Norenzayan 2010). Cross-cultural evidence on health correlates of prosociality (Calvo et al. 2012) is very important in this respect. Also within WEIRD countries participants in studies that include physiological measurements are not random samples of the population. The Henrich, Heine and Norenzayan diagnosis warning echoes McNemar's (1946) warning that the practice in psychology to use students as research participants was creating a "science of the behavior of sophomores". Within this particular population a volunteer bias is likely to occur such that individuals who are more sociable, less conventional, and more interested in the study will be more likely to participate (Rosenthal 1965; Rosnow and Rosenthal 1976). In longitudinal research on health, selective participation based on health status and deterioration is an additional problem. These problems reduce the potential for generalization of the findings to broader populations.

E. USABLE KNOWLEDGE

The fact that volunteers are in better health and ultimately live longer than non-volunteers demonstrates the potential relevance of physiological correlates of volunteering. If proven to be causal, the link between health and volunteering bears the promise of huge welfare advantage of volunteering. Programs that encourage volunteering, specifically among the elderly and among those at risk for health problems, could improve health and promote longevity.

F. FUTURE TRENDS AND NEEDED RESEARCH

Our review suggests a considerable potential for discovery in future research on physiological correlates of volunteering. In our view, some of the findings we have reviewed are outright exciting. The current phase of biosocial research is one of discovery, mapping hitherto uncharted territory where 'Here be dragons' used to be written. Just like the first maps drawn by cartographers were notoriously unreliable, new findings in biosocial science often fail to replicate in future studies (Freese 2011). The burgeoning literature in the biosocial sciences carries the risk of the 'decline effect' (Lehrer 2010; Schooler 2011): promising discoveries of associations between physiological characteristics and prosocial behavior will prove to be more complicated than initially conceived, or worse still: they may not be replicated in other samples. Attempts to replicate often fail, as a recent replication effort of genes previously reported to be involved in intelligence shows (Chabris et al. 2012). We should thus be careful not to generalize from single genetic association studies. The results may be false positives as a result of a low power (Davis-Stober and Dana 2013). Therefore we encourage the use of meta-analytic methods to uncover reliable patterns and moderators of gene-behavior associations. Some of these problems are also inherent in fMRI studies (Vul et al. 2009). There is also abundant evidence that non-significant findings are disappearing from the universe of journal publications in the social sciences (Fanelli 2012). Replication and open access publication of all relevant findings are therefore important to the advancement of knowledge in this area.

While the body of research on health correlates of volunteering is sizeable, research on neurochemicals, hormones and genes has often examined other forms of prosocial behavior such as charitable donations. Future research on these physiological correlates should focus specifically on volunteering.

We should be careful not to conclude from correlational evidence that volunteering promotes health because reverse causation (health promoting volunteering) is often difficult to rule out as an explanation of the findings. Nevertheless there is some promising experimental evidence that establishes volunteering as a causal factor in health promotion. Ideally, the effects of design features of such programs should be evaluated through randomized control trials.

Another aim for future research is to broaden the evidence base beyond samples from western, industrialized, rich and democratic (WEIRD) countries. Both research from non-WEIRD countries and cross-national comparative research is required to obtain knowledge on physiological correlates of prosociality in human nature.

Finally, we encourage researchers to consider the wide variety of forms of volunteering. Collapsing all volunteers into one group masks differential associations between physiological characteristics and helping in-group vs. out-group members, between volunteering for religious and non-religious groups, between intellectual and practical tasks, between volunteers with different motives, and between volunteering at different levels of intensity.

G. CROSS-REFERENCES

Chapter 34 on social background/social roles; Chapter 35 on psychological dispositions/factors; Chapter 55 on impacts on volunteers and association members.

H. REFERENCES

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